History of Ecological Sciences, Part 61B: Terrestrial Biogeography and Paleobiogeography, 1840s–1940s

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Biogeography is a strange discipline. In general, there are no institutes of biogeography; there are no departments of it. There are no professional biogeographers—no professors of it, no curators of it. It seems to have few traditions.

—Nelson 1978

And the term “biogeography” was only coined in 1891, by a geographer, not a biologist (Ratzel 1891:9).

Part 61A (Egerton 2018) explained that, after modest growth during the 1700s, Alexander Humboldt brought plant geography into botanical prominence with his South American study, Essai sur la géographie des plantes (1807), and that August de Candolle achieved a practical synthesis in his encyclopedia article, Géographie botanique (1820). Animal geography also progressed. Eberhard Zimmermann produced an early synthesis in two treatises (1777, 1778–1783), but sparked less follow-up by others in zoology than Humboldt’s and de Candolle’s works sparked in botany. There was some cross-stimulation between plant geography and animal geography. Keir Sterling compiled a very useful collection of 28 articles, Selections from the Literature of American Biogeography (1974), all but one of which fall within the time range of this Part 61B; Selections contains an 11-page (unnumbered) introduction in which Sterling provided an indication of how the individual articles fit in a larger context. This subject would require a book-length survey to encompass all its aspects, but McIntosh (1985:107–110) gave a brief summary. A discussion of North America’s four migratory flyways will be in part 62.

Europeans

Englishmen with an itch to travel abroad, collect specimens, and become prominent naturalists eagerly read Darwin’s Journal of Researches. Five who then went abroad and succeeded were botanists Joseph Dalton Hooker (1817–1911) and Richard Spruce (1817–1893), zoologists Alfred Russel Wallace (1823–1913), Thomas Henry Huxley (1825–1895), and entomologist Henry Walter Bates (1825–1892), all of whom followed Darwin’s excellent example of carefully collecting specimens and observations and producing both scientific reports and personal memoirs (von Hagen 1948:213–263, Woodcock 1969, Raby 1996:28–41, 76–177, Rice 1999:260–289, McCalman 2009, Egerton 2012a:168–175, 2012b, 2012c, Hemming 2015). Their publications were substantial contributions to biogeographical literature. Barbara Beddall (1969) republished selections from

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writings by Wallace and Bates, and Tony Rice (1999:260–289) published reproductions of Bates’ insect drawings and Wallace’s fish drawings from the Amazon. All of the above-mentioned naturalists excepting the frequently ill Spruce (Spruce 1908, Desmond 1975, Desmond 1977:578, Seward and Fitzgerald 1996, Raby 2004) became prominent Darwinian “warriors” in the evolution controversy.

Joseph Hooker perhaps published more on phytogeography than anyone else since Humboldt (Turrill 1953, 1963, Good 1955:748, Allan 1967:112–250, Desmond 1972, 1999, Browne 1983: see index, Endersby 2004b, Griggs 2011, Egerton 2012a:172–175, 2012c:125–138). As the son of a botanist, he had a head start, even in geographical botany (Hooker in Huxley 1918:I, 5):

...when still a child, my father used to take me [on] excursions in the Highlands, where I fished a good deal, but also botanized; and well I remember on one occasion, that, after returning home, I built up by a heap of stones a representation of one of the mountains I had ascended, and stuck upon it specimens of the mosses I had collected on it, at heights relative to those at which I had gathered them. This was the dawn of my love for geographical botany.

He went on to say that he read Mungo Park’s and other African travel books and developed a desire to conquer the Atlas Mountain in Morocco, which later he did. He went to the University of Glasgow, earned an M.D. degree (1839), which enabled his father to obtain a position for him as an assistant surgeon and naturalist on a naval ship, H.M.S. Erebus bound (with H.M.S. Terror) to the south seas, September 1839–September 1843, to map shorelines and discover the location of the magnetic south pole. The expedition leader was Captain James Clark Ross (1800–1862), who had located the magnetic north pole and would also find the magnetic south pole (Bravo 2004). Hooker was following Darwin’s example and took along a copy of Darwin’s Journal to read on the voyage (McCalman 2009:85–148). Besides many small islands, the ships visited Antarctica, Tasmania, New Zealand, and the Falkland Islands. Even before returning to England, his extensive reports to his father appeared in the London Journal of Botany (1843), which his father edited. Hooker’s main published reports from the voyage, 2 volumes each, were: Flora Antarctica (1844–1847), Flora Nouva-Zelandiae (1853–1855), and Flora Tasmaniae (1855–1860). Accompanying lithographs were based upon his specimens and sketches. His later contributions are discussed below.

Wallace’s struggles abroad are particularly noteworthy (Wallace 1905, 1916, George 1964, Mayr 1982:417–423, Browne 1983: Index, Quammen 1996: Index, Meams and Mearns 1998:315–320, Shermer 2002, Fichman 2004a, b, McCalman 2009:221–290). Wallace lacked Darwin’s advantage of university studies, but he had read closely both editions of Darwin’s Journal of Researches (1839, 1845) and many more relevant works. He left to explore the Amazon region in May 1848, the trip to be financed by a London agent selling his collected specimens. He was impressed by the fact that some mammal species, especially monkeys, were bounded by rivers. Although he did send some specimens to his agent, he embarked for England in July 1852 with most of his latest collections of live and dead animals and manuscripts, but the Helen burned and sank, and Wallace was later rescued from a lifeboat, with the few papers and drawings he had saved (Wallace 1905:I, 303–309, Desmond 1977:635–636, Camerini 1996, Daws and Fujita 1999:20–21, Knapp 1999, Wilson 2000, Raby 2001). He reached England on 1 October, and he published two books in 1853 based upon his
memories—Palm Trees on the Amazon, and A Narrative of Travels on the Amazon and the Rio Negro. He commented in Narrative (1853:326), “There is no part of natural history more interesting than the study of the geographical distribution of animals.” He had wanted to write a book on Amazon fish, and he saved six illustrations, which he gave to the British Museum, where they were identified, and later he published them, with names, in My Life (1905:I, facing 284, 286, 288). He met Darwin at the British Museum. In March 1854, he traveled to the Malay Archipelago on a Naval ship (no charge). His achievements there are discussed below.

Hewett Watson (1804–1881), whom we met in part 61A, served as naturalist on a naval expedition to map the Azores in 1842. His publications on the Azores (1843–1847, 1870) followed the examples of Humboldt and Darwin. Otherwise, he published a continuous series of articles and books on British phytogeography (Egerton 2003:241–250). On the significance of his work: British plant geographer Ronald Good (1964:279) called Watson’s Cybele Britannica (4 volumes, 1847–1859) “great.” The Botanical Society of the British Isles obviously agreed, for it named its journal Watsonia.
German botanist August H.R. Grisebach (1814–1879) was born and remained in a university town, Göttingen; he went to its university and later joined its faculty (von Hofsten 1916:315–316, Wagenitz 1972, Stafleu and Cowan 1976–2009:I, 1007–1011, Magnin-Gonze 2004:202, Egerton 2013b:343–344). Becoming acquainted with Humboldt, he became interested in phytogeography; his early contribution to it was Ueber den Einfluss des Climas auf die Begrenzung der natürlichen Floren (1838), which American plant ecologist Henry Gleason identified as the first discussion of integrated plant communities (Gleason 1939). Grisebach’s most detailed regional travel account and botanical study were in an area now in western Turkey: Reise durch Rumelien und nach Brussa im Jahre 1839 (2 volumes, 1841) and Spicilegium florae Rumelicæ et Bithynicæ (2 volumes, 1843–1844). He also began publishing annual updates on progress in phytogeography, for years 1842–1845, which were considered important enough by the Ray Society to publish translations of them (Grisebach 1846, 1849). He resumed his series of annual progress reports in 1868–1876.

German geographer Heinrich Berghaus (1797–1884) was already a geographer in the Prussian Army Reserve when he went to Paris in 1815 to meet Humboldt, who later became a regular correspondent (Humboldt and Berghaus 1863, 3 volumes, Hantzsch 1902). He was not a biogeographer, but their correspondence would have increased Humboldt’s geographical sophistication.

The Dutch ornithologist, Coenraad Jacob Temminck (1778–1858), campaigned successfully for establishment of the Rijksmuseum in Leiden and became its first director in 1823 (Stresemann 1951:117–130, 1975:110–125, Farber 1982: Index, Mearns and Mearns 1988:373–376, Gassó Miracle 2008). The government had already sent out a natural history expedition to the Dutch East Indies in 1820, consisting of two naturalists and two assistants (Stresemann 1951:130–155, 1975:126–152). That was the second expedition it had sent to the Malay Archipelago, and one of the naturalists died in less than three months, and the expedition artist died two days later. In December 1823, the king appointed two naturalists and an assistant, all Germans—Heinrich Boie (1794–1827) and Heinrich Christian Macklot (1799–1832), assisted by Salomon Müller (1804–1864)—to replace the deceased members of the previous expedition. They left home in December 1825 and reached Java on 6 June 1826. Boie and Macklot both did good work before they also died (most likely, three had malaria; Macklot died in a conflict). Only Müller survived, and he undertook the research of the naturalists, advised, no doubt, by Temminck. Müller returned to Leiden in 1837 and then organized his specimens and notes at the Rijksmuseum (Glaubrecht 2002:259–264). The article he published, Geographie der Thiere: Ueber die geographische Verbreitung der Säugethiere im Indischen Archipelagus (1842), included information later used by the geographer Heinrich Berghaus for a map showing what is now known as Wallace’s Line (reproduced by Camerini 1993a:708, 1993b:505), which now should be called the Müller-Wallace Line.

Nurnberg native (Johann) Andreas Wagner (1797–1861) earned a doctorate in 1826, and in 1832, he joined the faculty of the University of Munich, became Professor in 1836, and he also served as Curator of the university’s Zoologische Staatssammlung (von Hofsten 1916:281, Smith 2005). He published Die Geographische Verbreitung der Säugethiere Dargestellt (3 parts, 1844–1846), attempting to do for mammals what Schouw had done for plants (Kendeigh 1954:154):
He recognized three broad zones each divided into provinces. The northern zone included the polar province, the temperate province of the Old World, and the temperate province of North America. The middle zone was divided into a South Asian province, an African province, and a middle American province. The southern zone contained the Australian province and the Magellanian (southern South American) province. Wagner tried to correlate the distribution of animal groups with types of vegetation...

His also assisted Johann C.D. von Schreber with his Die Säugethiere in Abbildungen nach der Natur, mit Beschreibungen (Leipzig, 1840–1846; from Wood 1931:555).

The advance in knowledge of species distributions in South America by four Englishmen—Charles Darwin, Alfred Russel Wallace, Henry Walter Bates, and Richard Spruce—was discussed in parts 37 and 41 in this history (Egerton 2010d, 2012b). To those discussions, here I merely add: Jonathan Maslow, Footsteps in the Jungle: Adventures in the Scientific Exploration of the American Tropics (1996:58–138).

Bayreuth native (Friedrich Johann Carl) Moritz Wagner (1813–1887), was educated at the University of Augsburg and elsewhere, became an explorer in Algeria, 1836–1839; Armenia, 1842–1846; and North and Central America, 1852–1855 (Mayr 1982:562–564, Quammen 1996:130–135, Smith 2005, Wagner et al. 2012). In 1862, he became Professor of Geography and Ethnography at the University of Munich. His explorations were primarily on continents; he did not puzzle over species on islands. Like Wallace in the Amazon basin, he found that certain species’ range was limited by Algerian rivers, but
also by mountain ranges and deserts. He concluded, therefore, that species only form when a species that formerly had a larger range became divided geographically into different populations that can no longer interbreed. Darwin found his claim too dogmatic and believed there were exceptions to this generalization.

A Scot who merits a nod here was naturalist Andrew Murray (1812–1878), whose strongest interests were in botany and entomology, on which he published much (Boulger 1909, Desmond 1977:457, Wilson 2004). He participated in a botanical expedition to Oregon and published its findings (1853), and he also published The Geographical Distribution of Mammals (1866), which Casey Wood thought was “One of the most important contributions to zoogeography extant” (1931:476). It included 101 colored maps and 16 + 420 pages.

