Evolution, Biogeography, and Maps

An Early History of Wallace's Line

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A YEAR AFTER HIS RETURN from eight years of traveling and collecting animal specimens in the East Indian Archipelago, Alfred Russel Wallace presented a paper on the physical geography of the region to the Royal Geographical Society of London. The map accompanying the article (Figure 1) depicted the boundary between the Asian and Australian biotas by a single line, known shortly thereafter as "Wallace's line." Although Wallace's line is one of the most disputed topics in biogeography and his evolutionary theorizing has been the focus of intensive scrutiny, the close connection between the formulation of the line and Wallace's evolutionary hypotheses has been overlooked by historians of science.[1]

The relationship between Wallace's line and evolutionary theory is explored here. Contemporary descriptions of faunal regions referred vaguely to the area then known as the East Indian Archipelago as the place where the Asian and Australian biotas met. Wallace and Charles Darwin each struggled with the precise location of the boundary between these two faunal regions at a critical stage in the development of his evolutionary theory. Mapping the boundary between the Asian and Australian faunas served multiple functions: it was a method for organizing and communicating

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[1] Alfred R. Wallace, "On the Physical Geography of the Malay Archipelago," *Journal of the Royal Geographical Society,* 1863, *33*:217–234. To my knowledge, Thomas Huxley coined the term *Wallace's line* in his paper on gallinaceous birds, "On the Classification and Distribution of the Alectoromorphae and Heteromorphae," *Proceedings of the Zoological Society of London,* 1868, pp. 294–319. References to articles on Wallace's line can be found in Wilma George, "Wallace and His Line," in *Wallace's Line and Plate Tectonics,* ed. T. C. Whitmore (Oxford: Oxford Univ. Press, Clarendon, 1981), pp. 3–8; Ernst Mayr, "Wallace's Line in the Light of Recent Zoogeographic Studies," *Quarterly Review of Biology,* 1944, *19*:1–14; and George G. Simpson, "Too Many Lines: The Limits of the Oriental and Australian Zoogeographic Regions," *Proceedings of the American Philosophical Society,* 1977, *121*:107–120.

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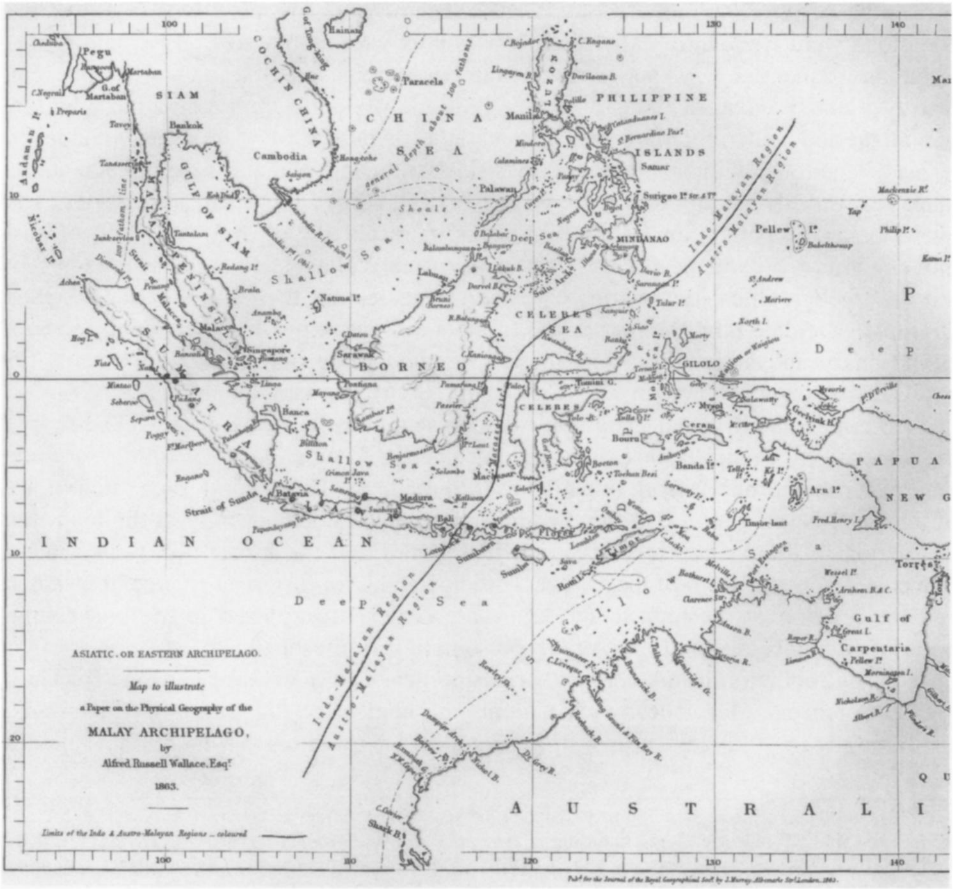

Figure 1. A portion of the first map showing "Wallace's line," published in the Proceedings of the Royal Geographical Society *in 1863.*

faunistic data, a potential device for predicting range limits of other species, a modern method of argumentation and representation that was familiar to their peers, and, most important, a method of analysis that tested positively with evolutionary hypotheses. In more general terms, maps of faunal regions served as instruments both of thought and of persuasion.

While I shall not ignore the relationship of Wallace's and Darwin's maps to those of other naturalists, or the role of maps as a means of biogeographic argumentation, my emphasis here is on maps as instruments of thought, as visual and flexible components of their proponents' conceptual frameworks. From this vantage point one can examine how Darwin and Wallace used both actual and mental maps in an effort to find order in a mass of complex biogeographical data. I emphasize actual *and mental* maps to encompass not only the maps the two men made or used, but also the map-based images that became elements of their thought.[2]

[2] Major references to theories of mind or of cognition that describe the role of visual imagery are discussed in Jane Camerini, "Darwin, Wallace, and Maps" (Ph.D. diss., Univ. Wisconsin, 1987), pp.

Map-based observations of, for example, discontinuous distributions or altitudinal zonations were frequently expressed in words as well as pictures. By studying different or sequential versions of such map-based conceptual frameworks, one can readily identify changes in map meaning. Maps of faunal regions in the pre-Darwinian period generally portrayed the static distribution of plants and animals in terms of "nations" with stable boundaries. Darwin's and Wallace's mental and actual maps showed the same stable regions, but theirs outlined the result of historical and evolutionary transmutation of the organisms themselves, not only the result of past movements of organisms. If it is fair to say that Wallace's line came to represent not only geographical boundaries of existing species but their history as well, then we must articulate how the map came to have this meaning. In other words, if both evolutionary and nonevolutionary faunal regions can be portrayed by the same (or similar) maps, then how can we speak about what the maps mean?

Two issues about visual geographical representations are raised here. The first is the capacity of a map to look the same but change in meaning over time, from one mapmaker to another or from one map user to the next. The second issue, a corollary of the first, is the notion that the meaning of a map resides not only in the map, but in relation to the written text of which it is a part and the larger historical context in which it appears. Both of these issues—the potential for historical change in meaning and the relation of the map to the text—are largely unexplored in the burgeoning body of literature devoted to visual representation in the history of science.[3]

In the introduction to his classic "The Emergence of a Visual Language for Geological Science," Martin Rudwick laments the neglect of illustration by historians, attributing it to "the lack of any strong intellectual tradition in which visual modes

4–6. In recent years interest in cognitive aspects of scientific practice has grown immensely; for references to this literature see David Gooding, *Experiment and the Making of Meaning* (Dordrecht: Kluwer, 1990); and Nancy J. Nersessian, "The Cognitive Sciences and the History of Science," Conference on Critical Problems and Research Frontiers in History of Science and History of Technology, 30 Oct.–3 Nov. 1991, Madison, Wis., pp. 92–115.