Scottish botanist Arthur Henfrey (1819–1859) (Geison 1972, Stafleu and Cowan 1976–2009:I, 154–155, Desmond 1977:301, Endersby 2004a, b) studied medicine and surgery, but poor health prevented a medical career, and so he taught botany in London. In 1854, he succeeded Forbes at Kings College, London. His popular books focused upon introducing European botany to the British. His Vegetation of Europe, its Conditions and Causes (1852) can be seen as in that tradition. The vegetation map in my reproduction of his book (1977) is faint, but the original was more legible. He provided two chapters on influences on the distribution of vegetation, but most of the book discussed vegetation in 10 regions into which he divided Europe. He included no bibliography. In 1857, he published An Elementary Course of Botany: Structural, Physiological, and Systematic, with a brief Outline of the Geographical and Geological Distribution of Plants, which Asa Gray stated in his review was “well-planned, compact, and comprehensive” (Gray 1857:434). However, Gray then spent the rest of his 10-page review correcting errors in Henfrey’s textbook. Henfrey might have made a stronger contribution to plant geography if he had not died at age 40. Neither Good (1955) nor Browne (1983) mentioned him.

Austrian zoologist Ludwig Karl Schmarda (1819–1908) studied at the University of Vienna and then held several academic positions (von Hofsten 1916:301). He was a productive researcher, mainly on invertebrates, and published seven books, the third being on the geographical distribution of animals (1853). Karl Schmidt (1955:767–769) found that his 1853 book discussed the same topics that one would expect in a modern book on zoogeography. Schmarda delimited 21 terrestrial regions and 10 marine regions; Schmidt reproduced his world map and listed names of his 31 regions. Ebach (2015:99) also reproduced the map, including the regions listed below it. He took a trip around the world, 1853–1857, and published a book on his discoveries (1861). In 1862, he became a professor at his alma mater. The Geographisches Jahrbuch for 1866 included articles by Schmarda on animal geography and Grisebach on plant geography (Ebach 2015:97).

Swiss botanist Alphonse Louis Pierre de Candolle (1806–1893), like his father, studied for a time in Paris (Christ 1893 [his bibliography, 224–234], Good 1955:748–749, Pilet 1971, Stafleu and Cowan 1976–2009:1, 433–437, Mayr 1982:444–445, Browne 1983:82–86, Naef 1987:352–355, Magnin-Gonze 2004:166–167). He did, however, also obtain a doctorate in law (1829), which no doubt came in handy when he published Lois de la nomenclature botanique (Paris, 1867), though it is unlikely he had thought of this when he decided to study law. In 1835, he succeeded his father as professor of natural history at the Academie de Genève. In 1850, he retired from teaching to con-
centrate on research. In our context, his most important work was Géographie botanique raisonnée (2 volumes, 1855, 1365 pages, 2 maps). It was by far the most detailed synthesis on plant geography written by then (and maybe, ever). Joseph Hooker provided an extensive review in seven issues of his father’s Journal of Botany (1856), which was mainly a summary with few comments, until the last part in which Hooker discussed de Candolle’s suggestion of special creations with some transmutations; Hooker offered instead possibilities on transmutation, reflecting his discussions with Darwin, who was not mentioned. Hooker also commented on plant geography’s vague principles and methods and a lack of universal standards for meteorology. Charles Darwin called de Candolle’s treatise “grand and noble” (11 November 1859, Darwin 1991:367). Alphonse de Candolle changed “the emphasis from regions to species” (Ebach 2015:97). Retrospectively, de Candolle’s 1855 treatise was in the ironic position of being a grand synthesis of a pre-Darwin’s Origin of Species perspective, just before Darwin published the Origin (Thiselton-Dyer 1893, 1909:298–299, Good 1955:748, Dajoz 1984:39–46). He was not an evolutionist in 1855, but he became one after reading Darwin’s Origin of Species (de Candolle 1862, Gray 1876:197–198, Baehni 1955:112–114, Drouin 1988:159–161, 1993:78–79, 2007:265).

Englishman Philip Sclater (1829–1913) was from the upper middle class and attended Oxford University (Austin 1975, Stresemann 1975:203–204, 225, 360, Mayr 1982:448, Mearns and Mearns 1992:394–397, Innes 2004, Bircham 2007:195–197). To earn a living, he practiced law in London, but his life interests were first to ornithology, and second to zoological organizations in London. His lasting influence was from his paper, On the General Geographical Distribution of the Members of the Class Aves (1858), despite the fact that, in the year before Darwin published The Origin, he
believed that all species were specially created in their current distributions. “In this paper Sclater delineated and named the zoogeographical regions that we know today, and which have stood the test of time” (Bircham 2007:219–220): Palaeartic, Nearctic (sometimes combined into Holarctic), Aethiopian (now Ethiopian or Afrotropical), Indian (now Oriental), and Australian (now sometimes Australasian). In 1875, he extended the scope of his survey to include all vertebrates, brief mention of leading references for each order, and indicated gaps where research was needed. Later, he collaborated with his son on a monograph on The Geography of Mammals (1899). His regions had the virtues of simplicity and plausibility, which is why they survived into the 1900s (Nelson 1978:291–292, Ebach 2015:131).

German-born Albert Günther (1830–1914) earned his M.D. degree from the University of Tubingen in 1858 and visited his mother in the London area, where he met two zoologists at the British Museum and was hired, initially, to prepare a catalog of the Museum’s snakes and amphibians (Thomson 1927, England 2004). He remained at the Museum for the rest of his career. The zoological community in London was not large, and Günther and Sclater would have known each other. In 1858, Günther published On the Geographical Distribution of Reptiles. He and Sclater undoubtedly read each other’s articles, but at the time, nothing further came of their forays into neighboring geographical studies. Günther thought his regions differed enough from Sclater’s to justify their defining two sets of regions (Ebach 2015:131). However, Karl Schmidt (1955:767) commented that there was “a very fair agreement between the two distinct approaches.” Their articles became resources for Wallace’s The Geographical Distribution of Animals (1876), discussed below.

Darwin began his contributions to biogeography by collecting biological specimens during his world travels on the Beagle, discussed above. Philip Darlington, Jr., argued (1959:307) that Darwin’s zoogeographical discoveries in South America and on Galapagos Islands gave him the clues he needed to take evolution seriously. His subsequent four monographs on barnacles (Darwin 1851a, b, 1854a, b) had
still broader coverage, since barnacles are not confined to tropics as corals are, and he included fossils (Egerton 2011a, b, c:353–355). He conducted the first biogeographical experiments: subjecting different kinds of seeds to immersion in salt water for 12–137 days (Darwin 1855, 1857). Biogeography became a prominent topic of discussion in Darwin’s correspondence, seen in the index of his Correspondence: volume 6, for years 1856–1857, about 1.5 columns and in volume 7, for years 1858–1859, almost a column (Darwin 1990:651–652, 1991:650).

A turning point was Darwin’s publication of Origin of Species (1859). The big breakthrough was establishing his theory of evolution by natural selection (Schmidt 1955:767, Mayr 1982:445–448, Browne 2003, 2004). Wallace had also arrived at that theory in 1858, with Darwin publishing jointly Wallace’s and his own essay on it (1858). Wallace appreciated that Darwin’s Origin went far beyond statement of a theory. Lomolino et al. published parts of both of Darwin’s two chapters on geographical distribution in Darwin’s Origin of Species (1859) to reproduce in their biogeography source book (2004:140–163); it was Darwin’s synthesis of this subject. Before publication of The Origin, zoologists had argued about how many centers of creation there were, but after publication, those arguments disappeared (Darlington 1959:309).

The importance of Darwin’s contribution is indicated in comments by Asa Gray’s biographer (Dupree 1959:237):

Hooker, Gray, and [Alphonse] De Candolle were all first-rate scientists, capable of establishing a new science of plant geography at the same time they contributed mightily to taxonomy. But Charles Darwin’s horizons were already so much broader than theirs [in 1850s] that even a single letter of his, written in haste, rearranged the facts of natural history into new and striking patterns. Hooker did not exaggerate when he confessed he would never have taken up the subjects of distribution and variation of species but for the advantages he “had derived from [Darwin’s] friendship and encouragement” (1853–1855:I, xxii).

Fig. 5. (a) Charles Robert Darwin, 46 in 1855. Wikipedia (b) Joseph Dalton Hooker, by Charles Henry Jeens. Wikipedia. (c) American Asa Gray in 1886. Gray 1894: II, frontispiece.
Unlike Darwin, one long voyage was not enough for Hooker. He next explored India, December 1847–February 1851 (Huxley 1918, Turrill 1963, Allan 1967:97–250, Desmond 1972, 1999, Stafleu and Cowan 1976–2009:II, 267–283, Desmond 1977:318, Endersby 2004, Egerton 2012a:172–175, 2012b:125–138), and later, he more briefly explored less extensive regions. Always he returned with herbarium specimens and published his findings. One approach to biogeographical studies was to seek “the geographical and topographical spread of organisms away from a centre of origin” (Fattorini 2016:5–6). Ernst Haeckel (1834–1919) named this approach “chorology” (1866:287). However, Joseph Hooker and Thomas Thomson (1817–1878, Desmond 1977:609–610) adopted it in their unfinished Flora Indica (1855) before Haeckel named it. Hooker’s explorations in Morocco and North America are discussed below.

In 1855, he became Deputy Director of the Royal Botanic Garden, Kew, and in 1865, he succeeded his father as Director. Research there was primarily on plant taxonomy, and Joseph duly followed along. However, he had a strong interest in plant geography, one example being his analysis in the introduction to Flora Tasmaniae on the Flora of Australia (Hooker 1859, Good 1955:748). Another example,
his “masterly essay,” A Sketch of the Flora of British India (1904), based upon both his travels in and previous publications on India (Turrill 1963:179–183).

A later Kew botanist, W.B. Turrill, compiled Pioneer Plant Geography: the Phytogeographical Researches of Sir Joseph Dalton Hooker (1953, xii + 267 pages), in which he arranged extracts under the headings of Arctic, Syria and Palestine, India, Africa, North America, Galapagos Islands (Darwin’s 1830s plant collection), Antarctica (including New Zealand, Australia, and Tasmania), and Miscellaneous (mostly on different islands). The extract which Lomolino et al. reproduced (2004:109–117) is from the introduction to Hooker’s Flora Novae Zelandiae (1853–1855).

Londoner Edward Blyth (1810–1873) ran a druggist shop, but his abiding interest was natural history, and his shop failed in 1836 (McKinney 1970, Brandon-Jones 1995, 1997, 2004, Mearns and Mearns 1998:67–72, Waller 2004). In 1841, he became curator of the museum of the Asiatic Society of Bengal and published a series of articles on India’s fauna in that Society’s Journal for the 21 years in which he lived in India. Both his articles and his encouragements of other zoologists in India were important contributions to Indian zoology. Darwin was glad to use Blyth’s publications in Origin of Species (1859), Animals and Plants under Domestication (1868), and Descent of Man (1871). Blyth also published A Suggested New Division of the Earth into Zoological Regions in Nature (1871), which offered improvements upon Sclater’s essay on geographical distributions of birds, especially for India. However, it did not attract the amount of attention which Sclater’s essay had received, despite appearing in Nature.

Austrian botanist Anton Kerner von Marilaün (1831–1898) wrote a notable work, Pflanzenleben der Daanulaender (1863, English, 1951), which was an excellent example of a regional vegetation study, with broader significance (Stafleu and Cowan 1976–2009:II, 525–530, Nicolson 1996:297–298, Egerton 2013b:342–343). He complained about a lack of a standard botanical terminology to describe all native plant formations (1951:5–6).