[3] Peter Taylor and Ann Blum note, in their introductory article "Pictorial Representation in Biology" (pp. 125–134), that these two issues are insufficiently addressed in the special issue of *Biology and Philosophy* (1991, *6*[2]) devoted to pictorial representation in biology and in the literature cited therein. Other recent work relevant to visual representation in biology is found in Barbara Maria Stafford, *Voyage into Substance: Art, Science, Nature, and the Illustrated Travel Account, 1760–1840* (Cambridge, Mass.: MIT Press, 1984); Bruno Latour and Steve Woolgar, *Laboratory Life: The Construction of Scientific Facts,* 2nd ed. (Princeton, N.J.: Princeton Univ. Press, 1986); Londa Schiebinger, "Skeletons in the Closet: The First Illustrations of the Female Skeleton in Eighteenth-Century Anatomy," *Representations,* 1986, *14*:42–82; Michael Lynch and Steve Woolgar, eds., *Representation in Scientific Practice* (Cambridge, Mass.: MIT Press, 1990); and Greg Myers, *Writing Biology: Texts in the Social Construction of Scientific Knowledge* (Madison: Univ. Wisconsin Press, 1990). Work on visual representations in physics includes Samuel Y. Edgerton, Jr., "The Renaissance Development of the Scientific Illustration," in *Science and the Arts in the Renaissance,* ed. John W. Shirley and F. David Hoeniger (Cranbury, N.J.: Associated Univ. Presses, 1985), pp. 168–197; Arthur I. Miller, *Imagery in Scientific Thought* (Cambridge, Mass.: MIT Press, 1986); Gooding, *Experiment and the Making of Meaning;* William Ashworth, Jr., "The Scientific Revolution: The Problem of Visual Authority," Conference on Critical Problems and Research Frontiers in History of Science and History of Technology, 30 Oct.–3 Nov. 1991, Madison, Wis., pp. 326–348; and Mary G. Winkler and Albert Van Helden, "Representing the Heavens: Galileo and Visual Astronomy," *Isis,* 1992, *83*:195–217. Also relevant are W. J. T. Mitchell, ed., *The Language of Images* (Chicago: Univ. Chicago Press, 1980); Mitchell, *Iconology: Image, Text, Ideology* (Chicago: Univ. Chicago Press, 1986); and Gordon Fyfe and John Law, eds., *Picturing Power: Visual Depiction and Social Relations* (London/New York: Routledge, 1988); Jan Golinski, "The Theory of Practice and the Practice of Theory: Sociological Approaches in the History of Science," *Isis,* 1990, *81*:492–505, on p. 498; and Andrew Pickering, ed., *Science as Practice and Culture* (Chicago: Univ. Chicago Press, 1992).

of communication are accepted as *essential for the historical analysis and understanding of scientific knowledge*." In the last twenty-five years or so, numerous historians have established the central, constitutive (as opposed to "merely illustrative") role of mapping in the emergence and practice of geology.[4]

Rudwick identified the striking discrepancy between the pervasive use of diverse visual tools in geological practice and their meager use in historical work. Not only is the use of maps in modern geology commonplace, but it is considered natural and unproblematic. The discrepancy is also true in biology, and evolutionary biology in particular, with the notable exception of a whole range of work on plant and animal illustrations.[5] Mapping in biology never became as conscious or explicit a goal as it did in geology, and biogeography never stabilized into a highly integrated or self-contained discipline. Thus, the nature of mapping remains far more tacit in biology than in geology, with the consequence that both the evidence for and arguments about "biocartography" are subtler. This does not render maps of biological themes any less essential to historical understanding than geological maps or visual representations in other physical sciences, but it partly explains why it has taken longer to establish connections between the history of pictorial representation and the history of evolutionary thought.

Recent work in cartography and geography demonstrates a newfound concern with manifold levels of map meaning, the rhetorical power of maps, and mapping as a mode of knowing.[6] Although this literature informs the present work, the former is

[4] Martin J. S. Rudwick, "The Emergence of a Visual Language for Geological Science, 1760–1840," *History of Science*, 1976, *14*:149–195, on p. 149 (emphasis added). For discussions of the role of mapping in geology see Rhoda Rappaport, "The Geological Atlas of Guettard, Lavoisier, and Monnet: Conflicting Views of the Nature of Geology," in *Toward a History of Geology*, ed. Cecil J. Schneer (Cambridge, Mass.: MIT Press, 1969), pp. 272–287; Marcia Pointon, "Geology and Landscape Painting in Nineteenth-Century England," *British Journal for the History of Science*, 1979, *1*:84–108; Rudwick, *The Great Devonian Controversy: The Shaping of Scientific Knowledge among Gentlemanly Specialists* (Chicago: Univ. Chicago Press, 1985); Rudwick, *Scenes from Deep Time: Early Pictorial Representations of the Prehistoric World* (Chicago: Univ. Chicago Press, 1992); Gordon L. Herries Davies, *Sheets of Many Colours: The Mapping of Ireland's Rocks, 1750–1890* (Dublin: Royal Dublin Society, 1983); James A. Secord, *Controversy in Victorian Geology: The Cambrian-Silurian Dispute* (Princeton, N.J.: Princeton Univ. Press, 1986); Homer E. Le Grand, "Is a Picture Worth a Thousand Experiments?" in *Experimental Inquiries: Historical, Philosophical, and Social Studies of Experimentation in Science*, ed. Le Grand (Dordrecht: Kluwer, 1990), pp. 241–271; Mark Hineline, "Beyond Mere Description: William Morris Davis, Block Diagrams, and Genetic Description," paper presented at the annual meeting of the History of Science Society, 30 Oct.–3 Nov. 1991, Madison, Wis.

[5] The most comprehensive references in this regard are Gavin D. R. Bridson and James J. White, *Plant, Animal, and Anatomical Illustration in Art and Science: A Bibliographical Guide from the Sixteenth Century to the Present Day* (Winchester: St. Paul's Bibliographies, 1990); Ann Shelby Blum, *Picturing Nature: American Nineteenth-Century Zoological Illustrations* (Princeton, N.J.: Princeton Univ. Press, 1993); and Brian Ford, *Images of Science: A History of Scientific Illustration* (London/New York: British Library and Oxford Univ. Press, 1992). See also L. Pearce Williams, *Album of Science: The Nineteenth Century* (New York: Scribner's, 1978); John E. Murdoch, *Album of Science: Antiquity and the Middle Ages* (New York: Scribner's, 1984); F. David Hoeniger, "How Plants and Animals Were Studied in the Mid-Sixteenth Century," in *Science and the Arts*, ed. Shirley and Hoeniger (cit. n. 3), pp. 130–148; Philip Ritterbush, "The Organism as Symbol: An Innovation in Art," *ibid.*, pp. 149–167; Evelyn Hutchinson, "Zoological Iconography in the West after A.D. 1200," *American Scientist*, 1978, *66*:675–684; David Knight, *Zoological Illustration: An Essay towards a History of Printed Zoological Pictures* (Folkstone, Kent: Dawson; Hamden, Conn.: Archon, 1977); and Knight, "Discourse in Pictures," in *The Age of Science* (Oxford/New York: Basil Blackwell, 1986), pp. 109–127.

[6] Arthur H. Robinson and Barbara B. Petchenik, *The Nature of Maps* (Chicago: Univ. Chicago Press, 1976); Stafford, *Voyage into Substance* (cit. n. 3); Dennis Wood with J. Fels, *The Power of Maps* (New York/London: Guilford, 1992); J. Brian Harley and David Woodward, *The History of Cartography*, Vol. 1 (Chicago: Univ. Chicago Press, 1987), Ch. 1; David Turnbull, *Maps Are Territories: Science as an Atlas* (Victoria, Australia: Deakin Univ. Press, 1989); Harley, "Deconstructing the Map," *Car-*

not concerned with how levels of map meaning participate in the development of particular sciences.

In reconstructing the story of Wallace's line, it is my purpose to examine part of a larger issue, the complex role of visual representation in the history of evolutionary biology. The legacy of the line, its numerous map progeny, and their role in shaping twentieth-century biogeographical thought is another, yet unwritten chapter in the history of evolutionary biogeography. Here I will simply try to demonstrate the integral relationship between mapping and Darwin's and Wallace's evolutionary understanding of the biogeography of the East Indian Archipelago. Because Darwin's work on the boundary between the Asian and Australian biotas is difficult to date with precision, it cannot be implicated as clearly in specific theoretical formulations as can Wallace's work. Wallace's articles of 1855 and 1858 on evolutionary theory, his formulation of the faunal line, and his 1863 paper on the physical geography of the Malay Archipelago are fundamentally interrelated, conceptually and temporally. The mapping of biological distributions was not merely coincident with the formulation of these men's theories, nor did it play a simple causal role; it was a pictorial embodiment of evolutionary processes, part and parcel of the conceptual framework that produced the theory of evolution. Wallace's line used available cartographic techniques to forge evolutionary meaning onto the familiar geographical map; pictures of faunal ranges became traces or "outcrops" of faunal histories.