The culmination of Grisebach’s research was his Vegetation der Erde nach ihrer klimatischen Anordnung (2 volumes, 1872, French, 1875). By 1870, traveling botanists had published accounts of enough vegetation of different places to make practicable such a synthesis. Ronald Good commented (1955:750): “the most striking thing about it now is how little it has been rendered obsolete by subsequent increase in our knowledge...” Grisebach’s son Eduard saw that his father’s shorter plant geographical writings were published the year following his father’s death, and there was also a posthumous second edition of Vegetation der Erde (1884–1885).

Wallace spent eight years (1854–1862) traveling about 14,000 miles in the Malay Archipelago, mostly by ship, despite suffering from tropical fever, probably malaria (Wallace 1905:I, 337–384, 1916:37–71, Daws and Fukita 1999:34). He later considered his Malay experience was “the central and controlling incident of my life” (Wallace 1905:I, 366), reminiscent of Darwin’s claim about the impact of his voyage on the Beagle on him (Darwin 1959:76). Wallace’s most important discovery, about January 1858, was the striking difference between the faunas of Borneo and Celebes across the Macassar Strait, which indicated a boundary between two major faunal realms of Asia and Australia (Wallace 1905:I, 356–359, Camerini 1993a, van Oosterzee 1997, Daws and Fukita 1999:74–79). However, as mentioned above, Salomon Müller had already drawn that line on his Malay Archipelago map in 1842, and Wallace’s line should now be called the Müller-Wallace Line. (Incidentally, it was at that point in his travels, in
1858, when he composed a letter to Darwin on his theory of the evolution of species by natural selection, which Darwin published along with his own writings on the subject.) Fifteen collaborators in 2013 improved upon Wallace’s zoogeographical regions of the world (Holt et al. 2013).
Three important works came from Wallace’s unrivaled tropical studies: The Malay Archipelago (2 volumes, 1869), The Geographical Distribution of Animals (2 volumes, 1876, mainly on land vertebrates), and Island Life (1880), which made him the most important contributor to zoogeography in the 1800s (Quammen 1996: Index, Smith and Beccoloni 2008). Wallace scholar John van Wyhe has thrown a bright light upon Wallace’s Malay experiences with three recent studies: Dispelling the Darkness: Voyage in the Malay Archipelago and the Discovery of Evolution by Wallace and Darwin (2013); an edited, annotated edition (with Kees Rookmaaker) of Alfred Russel Wallace: Letters from the Malay Archipelago (2013). Wallace’s letters began on 4 March 1854 and ended with letter 88, 31 March 1862; and The Annotated Malay Archipelago (1869, 2015). Darwin responded very positively to the 1876 volumes: a “grand and memorable work, which will last for years as the foundation for all future treatises” (5 June 76, Marchant 1916:235). Darwin was pleased that Wallace did not resort to land bridges to explain discontinuous distributions of species. A posthumous collection of Wallace’s letters contained three chapters on geographical distributions (1916:263–348). Lomolino et al. (2004:164–177) reprinted in their sourcebook chapter 23 from Geographical Distribution of Animals, Summary of the Distribution, and Lines of Migration, of the Several Classes of Animals, in which Wallace discussed not just amphibians, reptiles, birds, and mammals, but also fresh-water fish, insects, and terrestrial Mollusca. Schmidt (1955:769) suggested another source upon which Wallace built was the chapter on geographical distributions in Darwin’s Origin of Species (1859). Schmidt thought Wallace’s Island Life (1880) was more successful than his Geographical Distribution of Animals.

Wallace stated in the preface of his Geographical Distribution of Animals (1876:1, vi) that both Darwin and Alfred Newton had suggested he undertake this project about six years before. Wallace was the logical person to do so, because he had spent years in two tropical countries on different sides of the world studying vertebrate, and other animals, while also paying some attention to vegetation. It contains, in two volumes, seven color maps of the world’s zoogeographical regions and 20 black-and-white draw-
ings of typical animals and plants found in particular regions. He discussed fossil and extinct species as well as living ones, emphasizing birds and mammals, since they had been studied most, but including reptiles, amphibians, fresh-water fishes, and insects. He at times cited last names of authors and dates of publications, but did not often cite their publication titles, nor did he provide a bibliography. There are introductory chapters, but it was obviously written for practicing zoologists. He did cite (1876:1, 60–61) Murray’s Geographical Distribution of Mammals (1866) and Blyth’s Suggested New Division of the Earth into Zoological Divisions (1871), but offered a mild criticism of Murray book and slammed Blyth’s article: “Mr. Blyth’s scheme is one of the least natural, and also the most inconvenient.” Darwin was pleased with Wallace’s treatise, and Ernst Mayr (1982:449) observed that it became the bible of a regional school of biogeography (really, zoogeography). However, many naturalists thought Wallace’s Island Life (1880) was a better monograph, because it was a more manageable subject (Schmidt 1955:769–771, Barrow 2009:72–75). Wallace published two later notes on zoological regions (1883, 1894), not mentioning again Edward Blyth’s essay (1871), which he had previously discredited.

The Swiss paleontologist Karl Ludwig Rütimeyer (1825–1895) “in 1867, makes the suggestion of the former existence of a vast Antarctic continent, connecting all of the southern continents and New Zealand, and this idea received support from T.H. Huxley in 1870” (Schmidt 1955:773, Nelson 1975), though Eduard Suess coined the name Gonwandaland (Greene 1982:191; see below).

Finnish botanist Ragnar Hult (1857–1899) studied at Uppsala University before receiving his doctorate from Helsingfors University (Fries 1950:70, Collander 1965:74–77, Stafleu and Cowan 1976–2009:1, 361, Egerton 2013b:345). He investigated the physiognomy of vegetation and distinguished seven layers—ground layer, lower, middle and upper field layers, shrub layer, lower and upper forest layers—which he defined. In summer 1886, he taught a field course in plant geography, taken by Swedish student Rutger Sernander, who “adopted Hult’s ideas with great enthusiasm” (Fries 1950:70–71, Collander 1965:77). However, when Warming’s book appeared, it had a broad influence in Sweden, which would have included Sernander (Söderqvist 1986:50–51).
Another English naturalist, Henry Dresser (1838–1915), was a friend of Wallace’s. Dresser was a prosperous dealer in timber and iron, who traveled in Europe and North America and collected bird specimens wherever he went. Another specialist in bird studies, Richard Sharpe (1847–1909), proposed to Dresser in 1870 that they collaborate on a history of the birds of Europe, and Dresser agreed (McGhie 2017:98). Their plan was to publish *A History of the Birds of Europe* in parts, and they did so for 13 parts (Sharpe and Dresser 1871–1872). However, in September 1872, the British Museum hired Sharpe to work on its bird collection, and so he resigned from their shared authorship. Dresser continued alone, and by 1882, he had published parts 14–84, including 624 species from western Russia west to Britain and south to North Africa and the Near East and Azores, Canaries, and Madeira islands off north Africa’s west coast. Sharpe had participated in their examination of bird skins while he was a collaborator, but Dresser examined almost all of the 10,637 bird skins observed, from 102 collections besides his own (McGhie 2017:150). His monograph was highly praised by reviewers, and he later supplemented it with *Eggs of the Birds of Europe* (24 parts, 1905–1910), which included photographs of nests as well as eggs.

Two German botanists, discussed in part 48 (Egerton 2013b:345, 349), Adolf Engler (1844–1930) and Oscar Drude (1852–1933), contributed separately to phytogeography (Drude 1890, 1896, Engler 1899) and also collaborated in organizing and editing *Die Vegetation der Erde* (15 volumes, 1896–1923); each also wrote one of these volumes (Drude 1902, Engler 1910–1915). Two English-language volumes included are discussed also in part 48 (Egerton 2013b:349–350, 365) *The Vegetation of New Zealand* (1921) by Leonard Cockayne (1855–1934) and *Phytogeographic Survey of North America* (1911) by John Harshberger (1869–1929).

Engler was mainly a systematic botanist, but he was an early convert to Darwin’s revolution, and he developed a strong interest in plant geography (Stafleu and Cowan 1976–2009:II, 757–797, Stafleu 1978, Lack 2000, Magnin-Gonze 2004:197–199). In 1880, he founded *Botanische Jahrbücher für Systemataik, Pflanzengeschichte und Pflanzengeographie*, which he edited for almost 50 years. It was undoubtedly the first scientific journal to name phytogeography as one of its specializations. He also co-edited *Die Vegetation der Erde* (15 volumes, 1896–1923) and wrote one of the volumes, *Die Pflanzenwelt Afrikas* (1910–1915). Two of those recruited to write volumes in the series were John Harshberger, who wrote the North America volume (1911), and Leonard Cockayne, who wrote the New Zealand volume (1921, edition 2, 1928). Good (1955:754) merely mentioned Harshberger’s volume and made no mention of Cockayne’s; I previously discussed both (Egerton 2013b:349–350, 365). Although Fernald (1911) reviewed Harshberger’s book unfavourably, for present purposes, his bibliography on plant geography (1911:46–92) is truly monumental.

Drude (1852–1933) studied under Grisebach, earned his doctorate at Göttingen in 1873 (Stafleu and Cowan 1976–2009:1, 682–683, Matagne 2009: see index), and also updated Grisebach’s *Vegetation der Erde* with his own *Atlas der Pflanzen verbreitung* (1887), *Handbuch der Pflanzengeographie* (1890), and *Deutschlands Pflanzengeographie* (1896). Good (1955:751) explained that Drude’s atlas was “part of a larger physical atlas and consisted of a short series of excellently produced maps showing the ranges of various important plant elements, both vegetational and floristic, accompanied by a concise explanation.” He also collaborated with Engler in editing *Die Vegetation der Erde*. Still later, Drude wrote the earliest textbook on *Oekologie der Pflanzen* (1913), which Tansley reviewed (1914), but later forgot (Egerton 2013b:357–358).

An important resource for zoogeography which Schmidt cited (1955:773) was by University of Vienna geologist Eduard Suess (1831–1914): *Das Antlitz der Erde* (3 volumes, 1883–1909, French,
4 volumes, 1897–1918, English, 5 volumes, 1904–1924). Suess began his illustrious career as a paleontologist, and so his work was also a resource for paleoecology (Wegman 1976). The last chapter of this work was on distribution of life on the earth. Sea levels fluctuated, and there was evidence of land bridges at Beringia, Panama, and between Britain and France, and so one may assume land bridges at time existed between other land masses (Schmidt 1955:772–773, Wegman 1976:148).

Thanks to the prior syntheses in Alphonse de Candolle’s Géographie botanique (1855) and Grisebach’s Die Vegetation der Erde (1872), phytogeography flourished during the 1890s, exemplified not only in the work of Engler and Drude, but also in that of Warming, Flahault, Schröter, and Schimper. As explained in part 48 (Egerton 2013b), phytogeography was one of the roots of the broader science of plant ecology.

Danish botanist Eugenius Warming (1841–1924) studied at the University of Copenhagen. He took leave from his undergraduate education to become secretary to zoologist P.W. Lund for three years, 1863–1866, in Brazil, where Warming studied tropical vegetation, and that became the subject of two of his extensive publications (Goodland 1975, Müller 1976, Egerton 2013b:346–347). He earned his Ph.D. at the University of Copenhagen, and he taught elsewhere before he became professor and director of the botanic garden, 1886–1911, at the University of Copenhagen (Christensen 1932, Goodland 1975, Müller 1976, Egerton 2013b:346–348). His Pflantesamfund: Grundtræk af den ekologiske Pflantesgeografi (1895, German 1896) was called the first book that could be used as a plant ecology textbook (Coleman 1986); it had a stronger impact than Franz Meyen’s book (1836) had, because Warming had more accumulated knowledge on which to draw. The English translation (1909) dropped reference to plant geography in the title and substituted “plant communities.” The term he favored for groups was “formation,” for which I find no definition. The majority of sections in the English edition are organized under such titles as “Hydrophytes: Formations of Aquatic Plants,” “Helophytes: Formations of Marsh-Plants,” “Oxylophytes: Formations on Sour (Acid) Soil,” “Halophytes: Formations on Saline Soil.”