In order to place Darwin's and Wallace's use of faunal maps in perspective, I will briefly discuss the salient features of early nineteenth-century biological mapping and ideas about biological regions, both botanical and zoological. In the sections on Darwin and Wallace, only their work on zoological regions is analyzed.[7]

REGIONS AND MAPS

Natural historians in the late eighteenth and early nineteenth centuries increasingly focused on the description and explanation of plant and animal distribution.[8] Based on the groundwork laid by Carolus Linnaeus and Georges de Buffon, geographical distribution became a new object of study, and diverse approaches developed to make sense of a plethora of new information. One of these approaches, the regionalization

tographica, 1989, *26*:1–20; and Harley, "Cartography, Ethics, and Social Theory," *ibid.,* 1990, *27*:1–23. Of interest, although not bearing directly on the present study, is Wilma George, *Animals and Maps* (Berkeley: Univ. California Press, 1969), which deals with the meaning of animal drawings on maps before 1800.

[7] Darwin's interest in botanical geography is discussed in Janet Browne, *The Secular Ark: Studies in the History of Biogeography* (New Haven, Conn.: Yale Univ. Press, 1983). Wallace's work on the geography of human races is discussed by Martin Fichman, *Alfred Russel Wallace* (Boston: Twayne, 1981); references to and some excerpts from Wallace's publications on human geography are found in Charles H. Smith, ed., *Alfred Russel Wallace: An Anthology of His Shorter Writings* (Oxford: Oxford Univ. Press, 1991).

[8] The long tradition of identifying plants and animals with particular places is discussed in Janet Browne, "C. R. Darwin and J. D. Hooker: Episodes in the History of Plant Geography, 1840–1860" (Ph.D. diss., Univ. London, 1978), Ch. 3. Other works focusing on the history of biogeography include Browne, *Secular Ark;* Philip F. Rehbock, *The Philosophical Naturalists: Themes in Early Nineteenth-Century British Biology* (Madison: Univ. Wisconsin Press, 1983); James Larson, "Not without a Plan: Geography and Natural History in the Late Eighteenth Century," *Journal of the History of Biology,* 1986, *19*:447–488; and Gareth Nelson, "From Candolle to Croizat: Comments on the History of Biogeography," *ibid.,* 1978, *11*:269–305.

of plant and animal distribution, became a compelling object of study for a growing number of naturalists.

Biological regions formed the framework for Charles Lyell's discussion of geographical distribution in *The Principles of Geology*. His introductory comments to the first of three chapters devoted to geographical distribution are quoted here for their clear articulation of the importance of biogeography. The single most important element in his statements is the notion of regionalization. By this time, the 1830s, maps had become shared cultural images, and Lyell was able to refer to zoological and botanical regions without actually presenting a map:

> Next to determining the question of whether species have a real existence, the consideration of the laws which regulate their geographical distribution is a subject of primary importance to the geologist. . . .
>
> But the extent of this parceling out of the globe amongst different nations, as they have been termed, of plants and animals,—the universality of a phenomenon so extraordinary and unexpected, may be considered as one of the most interesting facts clearly established by the advance of modern science.

Regionalization was considered a remarkable fact, forming a paradigmatic basis for the study of geographical distribution. That different regions of the globe are inhabited by different organisms is partly explained by the environmental requirements of organisms. These factors, such as climate, moisture, and soil, define the station of a species (what we would call its habitat). The problem that Lyell stressed is that the known facts of distribution could not be accounted for by a study of stations alone; he cited Alexander von Humboldt as among the first to perceive that similar climates do not have identical productions. In order to explain the distribution of species, what was then called "habitation"—that is, the areas or regions (rather than the kinds of environments) over which they are distributed—Lyell discussed a different set of factors, the history of dispersal and migration of organisms in changing environments.[9]

Although Lyell did not advance a single scheme of regions, he thought that Augustin de Candolle's system of twenty great botanical provinces provided a trustworthy prose description of the "lines of demarcation" of native areas and was not likely to be substantially altered by new evidence.[10] Implicit in his discussion of plant provinces was that the lines of demarcation, the boundaries between the provinces, represented barriers to migration and dispersal over time.

Faunal provinces came under a separate discussion; there was no mention of the possibility that plant and animal regions might be the same. Lyell's demarcations of zoological provinces were based on the distribution of mammals and were loosely extended to other groups of animals. He mentioned some ten different provinces, referred to in approximated geographical terms: for example, "The whole arctic region has become one of the provinces of the animal kingdom" or "New Holland is well known to contain a most singular and characteristic assemblage of mammiferous

[9] Charles Lyell, *The Principles of Geology* (London: John Murray, 1832), Vol. 2, p. 66. Lyell's discussion of the distinction between stations and habitations is explicitly based on his reading of the "luminous" essay of 1820 by the renowned botanist Augustin de Candolle. In explaining the distinction between stations (the locality where each species grows in reference to climate, soil, etc.) and habitations (the geographical range of species), Lyell complained that the two terms have often been confused and emphasized that it was important to realize that they express two distinct ideas (p. 69).

[10] *Ibid.*, p. 71.

animals."[11] Lyell discussed birds, fish, reptiles, and marine organisms, all of which were known to differ from region to region, but he did not enumerate provinces.

Questions of species origin and species distribution were inextricably linked. Neither environmental requirements nor present-day geographical habitation (range) alone could explain the distribution or the origin of species. One had to consider the co-development, as it were, of the earth and its productions. The notion of "nations" of plants or animals was paradigmatic in that it prescribed a set of questions regarding species origin and distribution, carrying with it the assumption that geographical boundaries between regions of existing organisms were also critical barriers to migration over time.

Following the masterful lead of Humboldt, many other naturalists discussed regional plant and animal geography at length. In Britain, for example, we might point to James Cowles Prichard, known chiefly for his espousal of a quasi-evolutionary theory of human races; William Swainson, whose zoological works were widely read but only partly trusted; and Robert Chambers, whose *Vestiges of the Natural History of Creation* was scorned by scientists but was nonetheless a best-seller. Chambers's twelve-page essay on geographical distribution is among the earliest discussions of the importance of isolation for the maintenance of botanical and zoological provinces. Prichard's treatment of the subject is similar in broad outline to that of Lyell, both authors borrowing generously from one another in successive editions of their books. Prichard accepted de Candolle's twenty floristic provinces and described his own division of the earth into seven zoological provinces, based on the aggregation of endemic species.[12] Among these, he named Australia, the Indian Archipelago, and Polynesia (with its center in New Guinea) as separate provinces, but he did not describe precisely the boundaries between them.

The work of these authors reflects both the prevalence of a regional approach to geographical distribution and the substantial range of theoretical orientations within this approach from about 1805 to 1850. Regions were essential to creationist and evolutionist alike. When Darwin and Wallace read these overviews of biological regions, they became well informed of the basic problem: physically similar distant areas have different, characteristic species; therefore, the history of species and the history of the earth must be studied together to explain observed patterns of distribution. Lyell's emphasis on regions prepared the way for Darwin's and Wallace's research, but his description of biological regions, focusing on impassable barriers separating the major provinces, did not prepare them for the peculiar distribution of the mammals and birds of the East Indian Archipelago, where two widely different faunas are found in extreme proximity.

But this account of the regional approach to problems of geographical distribution does not present a complete picture of pre-Darwinian biogeography. The surge in mapping activities is one of the characteristic features of early nineteenth-century natural history.[13] With mapping, the notion of biological distribution became con-

[11] *Ibid.*, pp. 88, 89.

[12] Robert Chambers, *Vestiges of the Natural History of Creation* (London: Churchill, 1844), pp. 251–262; J. C. Prichard, *Researches into the Physical History of Mankind*, 3rd ed. (London: Sherwood, Gilbert & Piper, 1836), pp. 32–33, 68–71; and William Swainson, *A Treatise on the Geography and Classification of Animals* (Lardner's Cabinet Cyclopedia, 2) (London: Longman Rees, 1835).

[13] The sharp increase in mapping activities in the early nineteenth century was considered a central characteristic of "Humboldtian science" by Susan F. Cannon, *Science in Culture: The Early Victorian Period* (New York: Dawson, 1978).

crete. The cartographic representation of the range of a plant, animal, plant assemblage, or faunal region employs distinctive variables—color, shape, and area—that everyone can see. The emergence of sophisticated graphic representations of comparative social, economic, and political characteristics of states coincided with new methods in the study of the natural environment.[14] There was a remarkable expansion of science into the public domain, with museums, displays of experiments and inventions, and coffee-table narratives of exploration in exotic countries all playing a part in the popularization and visualization of scientific knowledge. The use of maps in popular as well as scientific documents was a pervasive and ubiquitous method for communicating scientific values in this "age of science." Distribution maps displaying spatial variations of an extensive range of objects, from star clusters and comets to minerals and forests, from occurrences of cholera to the correlation of drunkenness with income, were a characteristic feature of the visual culture.[15]

The iconography of this period is replete with cartographic "firsts" from virtually all fields of study, noteworthy among which was Eberhardt von Zimmermann's 1777 map of the distribution of mammals.[16] Zimmermann indicated major regions by outlining them in color; the map also portrayed range limits of numerous species. While naturalists in Germany, England, and France pursued the theme of animal and plant regions, few maps of zoological regions were made after Zimmermann's until the mid-nineteenth century. But other approaches to botanical distribution resulted in different kinds of maps, such as the map of botanical regions of France by de Candolle, Humboldt's map of the distribution of plant assemblages according to altitude, and the twelve maps of plant distribution by the Danish botanist J. F. Schouw, whose work became known through summaries published in English journals.[17] The legacy of these authors is their diverse approaches to mapping and the novel terminology they developed to describe biogeographical concepts. Thus, not only did regions

[14] The quantification of biogeographical phenomena, such as the development of botanical arithmetic, is not independent of the development of statistical thinking and of political and moral statistics. Several recent books treat the history of statistics in the nineteenth century, among them Theodore M. Porter, *The Rise of Statistical Thinking, 1820–1900* (Princeton, N.J.: Princeton Univ. Press, 1986). The development of new methods in the presentation of statistical information is described in Arthur H. Robinson, *Early Thematic Mapping in the History of Cartography* (Chicago: Univ. Chicago Press, 1982); and Edward R. Tufte, *The Visual Display of Quantitative Information* (Cheshire, Conn.: Graphics Press, 1983).

[15] The quotation marks acknowledge the title of David Knight's book on the scientific world view in the nineteenth century, *The Age of Science* (cit. n. 5). The term *visual culture* is attributed to Michael Baxandall in Svetlana Alpers, *The Art of Describing: Dutch Art in the Seventeenth Century* (Chicago: Univ. Chicago Press, 1983), p. xxv.

[16] The map first appeared in Eberhardt A. W. von Zimmermann, *Specimen zoologiae geographicae, quadrupedum domocilia et migrationes sistens* (Leiden/Batavia: Theodorum Haak, 1777), and in a slightly altered form in Zimmermann, *Geographische Geschichte des Menschen und der Allgemein Verbreiteten Vierfüssigen Thiere* (Leipzig: Weygandschen, 1778–1783). An explanation of the map in German was published separately: Zimmermann, *Tabula mundi geographico-zoologicae explicatio brevis* (Leipzig: N.p., 1783). The burgeoning of thematic cartography during this period is described in Robinson, *Early Thematic Mapping* (cit. n. 14).

[17] Augustin de Candolle and Jean B. A. P. M. de Lamarck, *Flore française . . .* , 3rd ed. (Paris: Desray, 1805); Alexander von Humboldt and Aimé Bonpland, *Essai sur la géographie des plants* (Paris: Levrault, Schoell, 1805); and Joachim F. Schouw, *Pflanzengeographischer Atlas zur Erläuterung von Schouws Grundzügen einer allgemeinen Pflanzengeographie* (Berlin: Reimer, 1823). Humboldt's maps are discussed in Thomas R. Detwyler, "Humboldt's *Essay on Plant Geography:* Its Relevance Today," *Michigan Academician,* 1969, *1*(3 and 4):113–122; Camerini, "Darwin, Wallace, and Maps" (cit. n. 2), Ch. 2; and Malcolm Nicolson, "Alexander von Humboldt and the Geography of Plants," in *Romanticism and the Sciences,* ed. Andrew Cunningham and Nicholas Jardine (Cambridge: Cambridge Univ. Press, 1990).

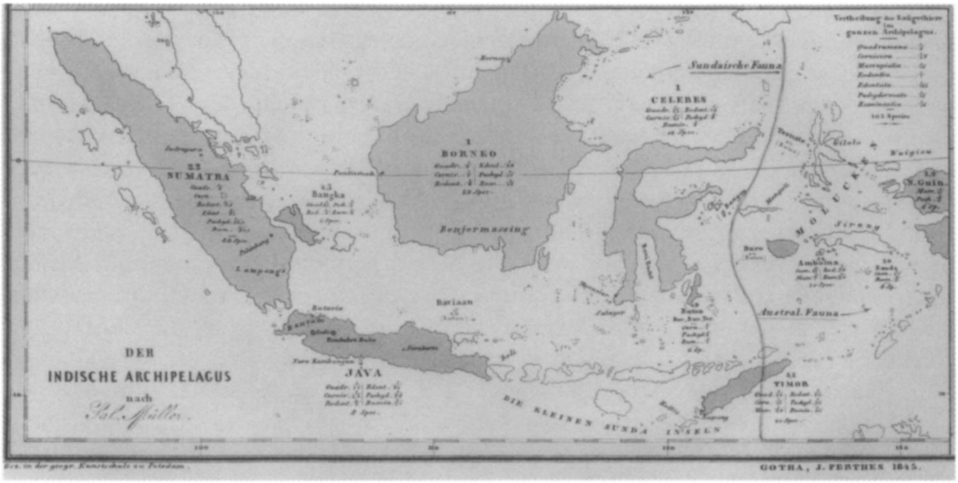

Figure 2. Heinrich Berghaus's "Mammalian Monograph" of the East Indian Archipelago, 1845, from the Physikalischer Atlas, *Section 6, Animal Geography Plate No. 6.*

become part of the discourse of natural history, but new terms—*isotherms, life zones, plant community, vegetation assemblage,* and *species range*—are additional evidence of the increasing role of map-based concepts in the study of geographical distribution.

The new role for cartographic representation in the study of plant and animal distributions was consolidated in the second quarter of the nineteenth century. New cartographic symbols continued to coevolve with novel concepts; mapping was now a recognized tool in the visual technology of natural history. A new genre of atlas, the physical atlas, contained only distribution maps, excluding political or "geographical" maps. Alexander K. Johnston's *Atlas of Natural Phenomena* was the most popular of these in England and was well known to both Darwin and Wallace.[18] It appeared in various editions from 1846 to 1856; a typical edition included twenty-four distribution maps, seven of which portrayed various themes of botanical and zoological geography.

The zoogeography of the East Indian Archipelago found its way onto a map in the first German physical atlas, Heinrich Berghaus's *Physikalischer Atlas* (Figure 2). The map was made by Berghaus in his effort to summarize and display the findings of the Dutch naturalist Salomon Müller. Berghaus called the map, along with another

[18] Darwin had already made use of the singly issued plates of the original German version of the atlas—Heinrich Berghaus, *Physikalischer Atlas* (Gotha: Justus Perthes, 1836–1848)—in research for *The Structure and Distribution of Coral Reefs: Being the First Part of the Geology of the Voyage of the Beagle, under the Command of Capt. Fitzroy, R.N., during the Years 1832 to 1836* (London: Smith Elder, 1842; rpt. Tucson: Univ. Arizona Press, 1984) (all quotations are from the 1984 reprint). Darwin made extensive notes on and references to several different editions of Alexander K. Johnston, *The Physical Atlas of Natural Phenomena* (Edinburgh/London: William Blackwood, 1848, 1850, 1856), in Darwin Archive (DAR), Manuscript Room, Cambridge University Library, Cambridge, England, 72:32–56, DAR 205.2.89, and Charles Darwin, *Natural Selection,* ed. Robert C. Stauffer (Cambridge: Cambridge Univ. Press, 1975), pp. 55, n. 1, 535, 539, n. 3. The 1850 edition of Johnston's *Physical Atlas* was in Wallace's personal library (now at the Linnean Society Library, London).

on mammals of Austria, "Mammalian Monographs.[19] Darwin, who saw some of the sheets of the Berghaus atlas as they were published, may well have seen the map; it is unlikely that Wallace was aware of it.

In sum, by the time Darwin and Wallace began to study geographical distribution, various schemes for plant and animal regions had been described verbally but few had been mapped, the exceptions being the maps of Zimmermann for mammalian regions and Schouw for botanical regions. Detailed information about animal distributions was accumulating rapidly. Why did Darwin and Wallace synthesize this knowledge by mapping zoological regions? Maps were clearly a necessary practical tool for traveling naturalists; what was their value as tools of biogeographical thought?