French botanist Charles-Henri-Marie Flahault (1852–1935) earned a doctorate at Paris in 1878, then traveled with fellow botanist Gaston Bonnier to Sweden, where they compared alpine and polar climates and plants (Emberger 1936, Jovet 1954:256–257, Good 1955:753, Staffleu and Cowan 1976–2009:1, 843, Matagne 1998:437–437). Flahault joined the University of Montpellier in 1881 and became professor of botany in 1883, founded an Institut de Botanique in 1890, and in 1891 started a school of Mediterranean phytogeography. In 1905, the International Botany Congress charged him and Swiss botanist Carl Schröter (1855–1939) with establishing a committee to establish terminology “that integrated the floristic and physiognomic components of botanical geography” (Matagne 1998:436) for the Third International Botany Congress (1910). Schröter’s Planzenleben der Alpen (1904–1908, 1288 pages) was a worthy companion to Kerner’s Pflanzenleben der Danaulaender (1863). Swiss botanist Josias Braun-Blanquet (1884–1980) studied under both Flahault and Schröter and became Flahault’s successor at Montpellier (Nicolson 1989:142–143, 146–148, 181).

Andreas Schimper (1856–1901) was the son of botanist Wilhelm Schimper, director of the Strasbourg Natural History Museum, in France until Prussia won the Franco-Prussian War (1871), and then, Wilhelm Schimper became Professor of Natural History at the Strasbourg University (Sanders 1975, Cittadino 1990:97–115, Egerton 2013b:346–347). Andreas earned his doctorate there and later traveled in Brazil, where he studied a symbiotic relationship between ants and Cecropia trees (1888). His encyclopedic Pflanzengeographie auf physiologischer Grundlage (1898, English, 1903, 870 pages, 4
folded colored maps) was one of the largest ecological treatises ever written by one author. He thought (1903:vi) that “The connexion between the forms of plants and the external conditions at different points on the earth’s surface forms the subject-matter of oecological plant-geography,” and that Grisebach’s approach was obsolete! Cowles (1909:356) judged Schimper “a prophet as well as an ecologist of the first magnitude.” Zoologist Schmidt (1955:783) acknowledged his importance. However, Schimper borrowed heavily from Warming, with scant acknowledgment (Goodland 1975:243). In my own check of

Fig. 11. (a) Acacia (b) Xerophilous (note captions) Schimper (1903:348, fig. 185; 349, fig. 186).
Schimper’s vast opus, I find that he did cite Warming in some chapter bibliographies and illustration captions; might Goodland have overlooked those citations?

Warming seems not to have noticed any slight by Schimper. Their books were more complementary than duplicative (Dajoz 1984:108–111). Schimper’s was encyclopedic and well illustrated with drawings and photographs. Warming’s was more of a textbook, half the size of Schimper’s and lacks illustrations. Warming’s greatly revised English edition (1909) had dropped the reference in its title to plant geography in favor of plant communities.

Fig. 12. Distribution of the most important types of formations on the Earth’s surface. Schimper (1903: map 3, third fold).

Falmouth, England native Henry Guppy (1854–1926) attended medical school in Birmingham and Edinburgh, then served as a surgeon in the Royal Navy, 1876–1885, and was in the western Pacific, 1881–1884, where he collected plants in the Solomon Islands, Keeling Island, and Java (Good 1955:754–755, Desmond 1977:276, Smith 2005). He published two volumes on the Solomon Islands in 1887. He collected in Hawaii and Fijian Islands, 1896–1900, and then published two volumes of Observations of a Naturalist in the Pacific between 1896 and 1899 (1903–1906). In 1906, he also published Plant Dispersal, followed by Studies in Seeds and Fruits (1912, 528 pages). His last large work was Plants, Seeds, and Currents in the West Indies and Azores (1917, 531 pages). Finally came two articles: The Island and the Continent (1919) and Plant Distribution from the Standpoint of an Idealist (1920). He was elected a member of the Royal Societies of London and Edinburgh.

Swedish ecologist-phytogeographer Rutgar Sernander (1866–1944) studied the vegetation of Gotland Island for his doctoral dissertation (Ph.D. 1894). In 1895, he became docent of phytogeography
at Uppsala University and in 1908 became professor of plant ecology (Fries 1950:70–71, Söderqvist 1986:46–47, Egerton 2013b:352–353). He ran a seminar on Swedish plant communities which began in 1908, and after the appearance of Types of British Vegetation which Tansley edited in 1911 (see below), that work exerted an influence on students in Sernander’s seminar (Söderqvist 1986:54–55). The students in his seminar would then write dissertations on Swedish vegetation.

Warming’s successor as professor of botany at the University of Copenhagen was Christen Raunkiaer (1860–1938). The English version of Warming’s book (1909:395) cited seven of Raunkiaer’s publications, 1889–1908. In 1934, 17 Raunkiaer publications (1904–1928) were published in English translation, plus a 54-page study in English not previously published, on Mediterranean vegetation. Raunkiaer’s main contribution was explained in his book, The Life Forms of Plants and Their Bearing on Geography (1907, English 1934). He focused upon the part of plants that survives its most unfavorable season, which he called its life form. He then classified 1,084 plant species of Denmark into 10 life forms and compared those numbers to 904 species from Danish West Indies and found conspicuous differences (1934:102). Such studies could be made in other places and create still different proportions of species in his 10 categories. These numbers could provide indications to geographical regions. That was interesting, though apparently not many others followed his example and conducted such studies. Yet, his studies seemed important enough to appear in English, and George Fuller (1935) thought it was an important book.

Plant ecology arose in Britain from influences of Warming, Schimper, and Flahault (Tansley 1947, Godwin 1977:4, 9). Scottish botanist Robert Smith (1873–1900) spent the school year 1896–1897 studying under Flahault and returned to Scotland with a desire to construct Flahault-type ecological maps (Good 1955:753, Desmond 1977:569, Ayres 2012:72). He had completed maps of Edinburgh and North Perth and begun maps of Forfar and Fife before his early death. His older brother, William Gardner Smith (1866–1928), completed those surveys, and then moved to Leeds, where he convinced the Yorkshire Naturalists’ Union to undertake a botanical survey under his direction (Desmond 1977:570, Ayres 2012:72). Yorkshire vegetation maps appeared in 1903, the first in England, which inspired formation of the British Vegetation Committee in 1904. Members of the Committee conducted surveys in various parts of Britain and constructed maps. That trend culminated in a massive Types of British Vegetation (1911) under editorship of botanist Arthur Tansley (1871–1955), who, by then, was also in charge of the Committee (Desmond 1977:598–599, Ayres 2012). However, he did not see that work as definitive. That would be The British Islands and Their Vegetation (930 pages, 418 photographs, 162 plates, 179 figures), which fortunately went to press in 1939 before World War II would have made it impractical to publish. He retired from Oxford University in 1937, yet continued publishing until 1954 (Ayres 2012:203–204).

Why not show other ecologists the British Isles as represented in Types of British Vegetation? Tansley organized an International Phytogeographic Excursion which was conducted in August 1911 (Sheail 1987:30–35, Fischedick 2000, Ayres 2012:83–86, Egerton 2013b:355–357). Foreign ecologists who participated were Drude, Ostenfeld, Rübel, and Schröter from Europe and Clements and Henry Cowles (1869–1939), with wives, from United States. On 1 August, the group assembled at the Cambridge Botany School and toured the University botanic garden. At the various places where local vegetation was studied, the Excursion was met by local botanists, mostly those who had contributed to the book.
The successful Excursion led, on the one hand, to Tansley organizing the British Ecological Society (BES) in 1913, the first ecological society in the world (Sheail 1987), and on the other hand, to Americans Cowles and Clements planning a sequel excursion in 1913. American botanists had been influenced by the Continental developments in phytogeography, just as British plant ecologists had (Egerton 1977b, Tobey 1981).

Leeds native Robert Francis Scharff (1858–1934) earned degrees at the universities of London, Edinburgh, and Heidelberg, and in 1887, he joined the Natural History Division, National Museum of Ireland, Dublin (Praeger 1949:152). He studied the recolonization of Ireland by mammals after the last ice age and wrote three books: *The History of the European Fauna* (1899), *European Animals: Their Geological History and Geographical Distribution* (1907), and *Distribution and Origin of Life in America*.
The last two works are roughly comparable to volumes which Engler and Drude edited on the vegetation of the earth (see above).

Finnish botanist Regnar Hult (1857–99) is relevant here, and what I said about him in part 48 (Egerton 2013b:344–345) fits here just as well.

French bacteriologist Charles J.H. Nicolle (1886–1936) was from Rouen, where his father was a doctor at the Rouen hospital. Charles earned his M.D. at the Pasteur Institute in 1893 and joined the medical faculty at Rouen. In 1896, he became director of the bacteriological laboratory. In 1903, he became Director of the Pasteur Institute of Tunis, where he remained. In 1909, he suspected that typhus bacteria were transmitted by lice. He tested his hypothesis by infecting an isolated chimpanzee with typhus and then transferring its lice to another isolated chimpanzee, which also got typhus. For this discovery, he received a Nobel Prize in 1928. François Dagognet (1977:151–163) discussed the significance of Nicolle’s work for biogeography.

German zoologist Hans Gadow (1855–1928) earned his Ph.D. under Haeckel at the University of Jena, 1878, and he went to London in 1880 at the invitation of Günther to catalog the bird collection at the British Museum (Smith 2005). In 1882, he moved to Cambridge University, where he later wrote The Wanderings of Animals (1913). It is a quite small book of 150 pages and 16 maps. Its historical significance lies in the fact that zoogeography had become well known enough for it to be competently summarized by a professional zoologist. In chapter 5, Former Configurations of Land and Water, he commented (Gadow 1913:76): “In the majority of cases the present distribution of animals cannot be accounted for without the assumption of enormous changes in the configuration of land and waters.” He thought that “instances of occasional dispersal (by the proverbial floating log, currents, storms and water-spouts)” was insignificant. He thought that land tortoises had reached Galapagos Islands by land. However, he was not so much advocating land bridges as he was arguing for the movement of continents (Gadow 1913:78–87).

An important developer of this idea, in 1915, was Berliner Alfred Wegener (1880–1930), who began his university education in astronomy (B.S. 1905). His interests shifted to meteorology and geology, and he joined a Danish expedition to northeastern Greenland, 1906–1908 (Schmidt 1955:775–777, Bullen 1976, Schwarzbach 1986, Greene 2015). He later went on three more Greenland expeditions, and he froze to death on the last one. In 1910, he became impressed by the corresponding east coast of South America and west coast of Africa, and in 1911, he learned of the similarities of fossils on those coasts, and in 1912, he announced his theory of continental drift. He was wounded in World War I, and during sick leave, he wrote Die Entstehung der Kontinente und Ozeane (1915), his most important work. It appeared, however, when the world was preoccupied with war (Hallam 1973:1–21, 1983:110–156, Colbert 1985, De Querioz 2014:34–42). In 1924, he became professor of meteorology and geophysics.

Wegener’s theory was incompatible with ideas on permanent locations of continents, and on the rise and fall of land bridges, aside from ideas on the rise and fall of ocean levels due to ice age fluctuations. He argued that continents are granite bodies afloat on a pliable medium. He added new evidence in later editions of 1920, 1922, and 1929. The 1922 edition was translated into English, French, Spanish, Swedish, and Russian. A major weakness was that he did not offer a plausible mechanism to explain how
continents moved. Controversy over his theory was considerable until the world was again diverted by war (Schmidt 1955:775–776). Henry N. Ridley avoided that controversy with his huge The Dispersal of Plants throughout the World (1930, 744 pages), which stuck to the facts (Good 1955:759, Desmond 1977:520). The same was true for a dozen authors who wrote important treatises on regional vegetation—including on New Zealand, South Africa, Philippines—whom Good (1955) cited. It was only after 1960 that continental drift gained widespread acceptance. A documentation of Wegener’s theory was the impressive 1990 symposium on Biological Relationships between Africa and South America, even if the scientists were so present-oriented that their published papers never mentioned him (Goldblatt 1993).

German zoogeographer Richard Hesse (1868–1944), from Nordhausen, earned his Ph.D. (1892) at the University of Tubingen and taught there and at two other universities before becoming professor of zoology at the University of Berlin, 1926–1935. He published Tiergeographie auf oekologischer Grundlage (1924); his monograph’s title is a paraphrase of Schimper’s on plants (1898). Thomas Park (1949:55) thought Hesse’s was the most important treatise on ecology during the 1920s. W.C. Allee and K.P. Schmidt translated Hesse’s original monograph and revised it into English (1937). These translators stated that it was the first attempt to apply ecological methods and principles to zoogeography. Schmidt (1955:767) later made a similar claim for Schmarda (1853). However, ecological understanding of zoogeographical principles had advanced significantly during 70 years between Schmarda’s and Hesse’s works. Hesse was first to use ecological understanding to account for distributions worldwide. Hesse et al. (1936) included oceanic life as well as land and inland water life; some chapters are well illustrated; citations are slightly better than in Wallace (1876) and Heilprin (1887), in that publishing locations were indicated in chapter bibliographies, though titles were omitted. The English-language edition was a success, which inspired Allee and Schmidt to publish a second edition, which their preface called “an essentially new work” (Allee, Schmidt and Hesse 1951:vii). Not only did new material replace some older comments, the second edition had also increased from 597 pages to 715 pages. The chapter bibliographies in the second edition included titles as well as locations of citations.

Fig. 14. (a) Pangaea. (b) Alfred Wegener. Wikipedia.
English botanist John Christopher Willis (1868–1958) attended Cambridge University (BA, 1891, D.Sc. 1905) before joining the faculty of Glasgow University, 1894–1896 (Good 1955:756–757, Desmond 1977:664, Smith 2005). Then, he traveled to Ceylon (Sri Lanka) to become director of the botanic garden at Peradeniya, 1896–1911. Next, he moved to the directorship of the botanic garden at Rio de Janeiro, Brazil, 1912–1915. Theoretically, he thought one could explain evolution by either natural selection or mutation, and he defended mutation (Good 1955:756–757). He thought that his contributions to phytogeography supported his theory: Age and area: a study in geographical distribution and origin of species (1922), The birth and spread of plants (1949).

Scottish zoogeographer Marion Newbigin (1869–1934) earned her B.Sc. and Ph.D. at the University of London (1893, 1898) and published Life by the Sea Shore (1901) before returning to Edinburgh in 1902 (Creese 2004). She became editor of Scottish Geographical Magazine in 1902 and continued as editor until she died. Her pioneer work was Animal Geography (1913), followed by her major work, Plant and Animal Geography (posthumous, 1936). In the latter work, she had been preceded by Emmanuel de Martonne (1873–1955), Traité de Geographie Physique (edition 4, volume 3, Biogéographie 1921, de Martonne et al. 1927). In her latter work, Newbigin depended for plant geography mainly on Warming, Schimper, and Tansley (Stott 1984:1). Her books were widely used in the UK.

Swedish botanist (Otto) Gunnar Erdtman (1897–1973) was a pioneer in palynology; he published his 1921 text on it in the German language. His Pollen Statistics: a New Research Method in Paleoecology (1931), published in Science, noted that plant ecology flourished in America, but not paleoecology, which would enhance plant ecological understanding. In Sweden, for about 20 years, G. Lagerheim and L. von Post had been using the Hiller peat auger to drill into peat deposits to gain an understanding of vegetation history from pollen grains that were preserved in the peat. Erdtman provided instructions and citations to the literature in a Swedish geological journal. This approach proved very fruitful.

Russian botanist Evgenii Wulff (1885–1941) in 1932 published An Introduction to Historical Plant Geography (English, 1943). He reviewed different suggestions to account for existing plant distributions and found Wegener’s theory most plausible. Englishman Ronald Good later stated (Good 1955:758) that he wrote The Geography of the Flowering Plants (1947) before World War II, but the war delayed its publication until afterward.

North Americans

Great Britain’s three naval world circumnavigations under James Cook, with naturalists, followed by the Beagle’s with Darwin influenced Americans to do likewise, though it was a struggle to organize it. No naval officers who had the proper rank to lead the expedition wanted to, and the one officer who wanted to go, young Lieutenant Charles Wilkes (1798–1877), lacked the rank and confidence to do so. The Secretary of Navy promised to make him an acting captain, but failed to deliver, which left Wilkes feeling vulnerable. He commanded six vessels, with 346 men, including naturalists, on the U.S. Exploring Expedition, 1838–1842 (Tyler 1968, Stanton 1975, Leonhart 1985, Stann 1985, Viola 1985, Sprague 1999, Philbrick 2003). He was very capable technically, but feeling insecure, he was not a diplomatic “people person,” and his relationships with those aboard were strained. Charles
Pickering (1805–1878), who had published a brief paper, On the Geographical Distribution of Plants (1830), became a zoologist during the expedition, though he mainly studied plants and human biogeography (Gray 1878, Kendeigh 1954:154, Eyde 1985:26, Harmond 1997, Burchsted 1999, Philbrick 2003). Another naturalist was Titian Ramsay Peale (1799–1885), son of prominent Philadelphia artist and museum owner-director, who was also an artist (Poesch 1961, 1974, Harmond 1997b, Philbrick 2003).

The Exploring Expedition did achieve outstanding results: discovery of Antarctica and mapping of 1,500 miles of its coastline, 40 tons of specimens and artifacts, discovery of 2,000 new species, and mapping coastlines of numerous south Pacific islands for the first time (Ehrenberg et al. 1985, Egerton 2011b:153–161, Egerton 2012a, b, c:149). Asa Gray, the botanist, resigned before the expedition began, and two gardeners were taken along, William Rich and William Brackenridge (Eyde 1985:27–33), collected plants at the places where the expedition went ashore. However, when it came time to write a botanical report, the expedition leader, Charles Wilkes, turned to Gray, who agreed to undertake the task (Eyde 1985:38–40). Gray’s work became part of the expedition’s official record (Gray 1854). Peale did write the volume on mammals and birds (1848), but Wilkes decided it was inadequate and only a few copies of it survive (Harmond 1997b:614). Wilkes then had Philadelphia ornithologist John Cassin (1813–1869) rewrite the volume (Thorsen 1997), still using Peale’s illustrations (1858).

Since the expedition’s achievements rivaled those of Captain Cook, Wilkes expected to receive comparable celebration to Cook’s upon return to the United States. Unfortunately, such a reception was close to non-existent, because of court martials of Wilkes for his harsh treatment of officers and others. His career survived, but he never became a hero and his expedition’s achievements were rather neglected. However, the expedition’s achievements were well documented in numerous publications (Haskell 1942, Philbrick 2003:435–436). One example of Wilkes’ strained interactions was his dismissal of conchologist Joseph Pitty Couthouy (1808–1864) and seizure of his journals and specimens, in October 1840 (see 61C).

French American naturalist John James Audubon (1785–1851), who is most famous for The Birds of America (4 volumes, 1827–1838) of paintings and text in his Ornithological Biography (5 volumes, 18),
but afterward he collaborated with John Bachman (1790–1874), and eventually also Audubon’s two sons, John Woodhouse Audubon and Victor Audubon, in publishing *Viviparous Quadrupeds of North America* (3 volumes, 1845–1848) of 160 paintings and text on 197 species in 3 volumes (1846–1854); they extended coverage west by taking a steamboat up the Missouri River (Hamilton 1955:663). A broader exploration of western biota came in the 1850s, when naturalists accompanied Federal-sponsored explorations for the best route for a transcontinental railroad (see below).

New Yorker John Torrey (1796–1873) became interested in plants in 1810 but earned a medical degree (1818) and taught chemistry (Rodgers 1942, Robbins 1968, Dupree 1976, Kenney 1999b). He published an ambitious first volume of *Flora of the Northern and Middle Sections of the United States* (1824) and, later with a protégé, Asa Gray, began an even more ambitious *Flora of North America* (2 volumes, 1836–1843) before being abandoned so he could complete a *Flora of the State of New York* (2 volumes, 1843). In the next forty years, he described plant specimens brought back by explorers from eighteen Federal expeditions into the American West.

New York State botanist Asa Gray (1810–1888) agreed to join the U.S. Exploring Expedition, but backed out when he received an appointment as a professor of botany at the University of Michigan, though that position never materialized and he went to Harvard University instead (Dupree 1959:67–72, 111, 1972:512, Kenney 1999a). In return for identifying Cyperaceae species for German botanist Joseph Zuccarini, Zuccarini gave him the first part of *Flora Japonica* (1835–1839), by Philipp Franz von Siebold and Zuccarina, which Gray then reviewed in the *American Journal of Science* (Gray 1840). Although that first part was limited to ornamental plants, Gray was struck by the similarities between 14 species and related temperate American species. He listed in parallel columns those Japanese species and similar American species, but at that point no explanation of these similarities was possible. In a subsequent note (Gray 1846), he expanded the list of similar species between Japan and United States, without an attempted explanation. He continued this line of research after Commodore Matthew Perry pushed open Japan in March 1854. Two members of Perry’s expedition collected plants that were given to Gray to describe (Gray 1856–1857). Gray also published possibly the first regional flora (more than one state) in North America, *A Manual of the Botany of the Northern United States* (1848, lxxii + 710 pages), as well
as assisting Torrey with his unfinished Flora of North America discussed above. Gray’s own early distant exploration was in the North Carolina mountains in summer 1841 (Gray 1842, Dupree 1959:96–97).

Although Hooker became Darwin’s most trusted friend, Darwin also came to trust Gray, whom he met in 1838, when Gray traveled to Britain and Continental Europe. However, it was too brief a meeting for them to get to know each other, and they met again at the Royal Botanic Garden, Kew, in 1851, after Joseph Hooker had become friends with both men (Dupree 1959:81, 192). Four years later, on 25 April 1855, Darwin initiated their correspondence by asking Gray about the ranges of alpine plants in America (Darwin 1990–1991:V, 322–323). Gray responded, 22 May 1855 (in Darwin 1990–1991:V, 334–336):

*I had always intended, when the Flora of N. America should be finished to work up the geographical and climatic relations of this flora, and to compare it critically with the N. European, & N. Asian floras. I was more sanguine in former years. Now I doubt I shall ever live to see this Flora finished (tho, I hope to complete the 2d vol. this year)...*

He then answered Darwin’s questions as best he could, and encouraged him to mention additional questions that he might be able to answer when revising his Manual of the Botany of the Northern United States (edition 1, 1848).

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Fig. 17. Frémont’s five western mapping expeditions. Egan (1977: inside front cover).
Other noteworthy American land explorations occurred soon after the Wilkes expedition. U.S. Topographical Engineer John C. Frémont (1813–1890) conducted five mapping expeditions into the West (1842–1853), the first three of which were quite successful, though the last two were not entirely, though he completed maps for all five (Nevins 1955, Egan 1977, Richmond 1989, Herr 1999, Roberts 2000, Chaffin 2002:95–430, Beidleman 2006:163–184, Egerton 2011b:161–165, 2012a:150). Frémont was interested in western plants, and he collected specimens and presented them to Torrey to describe (McKelvey 1955:753–769, 843–889, 914–931, 1039–47, Jackson and Spence 1970–1984:I, 758–775, III, 571–608).

Fig. 18. (a) Asa Gray, age 57 in 1867. Gray 1894:I, frontispiece. (b) John C. Frémont as a young U.S. Army explorer. Wikipedia. (c) Louis Agassiz at blackboard. Wikipedia.