DARWIN AND THE EAST INDIAN ARCHIPELAGO

In the course of his extensive writing and research in the decade following the voyage of the *Beagle* (1831–1836), Darwin confronted the complex distribution patterns of East Indian mammals. His published and unpublished writings reveal that the boundary between the Asian and Australian faunal regions was a focal point in his struggle to account for the regionality of organisms according to his developing theory of common descent. He attempted to delineate the location of this faunal boundary using tables, nautical charts, and maps, as well as verbal descriptions of species locations. From an evolutionary point of view, a naturalist would not expect an archipelago of physically similar islands to be populated with strikingly different animals on its western and eastern ends. Darwin would find the solution to this problem in the realization that deep water (rather than a large expanse) between certain islands could account for the observed differences in the fauna of the East Indian Archipelago.

Darwin employed the idea of regions as conceptual scaffolding for a complex combination of geological, biological, and geographical phenomena. He explicitly and repeatedly tried to account for the regionalization of animals, from the early entries in his first transmutation notebook ("I really think a very strong case might be made out of world before zoological divisions"), to notes for *Natural Selection,* and through the chapters on geographical distribution in the *Origin of Species.*[20] In his approach to biogeography, regional, map-based thinking appears as an instrument of thought rather than as an end in itself: Darwin's goal was to account for the

[19] Berghaus, *Physikalischer Atlas,* Vol. 2, text p. 21, cited his source as the classic overview of the fauna of the East Indian Archipelago by Salomon Müller in the *Annalen der Erdkunde*, 1842, pt. 1 (Mar.), pp. 251–266; pt. 2 (Apr.), pp. 289–333. A similar overview by Müller appeared the year after the map was printed: "Ueber den Charakter der Thierwelt auf den Inseln des Indisches Archipels," *Archiv für Naturgeschichte,* 1846, *12*:109–128. The Berghaus atlas and the plant and animal maps therein are discussed in Jane R. Camerini, "The Physical Atlas of Heinrich Berghaus: Distribution Maps as Scientific Knowledge," in *Non-Verbal Communication in the History of Science,* ed. R. Mazzolini (Florence: Olschki, 1993). Another Dutch student of the East Indian fauna was H. Zollinger, "Over het begtip enden omvang eener Flora Malesiana," *Natuurkundig Tidschrift voor Nederlandisch-Indie,* 1857, *13*:293–322. There is no evidence that Lyell, Darwin, or Wallace was aware of either Müller or Zollinger before 1863; Wallace cited Zollinger in Alfred R. Wallace, *The Malay Archipelago: The Land of the Orang-Utan and the Bird of Paradise* (1869; 6th ed., London: Macmillan, 1877), p. 202.

[20] Paul H. Barrett, Peter J. Gautrey, Sandra Herbert, David Kohn, and Sydney Smith, eds., *Charles Darwin's Notebooks, 1836–1844* (Ithaca, N.Y.: Cornell Univ. Press; London: British Museum [Natural History], 1987), B.95; Darwin, *Natural Selection,* ed. Stauffer (cit. n. 18), pp. 584–585; DAR 205.2.89v; and Charles Darwin, *On the Origin of Species by Means of Natural Selection* (London: John Murray, 1859; London: Penguin, 1968), p. 393 (summary of Chs. 11, 12).

accepted "fact" of zoological regions in a way that accorded with his evolutionary theory, not to define faunal boundaries. But an important fact was missing—the location of the boundary between the Asian and Australian faunas, in an area where there was no single obvious barrier to migration. Darwin eventually found the relationships that made sense of the phenomena—elevation and subsidence, formation of new species, barriers to mammalian distribution, and depth of water—that recur in conjunction with his efforts to locate this regional dividing line.

In spite of the many changes and refinements during the long gestation of his theory of evolution by natural selection, there is a stability in Darwin's maplike frame of reference for the study of patterns of animal geography. This backdrop, the geographical base map of his biogeography, grew out of his extensive experiences with maps on the journey of the *Beagle,* including the numerous geological profiles and maps he made himself. Most important, he carefully compiled a detailed world map of the distribution of coral reefs, which played a central role in *The Structure and Distribution of Coral Reefs*.[21] His manuscripts and published work provide substantial evidence that he also relied on published exploration and distribution maps, as well as on his own mental maps, during many phases in the development of his theories.[22]

Darwin's enduring interest in geographical distribution can be categorized into three loosely defined stages: these are represented by the notebooks and unbound notes of the late 1830s, his unpublished essays on species from the 1840s, and the manuscripts and books of the 1850s, including *On the Origin of Species*. During the post-*Beagle* decade, Darwin became extremely well versed in contemporary thought on geographical distribution through his voracious reading of natural history journals and books, travel reports, and exploration surveys and his voluminous correspondence and professional relationships with leading naturalists of the day. Darwin's collection of information and ideas about the occurrence and ranges of animals in the East Indian Archipelago is well documented in these notebooks and loose notes.[23]

[21] Darwin made two compilation maps of his coral reef map that hang in Down House; these are reproduced and discussed in Camerini, "Darwin, Wallace, and Maps" (cit. n. 2), pp. 95–98. *Structure and Distribution of Coral Reefs* is the first of Darwin's three volumes on his geological research from the *Beagle* voyage; the others are *Geological Observations on the Volcanic Islands Visited during the Voyage of H.M.S. Beagle, Together with Some Brief Notices of the Geology of Australia and the Cape of Good Hope: Being the Second Part of the Geology of the Voyage of the Beagle, under the Command of Capt. Fitzroy, R.N., during the Years 1832 to 1836* (London: Smith Elder, 1844); and *Geological Observations on South America: Being the Third Part of the Geology of the Voyage of the Beagle, under the Command of Capt. Fitzroy, R.N., during the Years 1832 to 1836* (London: Smith Elder, 1846). Darwin's numerous articles on his geological research are reproduced in Paul H. Barrett, ed., *The Collected Papers of Charles Darwin* (Chicago: Univ. Chicago Press, 1977).

[22] Darwin refers to scores of maps in *Structure and Distribution of Coral Reefs* (cit. n. 18); in addition to the profiles and maps published in the volumes on geology, two unpublished geological maps and numerous profiles are among his manuscripts in DAR 34.1, DAR 34.2, DAR 39.2, DAR 41, and DAR 44. These maps are discussed in Camerini, "Darwin, Wallace, and Maps," pp. 72–90, and in each of the three contributions to a special issue of the *British Journal for the History of Science* (1991, *24*) devoted to Darwin and geology: James A. Secord, "The Discovery of a Vocation: Darwin's Early Geology," pp. 133–157; Sandra Herbert, "Charles Darwin as a Prospective Geological Author," pp. 159–192; and Frank H. T. Rhodes, "Darwin's Search for a Theory of the Earth: Symmetry, Simplicity, and Speculation," pp. 193–229. Notable exceptions to the traditional neglect of visual representation in Darwin's thought are Michael T. Ghiselin, *The Triumph of the Darwinian Method* (Berkeley: Univ. California Press, 1969), pp. 13–24; and Howard E. Gruber, "Darwin's 'Tree of Nature' and Other Images of Wide Scope," in *Aesthetics in Science,* ed. J. Wechsler (Cambridge, Mass.: MIT Press, 1978).

[23] Camerini, "Darwin, Wallace, and Maps," App. 1, lists some forty references to the East Indian Archipelago in Darwin's notebooks and loose notes from before 1840. My analysis here is based pri-

He was concerned with the areal extent of species ranges, with ascribing animals to the Asian or Australian fauna, and with the pattern of species variation among the islands, drawing analogies to the pattern he saw in the Galapagos. Darwin sought information about animal distribution in the East Indian Archipelago from a wealth of sources, most notably James Horsburgh's *India Directory,* René Lesson and Prosper Garnot's *Zoologie* from the voyage of the *Coquille,* Jean-René Quoy and Paul Gaimard's *Zoologie* from the voyage of the *Astrolabe,* Jacques de Labillardière's account of the voyage of *La Pérouse,* Coenraad Temminck's contribution to the *Flora Japonica* of Phillip von Siebold, and Sir George Windsor Earl's book *The Eastern Seas.*[24] Many of these works were consulted in conjunction with his research on coral reefs, which occupied much of his time from late 1838 until early 1842.[25]

At an early stage in his evolutionary theory, Darwin imagined that isolation, brought about by subsidence of once-continuous land, was critical in differentiating the three forms of rhinoceros (Indian, Javanese, and Sumatran). He claimed that if Sumatra and Java were to be reunited by continued elevation of the islands, the two species would remain distinct. His research on the Malay region combined one of his major geological preoccupations, island elevation and subsidence, with his interest in the distribution of mammals. Because mammals have more difficulty in crossing presumably permanent oceanic barriers than do birds or insects, their island distribution took on greater importance. The mammal-rich East Indian Archipelago, in contrast to the mammal-poor Galapagos Islands, provided a unique setting for mammalian evolution. An example of the confluence of Darwin's interest in species distribution and in elevation and subsidence is found in Notebook B, the first of his transmutation notebooks, begun in the second half of 1837. Although somewhat cryptic, the following quotations show Darwin speculating about speciation as a result of repeated elevation and subsidence of islands in the East Indian Archipelago:

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marily on Darwin's writings as found in Barrett *et al.*, eds., *Darwin's Notebooks* (cit. n. 20); his essays of 1842 and 1844, in Sir Gavin De Beer, ed., *Charles Darwin and Alfred Russel Wallace: Evolution and Natural Selection* (Cambridge: Cambridge Univ. Press, 1958); his big book on species, *Natural Selection,* ed. Stauffer (cit. n. 18); and three volumes of his portfolio notes on geographic distribution bound in archival volumes DAR 205.2, 205.3, and 205.4. Darwin's interest in geographical distribution is analyzed by Philip J. Darlington, Jr., "Darwin and Zoogeography," *Proc. Amer. Phil. Soc.,* 1959, *103*(2):307–319; Ghiselin, *Triumph of the Darwinian Method*, pp. 32–45; Alan R. Richardson, "Biogeography and the Genesis of Darwin's Ideas on Transmutation," *J. Hist. Biol.,* 1981, *14*:1–41; and Browne, *Secular Ark* (cit. n. 7).

[24] James Horsburgh, *India Directory,* 4th ed., 2 vols. in one (London, 1836); René P. Lesson and Prosper Garnot, *Zoologie,* in Louis I. Duperrey, *Voyage autour du monde . . . sur la corvette de sa 'Majesté,' 'La Coquille' pendant les années 1822, 1823, 1824 et 1825,* 6 vols. (Paris, 1825–1830); Jean-René C. Quoy and Paul J. Gaimard, *Zoologie,* in J. S. C. Dumont d'Urville, *Voyage de la corvette 'l'Astrolabe' . . . pendant les années 1826–1827–1828–1829,* 14 vols. and atlas (Paris, 1830–1835); Jacques J. H. de Labillardière, *Relation du voyage à la recherche de 'La Pérouse' . . . pendant les années 1791, 1792, et pendant la 1ère et la 2ème année de la Republique française,* 2 vols. and atlas (Paris, 1800); Coenraad J. Temminck, *Discourse preliminaire: Coup-d'oeil sur la faune des îles de la Sonde et de l'empire du Japon,* in Phillip F. von Siebold, *Fauna Japonica; . . . conjunctis studiis C. J. Temminck et H. Schlegel pro vertebratis, atque W. de Haan pro invertebratis elaborata,* 6 vols. in four (Leiden/Batavia, 1833–1850); and George W. Earl, *The Eastern Seas, or Voyages and Adventures in the Indian Archipelago, in 1832–33–34 . . .* (London: W. H. Allen, 1837).

[25] Darwin had begun to theorize about coral reef formation while on the *Beagle*. See David R. Stoddart, "Coral Islands by Charles Darwin, with Introduction, Map, and Remarks," *Atoll Research Bulletin,* 1962, *88*:1–20; Stoddart, "Darwin, Lyell, and the Geological Significance of Coral Reefs," *Brit. J. Hist. Sci.,* 1976, *9*:199–218; and Frederick Burkhardt, "Darwin's Early Notes on Coral Reef Formation," *Earth Sciences History,* 1984, *3*:160–163.

Figure 3. *A portion of Darwin's table of mammals of the Malay Archipelago, from DAR 205.3.211.*

> The motion of the earth must be excessive up & down. —Elephants in Ceylon—East Indian archipelago.
>
> Species formed by subsidence. Java & Sumatra. Rhinoceros. Elevate & join keep distinct. two species made. elevation and subsidence continually forming species. —
>
> When breaking up (the primeval.) continent. Indian Rhinoceros. Java & Sumatra ones all different. —Join Sumatra & Java together, by elevations now in Progress, & you will have two.[26]

An interesting example of Darwin's notes on these matters is a table he drew comparing the mammalian fauna of Borneo, Sumatra, Java, Malacca, and other small isles (Figures 3 and 4; see Figure 5 to locate these places). The table is an undated entry among Darwin's portfolio "scraps"; it was almost certainly made in conjunction with his reading of Temminck's *Coup-d'oeil sur la faune des îles de la Sonde et de l'empire du Japon* in 1839.[27] This example illustrates his strong interest in variations among closely related island species. He noted whether a species was unique (endemic) to an island and whether or not it had a close relative on another island. On the same sheet Darwin made some notes of a more speculative nature (not shown in Figures 3 and 4), pointing to the ever-present theoretical problem of common descent. In searching for a solution to the relation of mammalian species in the archipelago, he looked to the depth of water between islands and the possibility

[26] See Barrett *et al.*, eds., *Darwin's Notebooks* (cit n. 20), B.80, B.82, and B.241, for Darwin's additions and deletions to these entries.

[27] DAR 205.3.211. The table is dated on the basis of an entry in Notebook E.170, which includes a note with a page reference to Temminck, *Coup-d'oeil sur la faune des îles de la sonde* (cit. n. 24). Darwin's table is drawn on the same large sheet of paper on which notes from Temminck were made. In the second column there is a page reference written alongside the small circles. Darwin's note here reads: "yet there are many species of these 2 genera p 9."

Borneo	Sumatra	Java	Malacca	Small isles near these great ones
Orang Outang	Orang Outang p. 6	0		Cervus Kuhlii proper to smaller isles
Semnopithecus nasique				of Bassian near Java, but never found
Gibbon NS				on Java. p. 11
Felis macrocelis				Muka Kambing (p. 12) has a
Tupaia 2 spe. NS				Pteromys 1/3 larger than P. nitratus
Semnopithecus 2 spec				so common in Java. — it is found
Ursus malaianus	Ursus	0	Ursus malaianus	in some other isd's but never
Felis 2 spec NS				in Java.
Hypsiprimnus ursinus				
	Elephant	0	Elephant	
	Tapir	0	0	
		1 spec	p. 8	
	Rhinoceros bicorna p. 8	Rhinoceros unicorna p. 8	Rhinoceros unicor. 2 Spe	
	Bos arni	Bos banting	Bos sylhetanus	
			[D'achii Cochin theas?]	
	Cervus russa p. 80	Cervus nipa		
	hippelaphus 90	0		
	Sus — 3 spec.? —	Sus verrucosus	Sus verrucosus	
		vittatus		
	—Yet there are 0 ___	Hylobates leuciscus		
	—many species 0 ___	Semnopth: mitratus (p. 9		
	—of these 2 0 ___	________ mauris		
	—genera p. 9 0 ___	________ auratus or pyrrhus		
	Galeopth: marmoratus	________ 0 ________		
	0	Galeopithecus variegatum		Found in all these isd's even to
				Amboina or Timor

Figure 4. A transcription of Darwin's table. The square brackets indicate uncertain transcriptions.

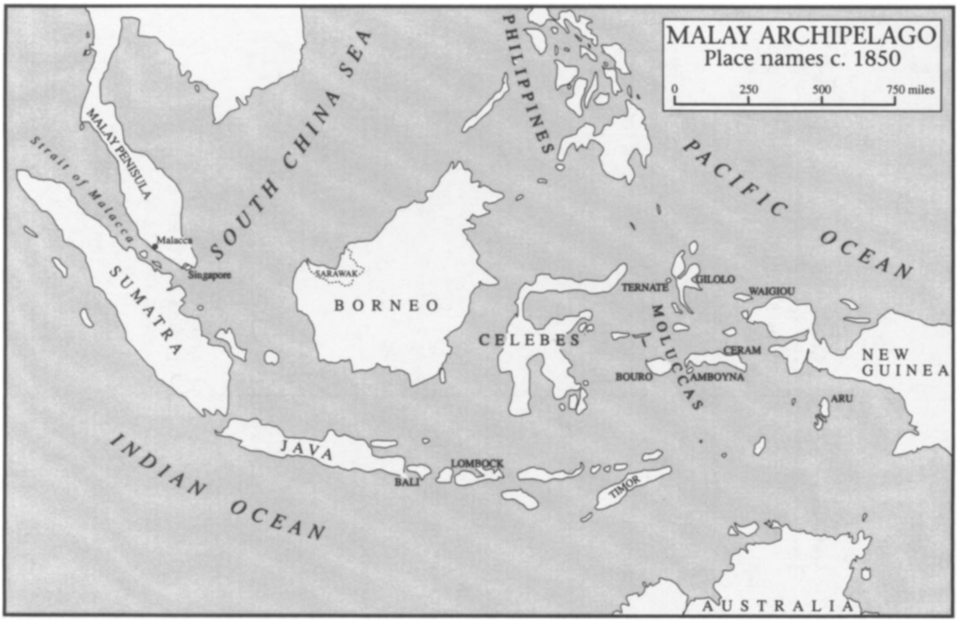

Figure 5. *Location of major places and contemporary place-names in the Malay Archipelago (East Indian Archipelago), circa 1850.*

of former land connections between them, penciling in the phrase "relation of character of quadrupeds to soundings."[28]