Congress established the General Land Office in 1812, to survey Federal lands. In 1849, it established the Department of Interior to manage public lands. By the 1840s, railroad technology was sufficient for Congress to envision a transcontinental railroad. That immediately resulted in a controversy over location for its eastern and western terminals. Seven proposals for its route were submitted to Congress, none of which received a majority vote, and so Congress voted to sponsor multiple surveys, in hopes that one route would seem obviously superior to the others. That was a bonus for geographical botany and zoology, because these surveys included naturalists who collected records and specimens along the lines surveyed. Edward Wallace described this aspect of the surveys in The Great Reconnaissance: Soldiers, Artists and Scientists on the Frontier, 1848–1961 (1855), with 24 illustrations reproduced from the survey reports discussed. William Goetzmann included accounts of the same explorations in his even broader account, Exploration and Empire: the Explorer and the Scientist in the Winning of the American West (1967:231–347), which included numerous contemporary illustrations and maps. On the relevance for these surveys for history of ecology, I have discussed them in part 38B (Egerton 2011b:167–173; also 2012a:151). Here, I only add a relevant work: Paul D. McDermott, Ronald E. Grim, and Philip Mobley, Eye of the Explorer: Views of the Northern Pacific Railroad Survey, 1853–1854 (2010). Other surveys, for other reasons, also occurred after the Civil War, 1867–1879, described by Richard Bartlett, Great Surveys of the American West (1962, Rodgers 1944:21–80), with many contemporary illustrations—almost all of which are photographs. Goetzmann also included those surveys in his broader account (1967:355–576).
Swiss zoologist Louis Agassiz (1807–1873) was son of a Protestant minister, and although Louis never adhered to a particular religion, his conservative religious faith was too strong for him to accept Darwin’s revolution of 1859 (Agassiz 1886, Lurie 1960, 1970, Mayr 1982: Index, Solomon 1997, Irmscher 2013). He had been the first zoologist to accept the glacial theory of climatic change in the past history of continents, which had not threatened his beliefs, but had been compatible with Cuvier’s theory of past catastrophic extinctions which Agassiz accepted. (An extract from Agassiz’s Études sur les glaciers [1840] is translated in Mather and Mason 1939:329–335.) He went to Boston and Cambridge, Massachusetts, to lecture in 1846 and received such a positive reception that Harvard University offered him a professorship which he accepted. In 1848, he led an expedition to the north shore of Lake Superior; it included nine students, two European naturalists, American naturalist John Le Conte, and others. Agassiz was an effective leader, and a well-illustrated, multi-authored volume recorded the expedition’s discoveries (Agassiz 1850a, Lurie 1960:148–152, Irmscher 2013:95–98). A Bostonian participant, J. Elliot Cabot, wrote the narrative of the expedition (pages 9–133) and drew landscape illustrations; Agassiz wrote most of the remaining portions of the report, but there were four specialized reports—on Coleoptera, Lepidoptera, Mollusca, and Birds—by other members of the expedition. In 1859, Agassiz established Harvard’s Museum of Comparative Zoology, with a substantial public–private endowment (Winsor 1991), and it probably contains specimens from the 1850 expedition. Darwin was very pleased to receive a copy from Agassiz, but if he read pages 375–376, he would have been disappointed to learn that Agassiz thought the fish and other aquatic species in that lake had been created there (Browne 1983:138–144). Geology professor Albert V. Carozzi wrote a 21-page geological introduction to the 1974 edition, claiming the chapter on glacial boulders on the lake shore was its most important contribution.

Agassiz’s interest in biogeography was not limited to his Lake Superior expedition (von Hofsten 1916:293, 297–298, Browne 1983:138–144). His own account of the vegetation around the lake shore (1850a:137–190) compared it to Alpine vegetation in Switzerland, and he soon published two other relevant essays: Geographical Distribution of Animals (1850b) and Sketch of the Natural Provinces of the Animal World and Their Relation to the Different Types of Man (1854a, b), which included a North American map (1854: reproduced in Kendeigh 1954:155). François Vuilleumier and Allison Andors (1999:389) called Agassiz “founder of American biogeography.” They noted his influence upon later founders of zoological museums.

New Yorker Jacob P. Giraud, Jr. (b. 1811), was an early example of what historian Mark Barrow (1998:9–13) called a culture of collecting in which middle-class men came to think that they could enhance their appreciation of nature by collecting whatever aspect of it interested them. In 1844, Giraud was living on Long Island, and he used his collection as a basis for writing The Birds of Long Island. Very little is known about him, but on 22 April 1867, he presented his bird collection to Vassar College, Poughkeepsie, New York (Johnson 1921).

Although Gray traveled less widely than did Hooker, he still managed to develop a broad perspective on phytogeography (Good 1955:748, Dupree 1959, 1972). One example was Gray’s studies on the relations between Japanese and North American plants, begun in the 1840s and continuing in the 1850s (Hung 2010). That interest was encouraged by Darwin, who wrote to Gray in April 1855, with enquiries about the range of alpine plants in America (Darwin). Gray answered Darwin’s questions as best he could. On 4 May 1857, Gray wrote English botanist George Bentham (in Gray 1893:II, 429):
When [Charles] Wright comes home from Cuba I expect to get hold of his considerable north Japan collection, which I expect to find very interesting on questions of distribution…

Charles Wright (1811–1885) had graduated from Yale in 1835, and he decided to become a plant collector and explorer (Mearns and Mearns 1992:496–500, Hung 2017:86–87). He had previously collected plants for Gray, 1849–1851, in Texas. He became the botanist in the U.S. North Pacific Exploring Expedition (NPEE), 1853–1856. (The zoologist of NPEE was William Stimpson, who is discussed in part 61C, because his collection was primarily on marine invertebrates.) Wright collected terrestrial plants.

Gray gained access to Wright’s Japanese collection, which became the subject of his detailed descriptions, followed by his explanation of the similarities between parts of the floras of Japan and eastern North America based upon wide-ranging arguments from the fossil record (Gray 1859, Hung 2017). Nor was that the last time he pondered this puzzle, which his biographer considered his “greatest theoretical contribution to science” (Dupree note 5 on page 185 of Gray 1963). Darwin wrote to Gray on 20 July 1857 and briefly explained his theory on the origin of species (Darwin 1990–1991:VI, 431–433).

New Yorker James Graham Cooper (1830–1902) was son of naturalist William Cooper, who helped establish the Lyceum of Natural History of New York in 1817 (Grinnell 1930, Coan 1982:14–16, Brodhead 1999). The son earned a medical doctorate in 1851 from the College of Physicians and Surgeons, practiced medicine at the New York City Hospital for two years, then joined the Isaac Stevens Expedition, the northern-most exploration of a route for a transcontinental railroad (Grinnell 1930, Coan 1982:19–58). He served as physician-naturalist, and his interests encompassed both plants and animals. James followed his father’s example of becoming a frequent publisher of rather brief natural history reports (Coan 1982:232–233 on William’s publications; 223–232 on James’ publications). James’ lon-
gest report seemed to be On the Distribution of Forests and Trees of North America, with Notes on its Physical Geography (1859). Those 35 pages + map described six Natural Provinces, which in turn were subdivided into 27 regions (with Arctic and Nevadian Provinces having one region each). Cooper settled in California, and the Cooper Ornithological Club was named for him.

James S. Lippincott (1819–1885) was from Philadelphia and attended Haverford College, 1834–1835 (Mack 1933). He began work as a teacher, switched to farming, and then became interested in science applied to agriculture. His essay, Geography of Plants, in the Report of the Commissioner of Agriculture (Washington, 1863) was part of that endeavor. It shows he was well informed about the subject, mentioning that this science originated with Humboldt, and citing also works by Joseph Hooker, Asa Gray, Alphonse de Candolle, and many others not included in this history. Having shown that he had done his “homework,” he turned to the practical applications of this knowledge. He wrote long before Alphonse de Candolle published Origine des Plantes Cultivées (1883), but Candolle was already one of Lippincott’s authorities.

In America, four ornithological societies, with journals, were founded within two decades, and all continue to flourish (Barrow 1998:47–73): Nuttall Ornithological Club (NOC, 1873, named for Thomas Nuttall), American Ornithologists Union (AOU, 1883), Wilson Ornithological Club (WOC, 1888, named for Alexander Wilson), and Cooper Ornithological Club (COC, 1893, named for J.G. Cooper). None were devoted mainly to zoogeography of birds, but all were receptive to such studies. AOU published its early history (Chapman and Palmer 1933), which includes two articles on museum collections of birds, which facilitate zoogeographical studies. NOC published two volumes on its history (Batchelder 1937, Davis 1987), and three authors wrote on history of WOC (Hall 1988, Jackson 1988, Jackson, Mayfield and Hall 1988, Mayfield 1988). COC later became COS, which merged with AOU in 2016 under a new

Fig. 20. Phytogeographical explorations in the U.S. Rocky Mountains, 1877, led by Asa Gray and Joseph Hooker. From Huxley (1918:II, facing 208).
name, American Ornithologists Society. The National Audubon Society was named for J.J. Audubon, but it is a popular (not scientific) society, and its concerns are not limited to birds (Graham 1990).

Reading, Pennsylvania native Spencer Fullerton Baird (1823–1887), moved with family in 1833 to Carlisle, where he later attended Dickinson College (B.A., 1840, M.A., 1843). He decided to become a zoologist, and in 1846, he became professor of natural history at Dickinson (Allard 1970, 1997). In 1850, he became assistant to Joseph Henry, head of the new Smithsonian Institution (Bruce 1987: Index, Rivinus and Youssef 1992:56–80). In 1878, he succeeded Henry as secretary of the Smithsonian. One of Baird’s important activities was to find naturalists who were either private collectors or naturalists on government expeditions who would provide specimens of birds and mammals for Smithsonian scientific collections (Stresemann 1975:243–245, Rivinus and Youssef 1992:81–97, Barrow 1998: Index, Jackson 1999). These specimens had tags indicating where collected, which became data for biogeographical

**Fig. 21.** Natural Provinces and Regions of North America, by James Graham Cooper. Kendeigh (1954:155–157).
studies. Baird himself participated in such studies; he synthesized Mammals: General Report upon the Zoology of the Several Pacific Railroad Routes Reports on Surveys for Railroad Route from Mississippi River to Pacific Ocean (1857). He was also senior co-author, with John Cassin, and George Lawrence in producing The Birds of North America (1860, Barrow 1998: Index). François Vuilleumier and Allison Andors state (1995:389) that Baird in 1866 was probably “The first ornithologist to divide North America into faunal districts,” though he “followed a regional classification proposed by Louis Agassiz.” A masterpiece of ambiguity! They then quote Baird who was also ambiguous. From 1871 until his death, he was also head of the new U.S. Fish Commission, which will be discussed in part 61C.

Another notable “museum man” specializing in birds and mammals was Springfield, Massachusetts native Joel Asaph Allen (1838–1921), who persuaded his father to give him a gun when he was 13, with which he collected specimens of local birds, but had no reference work, until later when a teacher gave him a copy of Brewer’s edition of Wilson, and at the public library, he found Audubon and Nuttall’s works (Allen 1916, Chapman 1927 [1922], Stresemann 1975: Index, Sulloway 1990, Hamilton 1995:391–393, Sterling 1997a, b, Barrow 1998: Index, 2009:78–84, Smith 2005). He attended a local academy, and then in February 1862, he became a special student under Louis Agassiz and his assistant at Harvard University’s Museum of Comparative Zoology. In March 1865, he joined Agassiz’s expedition to Brazil, where he collected numerous animal specimens before returning to Agassiz’s Museum of Comparative Zoology (MCZ) with his collections. He later went on collecting trips to Florida and out west to Utah. In 1885, he left MCZ for the American Museum of Natural History. In 1876, he was one of the naturalists who organized the Nuttall Ornithological Club and edited its Bulletin until 1883, when the American Ornithological Union obtained that bulletin and changed its name to Auk, which Allen edited for 28 years. In 1878, he published The Geographical Distribution of the Mammalia, which was two years after Wallace had published his Geographical Distribution of Animals, which also emphasized mammals. His publications constituted a very important contribution to the zoogeography of birds and mammals (Allen 1974).

Theodore Gill was president of the Biological Society of Washington in 1883, and for his presidential address, he chose to discuss Wallace and Allen’s geographical regions, which were rather different (Gill 1885). It is unlikely that Allen had seen Wallace’s work until he had written his own. Gill made some concluding observations, but he did not state a preference of one system over the other.

Hungarian Angelo Heilprin (1853–1907) immigrated to America in 1856, with his father and brother. He studied science in America, then in Europe in 1876–1878, and he became professor of invertebrate paleontology at the Academy of Natural Science, Philadelphia, 1880–1900. He traveled throughout the world and was a prolific author. His Geographical and Geological Distribution of Animals (1887) could perhaps have served as a textbook for advanced students in paleontology and zoology. His citations were little better than those of Wallace (1876); his first citation was: Wallace, “Island Life,” p. 3 (Heilprin 1887:2). As an invertebrate paleontologist, he discussed some topics which vertebrate zoologist Wallace had omitted.

Two examples later than Giraud of Barrow’s culture of collection were New Yorker Theodore Roosevelt (1858–1919) and Bostonian Henry Davis Minot (1859–1890), who met as freshmen at Harvard College in September 1876 (Lunde 2016:66–67). Perhaps Roosevelt was the more ambitious of the two, but Minot at age 17 was on the verge of publishing The Land and Game Birds of New England (1877).
spring 1877, these bird enthusiasts planned a trip to the Adirondack Mountains soon after spring semester. Roosevelt’s family had spent two vacations there in 1874 and ’75, where Roosevelt had taken notes on his nature observations. So, he could lead their adventure. After a week, Minot had had enough and went home. Roosevelt stayed and collected more notes, enabling him to publish (with Minot generously listed as co-author) The Summer Birds of the Adirondacks in Franklin County, N.Y. (1877, 4 pages), which Roosevelt had privately printed and distributed. Hart Merriam reviewed it along with other amateur publications for Bulletin of the Nuttall Ornithological Club (spring 1878) and praised it as the best of the group (Lunde 2016:69–70). Needless to say, both authors became members of NOC. Midway into their sophomore year, Minot left Harvard to study law, but these friends continued corresponding at least until 1880 (Brinkley 2009:123). Roosevelt graduated magna cum laude in 1880, and then, he too studied law, at Columbia University (Lunde 2016:90–92). However, he became disillusioned, because he concluded that lawyers served their clients rather than justice (McCullough 1981:279–280). He never finished law school. Instead, he entered politics, first in the New York State Legislature, Governor, Vice-President, and President. During that period, wildlife received only a modest amount of his time (Cutright 1956, Lunde 2016). However, Roosevelt’s term as president ended in 1909, and he was soon planning an expedition to Africa, which was a large-scale operation that also occurred in 1909. It was a big game expedition, with his trophies going to the Museum of Natural History in New York and the Smithsonian Institution in Washington. In 1914, he also organized a river expedition down an unexplored tributary of the Amazon (River of Doubt) that subsequently was named for him (Millard 2005). Those two expeditions presumably were his most important contributions to zoography.

C. Hart Merriam (1855–1942) was from a prosperous family in New York State that spent winters in New York City (Osgood [including Grinnell] 1944, Sterling 1977, 1997a, b, 1999, Barrow 1998: see index, Hermann 2009, Egerton 2014a:66–69). He grew up with a strong interest in wildlife. In 1871, his congressman father took him to chat with Spencer Baird at the Smithsonian. Baird examined Merriam’s stuffed bird and mammal specimens, and Baird arranged for him to accompany Hayden’s U.S Geological Survey of Yellowstone in summer 1872, and Merriam published a Report on the Mammals and Birds of the Expedition (1873). He studied zoology for three years at Yale, then received an M.D. degree from the New York College of Physicians and Surgeons (1879), and practiced medicine for six years. That practice did not occupy all of his time, for in 1884 he published The Mammals of the Adirondack Region. It began with what we can call an ecological introduction, including soil, topography, climate, general features, vegetation, and brief account of other animals (1884:10–26). In 1885, he became head of a division of USDA to study birds and mammals, where he remained until 1910. In 1889, he led an expedition to survey San Francisco Peak and nearby Little Colorado River, Arizona (Sterling 1977:204–240). In his report, he explained that (1890:1):

"The area carefully surveyed comprises about 13,000 square kilometers (5,000 square miles), and enough additional territory was roughly examined to make in all about 30,000 square kilometers (nearly 12,000 square miles), of which a biological map has been prepared."

He measured elevations and recorded species ranges, but he did not also measure temperatures at different elevations. Humboldt had published similar data for Chimborazo and Cotopaxi in 1807, but also included climatological data (Egerton 2009:268–269, 2012a:123–124). Merriam used his data to construct a Provisional Biological Map of North America Showing Principal Life Areas (1890 version in Kendeigh 1954:161, 1893 version in Egerton 2014a:67), and in the absence of an alternative,
his scheme was widely used, and it provoked more published reactions than any other contribution to American biogeography. Victor Shelford (1932) and Schmidt (1955:783–784) did criticize his scheme as simplistic, but Rexford Daubenmire (1938) praised Merriam for at least using data from both plants and animals in constructing his life zones, which continue to be pragmatically useful in the West (Dice 1923, Peterson 1942, Shelford 1945).

Fig. 22. Profile of San Francisco and O’Leary Peaks showing life zones. Merriam (1890: Plate 1).

In March 1899, the railroad tycoon, Edward H. Harriman (1848–1909), walked into Merriam’s office at the Department of Agriculture, introduced himself and invited Merriam to help organize an expedition to Alaska, to last two months (Sterling 1977:119–123, Goetzmann and Sloan 1982:8–14). Merriam was glad to organize a group of scientists and support staff, but was uncertain whether he could take off that long. A word from Harriman to the leaders at USDA ended that anxiety. Merriam obtained commitments from 23 leading scientists, three artists, two photographers, and two taxidermists. In May, the east-coast members of the expedition traveled in luxury cars on a special Harriman train that enabled them to sight-see across the continent to Seattle, with side tours along the way (Goetzmann and Sloan 1982:16–30). A specially renovated steamship awaited them, the George W. Elder. Harriman’s family was along for a vacation, but he let the scientists decide where to stop along the Alaskan coast. Harriman wanted useful scientific observations and specimens to be obtained, which was done, and then, Merriam spent 12 years, at Harriman’s expense, first, sending specimens to relevant authorities to describe, and then publishing 13 substantial volumes of reports (1901–1914). The Expedition historians, William Goetzmann and Kay Sloan, devoted their final chapter to discussing the results (1982:193–206). There is also historical information in George Bird Grinnell (1995) and in Thomas Litwin, editor, The Harriman Alaska Expedition Retraced: a Century of Change (2005).
Our earliest knowledge of the biogeography of Mexico came from two Americans with the U.S. Biological Survey, Edward William Nelson (1855–1934), and his protégé, Edward A. Goldman (1873–1946). Nelson was from the Amoskeag district of Manchester, New Hampshire (Goldman 1935, Glenn 1997). His father died in the Civil War, and after the war, he and his mother moved to Chicago, where she opened a dress-making business. In 1871, his large insect collection was burned in the Chicago fire, and he turned his attention to birds. In 1877, he joined the U.S. Army Signal Corps, and Spencer Baird recommended he be sent to St. Michael, Alaska, where he could study the flora and fauna. He later published Report upon Natural History Collections Made in Alaska between the Years 1877–1881 (1887). In 1890, he went on the Death Valley Expedition, led by Merriam’s assistant, Theodore Palmer (Sterling 1977:94). Afterward, Nelson’s wagon broke down as he was leaving the expedition, and he stopped at a California ranch for repairs. The ranch belonged to Ed Goldman’s father, who was an amateur naturalist, and as Nelson and Jacob Goldman discussed mutual interests, Nelson mentioned he needed an assistant (Young 1947:92, Reeves 1984:96). Goldman suggested his son, Edward, whom Nelson accepted. Edward Goldman became Nelson’s valuable collaborator (Nelson and Goldman 1926, Leopold 1950:518).

In United States, German plant ecology exerted an influence on pioneer plant ecologists in the Midwest. Since Midwestern colleges and universities were founded long after most eastern ones and were still expanding around 1900, they more easily added faculty in a new field like ecology. Michigan native Albert Hitchcock (1865–1935) studied at Iowa State Agricultural College, at Ames, under Charles E. Bessey, a leading botanist with ecological interests and Hitchcock earned two degrees (B.S.A., 1884, M.S. 1886), and belatedly after Bessey’s death, a Sc.D. (1920). Hitchcock’s Ecological Plant Geography of Kansas (1898) possibly became his doctoral dissertation. The only citation in it of previous literature (1898:68) was to: Mason, A Preliminary Report upon the Variety and Distribution of Kansas Trees. Hitchcock joined the U.S. Department of Agriculture in 1901, and he encouraged establishment of Barro Colorado Island field station, Panama Canal Zone. He is remembered for his Manual of the Grasses of the United States (Hitchcock 1935).

At about the same time Hitchcock began his researches, two plant ecology students at the University of Nebraska, Roscoe Pound and Frederic E. Clements, wrote their joint dissertation on the Phytogeography of Nebraska (1898, edition 2, 1900). Pound went on to a legal career and became Dean of the Harvard University Law School. Clements (1874–1945) had a career as a leading plant ecologist in United States, with worldwide influence (Clements 1960, Ewan 1971, Stafleu and Cowan 1976–2009: I, 510–511, Tobey 1981:51–58, Burgess 1996:26–27, Hagen 1999, Egerton 2009, 2013a, b:358–360). Subsequently, plant succession rather than phytogeography became the main focus of Clements’ research.

Clements and Chicago plant ecologist Henry Cowles (1869–1939) organized an American International Phytogeographic Excursion (1913), which encompassed a much larger territory than had the British one, but was equally successful, lasting from late July to early October (Nichols 1914, Fischedick and Shinn 1993, Cassidy 2007:51–52, 278–279, Beidleman 2009, Ayres 2012:87–90, Egerton 2013b:365–366). Tansley and his wife were impressed, and he published a rather detailed account on it (Tansley 1913–1914). Bob Burgess (1977:2) thought that the forming of the BES in 1913 may have provided momentum for forming the Ecological Society of America in 1915. However, there was a difference: The initiative for organizing BES came from plant ecologists, but in America, the initial impulse for ESA came from animal ecologists, though a plant ecologist, Cowles, implemented their suggestion (Burgess 1977, Crocker 1991:120–121, Cassidy 2007:77–80, Egerton 2015a, 2015b).
However, for Karl Schmidt, “the modern period in zoogeography must be dated from 1915,” (1955:778), because of publication of Matthew’s Climate and Evolution. William Matthew (1871–1930) was from New Brunswick, Canada, and earned his B.A. degree in geology at its university (1889), before moving to Columbia University for his M.S. (1894) and Ph.D. (1895). A course at Columbia under Henry F. Osborn (1857–1935) on evolution of vertebrates diverted him from geology to vertebrate paleontology, and when Osborn moved to the American Museum of Natural History as curator of vertebrate paleontology in 1901, he took along Matthew as his assistant (Simpson 1944, Colbert 1974, Shoshani 1997). In 1900, Osborn published “Geological and Faunal Relations of Europe and America” (Science, number 276, April), and in December, the German scientist Hermann von Ihering (1840–1930), who worked in Brazil 1880–1920, challenged Osborn’s on grounds that he ignored nine of his relevant articles on South American fossils (all fully cited), published in German or Portuguese. When Osborn retired in 1911 Matthew replaced him (Granger 1933, De Querioz 2014:43–45). In 1927, Matthew became professor of paleontology at the University of California, Berkeley. Of his approximately 240 publications, Climate and Evolution (1915) was most important. His contribution was widely appreciated at the time (Darlington 1938, 1948, Schmidt 1955:778–780), but decades later he would be judged as merely part of the obsolete “dispersalist” perspective by Gareth Nelson, Norman Platnick, Donn Rosen, and others (G. Mayer, personal communication).