Darwin struggled with the role of elevation and subsidence in the formation of new species, at times finding subsidence or elevation the critical factor favoring speciation, at times emphasizing both. In the course of his research for *The Structure and Distribution of Coral Reefs,* Darwin found evidence of recent elevation in the East Indian Archipelago and came to the conclusion that changes in land elevation over time were the key factor in speciation.[29] His interest in elevation and subsidence led Darwin to focus on the depth of water between adjacent islands in the region. He was concerned with soundings because he inferred (correctly) that shallow depths between islands meant that they had been united in the not-too-distant past. Shallow water indicated a recent land connection and close biological affinities, deep water a far more ancient barrier to migration and more distant biological relationships.

Elevation and subsidence were of fundamental importance in explaining the diversity of species because Darwin's theory at this time still required new physical conditions to stimulate variations within a species; he did not yet see the tendency to vary as an inherent (genetic) trait in wild species. Elevation and subsidence were also important in favoring or impeding migration: subsidence would isolate individuals, elevation would allow them to vary as they expanded their ranges into newly

[28] This portion of Darwin's note reads: "Relation of character of quadrupeds to soundings is explicable when same species occurs on the opposite sides, as Britain & Sicily etc—but what relation a creationist. —but these obviously differing in this troubled region of the world studded with craters, in correction on my theory for they might formerly have been connected and the same parent species" (DAR 205.3.209).

[29] Proofs of recent elevation in the East Indian Archipelago are summarized in Darwin, *Structure and Distribution of Coral Reefs* (cit. n. 18), pp. 134–135.

emerged land, and repeated oscillations would favor the creation of a great number of new species. His theory at this stage was based in his highly visual geological view of the world; it was largely dependent upon isolation for the production of new species.[30]

As part of his research on elevation, Darwin studied a Dutch chart of the region that listed measurements of soundings between the islands of the archipelago.[31] On this list, made as early as 1839, he noted deep water in several places, including on the west coast of Celebes (between Celebes and Borneo) and between Gilolo and Celebes, Bali and Lombock, Ceram and New Guinea, and Gilolo and the Philippine Islands. Remarkably, three of these locations are on the line Wallace later drew dividing the Asian and Australian biotic regions. Darwin's conclusions from these charts, tables, and musings on the relation of water depth to mammalian distribution were roughly drawn together in his two essays on species.

All of the above-mentioned threads woven into Darwin's theoretical framework appear in these essays (known as the pencil sketch of 1842 and the essay of 1844). Again we find the major faunal regions, depth of water, and elevation and subsidence as central themes. Here the story of three closely related oriental species of rhinoceros, descendants of their more distant African ancestor, provided one of his strongest arguments in the summary of his theory of common descent. In this discussion he sarcastically refuted Chambers's evolutionary hypothesis, which was based on inorganic origins of species. Darwin wrote: "Shall we then allow that the three distinct species of Rhinoceros which separately inhabit Java and Sumatra and the neighboring mainland of Malacca were created, male and female, out of the inorganic materials of these countries?"[32]

The regionalization of mammalian distribution provided a conceptual and at the same time visual framework for Darwin's first attempts at presenting his theory. In both of these essays Darwin began his discussion of geographical distribution with the concept of mammalian regions. He suggested initially that there were three or four main regions, with the East Indian Archipelago forming a single region along with North America, Europe, and Asia. In the essay of 1844 Darwin discusses two-, three-, and fourfold divisions of the globe before settling on a scheme of five regions: Australia and New Guinea, South America, North America and Eurasia, Madagascar, and Africa.[33]

In the essay of 1844 Darwin revealed one of his cognitive schemes by "placing" his five regions on a base map. "Inspection of a map of the world at once shows that the five divisions, separated according to the greatest amount of difference in the mammifers inhabiting them, are likewise those most widely separated from each other by barriers which mammifers cannot pass."[34] With either an actual or a mental

[30] Frank Sulloway, "Geographic Isolation in Darwin's Thinking: The Vicissitudes of a Crucial Idea," *Studies in the History of Biology,* 1979, *3*:23–65, treats the changing role of isolation in Darwin's thinking from the Notebooks of the late 1830s through later editions of the *Origin.*

[31] DAR 205.3.59; watermark on paper is 1839. The chart he took notes from is very likely one he referred to in *Structure and Distribution of Coral Reefs* (cit. n. 18), p. 175: "In a Dutch MS. chart on a large scale of Java, which was brought from that island by Dr. Horsfield, who had the kindness to show it me at the India-House."

[32] De Beer, ed., *Darwin and Wallace* (cit. n. 23), pp. 83, 249. Dov Ospovat, *The Development of Darwin's Theory* (Cambridge: Cambridge Univ. Press, 1981), treats in depth the development of Darwin's theories and emphasizes the geological basis of the essay of 1844.

[33] De Beer, ed., *Darwin and Wallace,* pp. 65, 169, 170.

[34] *Ibid.,* p. 171.

map of the world before him, he overlaid an image of the regional distributions of mammals, and then saw the congruence of the boundaries of the regions and major barriers to migration of mammals. As his theory began to take shape, he tested the zoological regions according to his ideas of dispersal from a single point of origin and common descent. Darwin synthesized all of the geological and biological patterns and processes he believed were involved, and then saw that the regions were in fact following an expected pattern.

Although Darwin's notes display some uncertainty as to the exact location of the line between the Eurasian and Australian regions, he had, by 1844, settled on the idea of deep water as forming the critical boundary. He concluded that "New Guinea and its adjoining islets are cut off from the other East Indian islands by deep water."[35]

In the 1844 essay Darwin pointed to deep water separating the Australian region from the other East Indian islands. He did not, however, specifically mention Celebes. The placement of Celebes in one or the other region would concern Darwin for some time, and several of his loose notes from the 1840s and 1850s dealt with affinities of the Celebes fauna and with the connection of Celebes with New Guinea and nearby smaller islands.[36] In the following year he read Earl's article "On the Physical Structure and Arrangement of the Islands in the Indian Archipelago" and began to rely on Earl and other authorities for their placement of Celebes.[37]

Earl grouped most of the islands separated by shallow depths into either the Great Asiatic or the Great Australian Bank. Those islands separated by deeper channels he took to be younger and of volcanic origin. The map accompanying the article, which was noted by Darwin, shows the banks as stippled areas (Figure 6). Earl found these geographic results significant in that "all the countries lying upon these banks partake of the character of the continents to which they are attached"; he offered evidence from plant, animal, and mineral distributions.[38]

Some years later, in a letter to Wallace, Darwin referred to soundings in the archipelago, indicating how important Earl's remarks had been to him. "Are you aware that Mr. W. Earl published years ago the view of distribution of animals in the Malay

[35] *Ibid.*

[36] Notes on alliances of Celebes forms to other species are found in Barrett *et al.*, eds., *Darwin's Notebooks* (cit. n. 20), C.13, 14; and in DAR 205.2.112, DAR 205.3.179. References to former land connections with Celebes are found in DAR 205.2.112 (Celebes and Philippines), DAR 205.2.129 ("Crawford tells me . . . Earl has written on connection of the Bank of Borneo with Celebes," dated 5 May [no year is given]), DAR 205.3.113 (Celebes and New Guinea, dated Aug. 1844), and DAR 205.3.182 (Celebes and New Guinea, dated Aug. 1856). When Darwin consulted Johnston's *Atlas* he noted that "Celebes is outlier (as far as soundings concerned) in map—Ceram and Timor being boundary to west, —& belongs to Australia" (DAR 72.35; phrase in parentheses inserted by Darwin). Darwin's and Wallace's sensitivity to the significance of deep water as a barrier to migration and their attention to the difficulties of placing Celebes in one region or another are all the more interesting in light of recent findings of plate tectonics. See T. C. Whitmore, "Introduction," in *Wallace's Line and Plate Tectonics,* ed. Whitmore (cit. n. 1), pp. 1–2; and M. G. Audley-Charles, "Geological History of the Region of Wallace's Line," *ibid.*, pp. 24–36.