The family of Joseph Grinnell (1877–1939) eventually settled in Pasadena, California, where he graduated and studied at what is now California Institute of Technology (B.A., 1897, M.A., 1901), where he also taught, 1903–1908 (Shor 1972, Chambers 1997, Barrow 1998:186–187). In 1907, he met the philanthropist Annie Alexander (1864–1950), who wanted to establish a Museum of Vertebrate Zoology at the University of California (Stein 1997, 2001:65). In 1908, he became its director, at the Berkeley campus, where he remained. He devoted his career to studying terrestrial vertebrates of California, emphasizing birds and mammals and focusing on distributions. An example of his work is: botanist Harvey Hall and Grinnell, Life Zone Indicators in California (1919), which cited five previous articles by Grinnell.

Illinoisan botanist Henry A. Gleason (1882–1975) conducted his formative research on the Midwestern prairies (Tobey 1981: Index, McIntosh 1985:137–140, Hagen 1992:28–31, Burgess 1996:46, Kingsland 2005: Index, Egerton 2013:b:366–367). Whether or not his research can be called biogeographical is debatable. He focused upon distributions of various associated species in particular areas and regions (Gleason 1936, Whittaker 1962:78–83, Drouin 1993, Nicolson and McIntosh 2002). He is most remembered among ecologists for his challenge to Clements (1916) concept of plant communities as species being integrated into a supra-organism, which experiences succession in one direction, analogous to an organism aging.

In 1926, ecologist Victor E. Shelford edited Naturalist’s Guide to the Americas, which encompassed lands north of the Amazon River and some islands in both the Atlantic and Pacific Oceans. It was detailed (xv + 761 pages), and written by many ecologists, known to Shelford through memberships in ESA. It included 15 maps of vegetation, each on a portion of that region. It was a great summation of terrestrial biogeography.

In 1928, the American Geographical Society published Problems of Polar Research: a Series of Papers by Thirty-one Authors (Joerg 1928). In order to answer questions of what problems should be
addressed in the future, authors had to explain what had already been achieved—amounting to progress reports. Four papers considered: Arctic plant geography (Harshberger 1928) and animal geography (Stejneger 1928); and Antarctic plant (Brown 1928) and animal geography (Murphy 1928). John Harshberger surveyed a good number of topics, each rather briefly; his implicit message was: If you want a research topic, take your pick. Norwegian native Leonhard Stejneger explored fewer topics on animal geography and showed an interest in theoretical questions. He had explored Arctic regions for the U.S. National Museum, Washington. English botanist Rudmose Brown had been on expeditions to both poles and published The Polar Regions (1927), which was “the first adequate textbook in English on the Arctic and Antarctic written from the standpoint of modern geography” (Brown 1928:342). He emphasized the limited kinds of Antarctic plants—limited by climate and by penguins eating them—mosses (over 50 species), lichens (over 100 species), and a few kinds of hepatics and liverworts. Mosses were frozen eight to eleven months a year. On the South Shetland Islands, there was a grass (Deschampsia antarctica) and a small associated caryophyllaceous plant (Colobanthus crassifolius). In the South Orkney Islands, there were about 70 species of fresh-water algae. Both unicellular and multicellular marine algae were very abundant. Diatoms are very abundant in Arctic and Antarctic seas. Some moss species are known from both Arctic and Antarctic lands, some of which might have spread on feet or feathers of migrating birds.

Minnesotan Royal N. Chapman (1889–1939) earned his B.A. and M.A. degrees (1914, 1915) at the University of Minnesota (Cattell and Cattell 1938:242, Graham 1941, Burgess 1996:25), studied for his Ph.D. (1917) at Cornell University under Professor John H. Comstock (Howard 1930:60), then returned to the University of Minnesota, joining the Entomology Department. In 1930, at age 49, he moved to the University of Hawaii to become dean of the Graduate School of Tropical Agriculture, and also director of the Pineapple Producers Cooperative Association’s Experimental Station, with a salary from the latter association reportedly of $20,000 a year (Howard 1930:182). Chapman’s Animal Ecology (1931) was obviously written in Minnesota, which he acknowledged by indicating he was formerly at the University of Minnesota, and in his dedication of the book to his former graduate students. The chapter in his textbook devoted to “zoogeography” is well illustrated, mostly with maps and diagrams from other printed sources, which he cited. It was a good summary of knowledge on this subject at the time (Chapman 1931:219–231).

Chicago zoologist-paleontologist George Gaylord Simpson (1902–1984) earned his higher degrees at Yale University, including his Ph.D. in geology, in the 1920s. He is notable for being the leading paleontologist during the 1900s (Laporte 2000). He wrote four autobiographical works, though the last was compiled after his death (1934, 1964, 1978, 1987, see also Olson 1991). Simpson explored Patagonia about a century after Darwin had, but that fact received no comment in Attending Marvels: a Patagonian Journal (1934). Darwin had had Richard Owen study the mammal bones he collected, but Simpson seemed to think those fossils were too few to interest him. Instead, he was captivated by bones which the Ameghino brothers, Florentino (1853–1911) and Carlos (1865–1936), found (Garate 1970). They, as children, emigrated from Italy to Buenos Aires, Argentina, where one of Florentino’s teachers was impressed with his intelligence and helped him enroll in the Escuela Normal de Preceptores to become a teacher. However, Florentino became more interested in paleontology than in teaching, and he developed a business that supported both he and Carlos, who dug for fossils and turned them over to Florentino to describe. What Simpson learned from his own early studies and from the Ameghino brothers’ studies he summarized in Attending Marvels. For example, after the Panama Isthmus emerged, North American mammals invaded South America (Simpson 1934:67):
This irruption of animals from North America spelled the doom of most South America’s native fauna. In their continent-asylum they had never had to face such fierce and efficient competition, and relatively few of them were equal to it. The northern animals had already faced rivals and enemies from Europe, Asia, and Africa and had survived. They had learned to run a little faster, or to think a little better, or otherwise to take care of themselves a little more efficiently than the South American stay-at-homes, and it was not long, geologically speaking, before the latter became extinct.

The time period during which the Panama land bridge rose above sea level probably came from geological studies, but the impact of that bridge for North America’s land fauna’s invasion of South America was documented by Simpson (1940). Fittingly, Lomolino et al. (2004:339–365) reprinted Simpson’s slightly later Mammals and Land Bridges (Simpson 1940), a notable contribution which not only marshaled convincing evidence to support his interpretations, but also critiqued other alternatives. Simpson’s paleozoogeographical investigations continued until 1963 (Schmidt 1955:793, Simpson 1965:69–234). However, his publications continued to appear for the rest of his life and beyond (Laporte 2000:313–317).
Indianan plant ecologist Stanley Cain (1902–1995) earned his B.S. degree (1924) at Butler University and then moved to the University of Chicago for his M.S. (1927) and Ph.D. (1930). He held a variety of positions both within and without academia (Burgess 1996:21, Harmond 1997a, Edens 2009, Egerton 2015a, b:50) and published Foundations of Plant Geography (1944). Cain served as ESA president in 1958.

Cincinnati, Ohio botanist (Emma) Lucy Braun (1889–1971) was the first woman president of the Ecological Society of America, in 1950 (Stuckey 1997, 2001, Neumann 2009, Egerton 2015a:62–63, 2015b:455). She earned her three degrees (B.A. 1910, M.A. 1912, Ph.D. 1914) at the University of Cincinnati and then taught there for her entire career. She studied two nearby environments: eastern deciduous forests and Midwestern prairies. Her publications on the former culminated in her important monograph, Deciduous Forests of Eastern North America (1950). Her biographer, Ronald Stuckey, collected her papers on prairies in E. Lucy Braun (1889–1971): Ohio’s Foremost Woman Botanist: Her Studies of Prairies and Their Phytogeographical Relationships (2001). Her publications on both regions were important contributions to North American phytogeography. Stuckey cited (2001:90–91) one example in which she challenged conclusions of another ecologist, Edward Deevey, Jr. (1914–1988), who studied pollen grains from a lake bottom for his dissertation under G. Evelyn Hutchinson at Yale University (Deevey 1949, Burgess 1996:36, Egerton 2015a:115). Stuckey’s presentation seems to indicate that Deevey projected his evidence much further geographically than warranted, which implicitly challenged Braun’s 1950 account, and so she wrote an article (1951) to explain her evidence and how it invalidated Deevey’s projections. Stuckey stated that Deevey did not respond to Braun’s arguments, indicating he realized she had won the argument.

Fighting a worldwide war might have been expected to expand knowledge of plant geography, but E.D. Merrill’s Plant life of the Pacific World (1945) was based upon pre-war publications; the war also constrained civilian travel (Miyanishi 2014). George Gaylord Simpson’s 20-page lecture, Mammals Around the Pacific (1966) cited no references and no authors except Darwin and Wallace—mostly it summarized his own work.

Conclusions on terrestrial biogeography

Plant geography and animal geography developed as separate, though parallel, sciences for more than two centuries. John Ray had contributed to both sciences in the late 1600s and early 1700s without attempting to synthesize them. Emmanuel de Martonne et al. produced a biogeographical synthesis in French (1921) and zoologist Marion Newbigin did likewise in English (posthumous, 1936). Even then, the two sciences continued to develop separately; it was another two decades before plant ecologist Pierre Dansereau published his Biogeography (1957). Although it seemed convenient here to discuss European and North American contributions separately, they frequently noted findings of biogeographers on the other continent. Europeans were more apt to conduct studies in Africa and Asia than Americans, and Americans were more apt to conduct studies in Central and South America than Europeans.

There was a steady stream of studies, with important ones discussed in parts 61A and 61B. However, the botanists and zoologists who conducted these studies were never numerous, and theoretical landmarks came from outside these studies: Darwin’s theory of evolving species (1859) and Wegener’s theory of moving continents (1915). Oceanic voyages of discovery by British, French, and Russian navies were important for history of aquatic biogeography, the subject of Part 61C, but also for terres-
trial biogeography. Darwin’s exploring on the South American continent is an obvious example, as also is Wallace’s later exploring in both South America and Southeast Asia. The 1800s saw the growth of both universities and natural history museums, both of which had biologists interested in some aspect of biogeography. Governments also grew and had biologists interested also, such as C. Hart Merriam in the U.S. Department of Agriculture and others in Department of Interior.

After Humboldt’s contributions during the early 1800s, the leading plant geographer during the later 1800s was Joseph Hooker, and the leading animal geographer was Alfred Wallace. Both Englishmen, like Humboldt, traveled widely and published extensively in their fields. Wallace published a synthesis of his field (1876), but Hooker could not do likewise since Alphonse de Candolle (1855) and Grisebach (1872) did so. At the end of the century, Engler and Drude began editing an encyclopedia, and Die Vegetation der Erde (15 volumes, 1896–1923) and Schimper published his one-volume encyclopedic Pflanzengeographie auf physiologischer Grundlage (1898). Two English-language participants in Engler and Drude’s encyclopedia were John Harsberger, who wrote on North America’s phytogeography (1911), and Leonard Cockayne, who wrote New Zealand’s (1921).

Tansley had the excellent idea of inviting plant ecologists from Europe and America to visit Britain to participate in an International Phytogeographical Excursion through some of Britain’s distinctive plant environments (1911). Cowles and Clements were interested American participants, and they followed Tansley’s example of hosting an American International Phytogeographical Congress (1913). European plant ecologists wanted to continue that tradition, and there were eventually some held in Europe, but two world wars interrupted that tradition. The two that did originally occur undoubtedly encouraged establishment of the British Ecological Society in 1913 and the Ecological Society of America in 1915. The American Geographical Society’s volume on polar research (1928) is of interest for containing papers by both American and British scientists, in both biological and physical sciences.

Acknowledgments

I thank Professor Gregory Mayer, Department of Biological Sciences, University of Wisconsin-Parkside, Kenosha, for comments on this survey; Jean-Marc and Anne-Marie Drouin, retired, France, for comments on aspects of this survey; Malte Ebach, Palaeontology, Geobiology and Earth Archives Research Centre, UNSW Australia, Sydney, Australia, for sending me pdf copies of his works, cited below; Kuang-chi Hung, National Taiwan University, for sending me pdf copies of his articles, cited below. Jerry Hershberger for computer assistance and Laura Mason for illustrations reproduction.

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