[37] George Windsor Earl, "On the Physical Structure and Arrangement of the Islands in the Indian Archipelago," *J. Roy. Geogr. Soc.*, 1845, *15*:358–365. The spelling of Earl(e)'s name varies in his publications and in Darwin's references to him. Darwin notes Earl's *Eastern Seas* (cit. n. 24) in Notebook E.18 and E.182; he refers to the 1845 article in DAR 205.2.50, DAR 205.2.129, and DAR 205.3.153 (entry dated 1845). On Earl's map Celebes falls (almost) in the Asian bank but is colored green, as are Borneo and New Guinea, to indicate volcanic land.

[38] Earl, "Physical Structure and Arrangement," p. 359. According to Wallace, "Physical Geography of the Malay Archipelago" (cit. n. 1), p. 226, Earl believed that there had been a former connection between Asia and Australia.

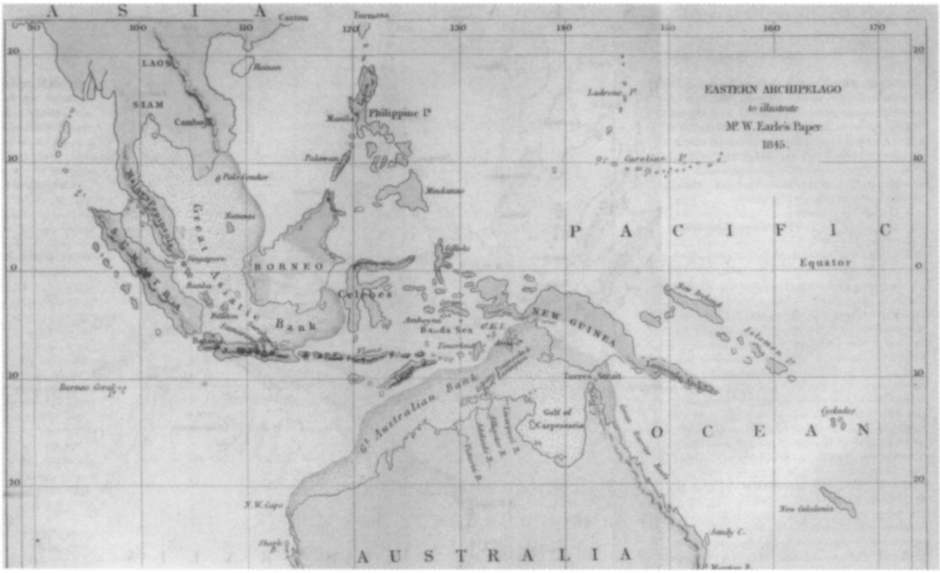

Figure 6. Map accompanying Sir George Windsor Earl(e)'s article "On the Structure and Arrangement of the Islands in the Indian Archipelago," published in the Journal of the Royal Geographical Society *in 1845.*

Archipelago in relation to the depth of the sea between the islands? I was much struck with this, and have been in the habit of noting down all facts on distribution in the Archipelago and elsewhere in this relation." It seems that Earl's article, rather than his own research, became a firm reference point for this correlation, and Darwin would later point to "the relation between soundings and distribution," invoking Earl's name.[39]

Darwin's lasting insight into mammalian distribution in the East Indian Archipelago was his (and Earl's) idea of relating depth of water to degree of biological affinity. The record of soundings was a shorthand for a history of repeated elevation, subsidence, and changes of sea level. "The distribution of mammals with relation to soundings" is a phrase found repeatedly in Darwin's drafts from the mid 1850s for his longer book on evolution, *Natural Selection*.[40] By this time, the phrase seems to have solidified in his mind, its significance being that water depth, rather than visible barriers to migration, could in fact account for the known patterns of mammalian distribution; his theory of common descent from a single pair of ancestors was thereby sustainable.

By the time Darwin wrote the *Natural Selection* manuscript and the *Origin of Species* itself, zoological regions were not of importance as areas per se; it was the barriers between them that were critical to his argument on geographical distribution. He noted for the first time in print that the region comprising Australia, New Guinea, and its adjoining islets was separated from the islands of the East Indian Archipelago

[39] Charles Darwin to Alfred Russel Wallace, 9 Aug. 1859, in James Marchant, *Alfred Russel Wallace: Letters and Reminiscences* (New York/London: Harper, 1916), p. 114; and DAR 205.2.89.

[40] The phrase is found in DAR 205.2.89, DAR 205.2.91 (in two places; see "On Barriers" in Darwin, *Natural Selection*, ed. Stauffer [cit. n. 18], pp. 585, 585 n), and DAR 205.3.171.

and the rest of the Eurasian region by deep water. He referred to the deep ocean near Celebes as the boundary between these major faunal regions:

> There is also a relation, to a certain extent independent of distance, between the depth of the sea separating an island from the neighbouring mainland, and the presence in both of the same mammiferous species or of allied species in a more or less modified condition. Mr. Windsor Earl has made some striking observations on this head in regard to the great Malay Archipelago, which is traversed near Celebes by a space of deep ocean; and this space separates two widely distinct mammalian faunas. On either side the islands are situated on moderately deep submarine banks and they are inhabited by closely allied or identical quadrupeds.[41]

Zoological regions were a necessary step in the development of Darwin's theory. Although he used the concept and a map image of mammalian regions in the early formulation of his argument for common descent and continued to be interested in regional schemes, the regions themselves faded from his writing after the 1850s.[42] He became more interested in the process of natural selection, in the origin of adaptations, and in explaining the evolutionary significance of certain distributional patterns, such as disjunct alpine distributions, than in the overall geographic regional patterns that resulted.

WALLACE DRAWS THE LINE

Even before he set sail on his journey in the Amazon (1848–1852), Wallace wrote to his friend Henry Walter Bates that his principal interest was in resolving the problem of the origin of species through detailed study of his favorite subject, "the variations, arrangements, distribution, etc., of species."[43] Knowledge of animal distribution was a major goal of his Amazonian research, and his publications from this journey clearly demonstrate his emphatic concern with detailed and accurate geographical information."[44] In 1854, when he began his extensive travels in the East Indian Archipelago, Wallace was equipped with an awareness of contemporary views on geographical distribution, as well as his firsthand knowledge of the practical difficulties of fieldwork. In the course of the eight years he spent in the Malay Archipelago (1854–1862), he published some thirty-eight papers and letters in British

[41] Darwin, *Origin of Species* (cit. n. 20), p. 383.

[42] His ongoing interest is evidenced by an annotated clipping of an article from *Nature,* 30 Mar. 1871, on a suggested new division of the earth into zoological regions (DAR 205.3.17).

[43] Alfred R. Wallace, *My Life: A Record of Events and Opinions* (London: Chapman & Hall, 1905), Vol. 1, p. 257. The standard references on Wallace's life and work are Marchant, *Alfred Russel Wallace* (cit. n. 39); Wilma George, *Biologist Philosopher: A Study of the Life and Writings of Alfred Russel Wallace* (London: Abelard-Schuman, 1964); H. Lewis McKinney, *Wallace and Natural Selection* (New Haven, Conn.: Yale Univ. Press, 1972); Arnold C. Brackman, *A Delicate Arrangement* (New York: Times Books, 1980); Fichman, *Alfred Russel Wallace* (cit. n. 7); John L. Brooks, *Just Before the Origin: Alfred Russel Wallace's Theory of Evolution* (New York: Columbia Univ. Press, 1984); and Smith, ed., *Wallace: Shorter Writings* (cit. n. 7).

[44] Alfred Russel Wallace, "On the Monkeys of the Amazon," *Proc. Zool. Soc. Lond.,* 1852, pt. 20, pp. 107–110; Wallace, "On the Habits of the Butterflies of the Amazon Valley," *Transactions of the Entomological Society of London,* N.S., 1854, *2*(8):253–264; and Wallace, *Palm Trees of the Amazon* (London: Van Voorst, 1853). Wallace's emphasis on geographical distribution is discussed in McKinney, *Wallace and Natural Selection,* pp. 13–26; and Brooks, *Just Before the Origin,* pp. 32–55.

natural history journals, including the historic sketch of his theory of evolution by natural selection that induced Darwin to get his own theory into print quickly.[45]

Small and large fragments representing Wallace's extraordinary intellectual activity in the course of his Malay travels are extant in two field notebooks, four journals, and two species registers. Wallace traveled about 14,000 miles within the archipelago, collected well over 100,000 specimens, and persevered in his speculations and theories in spite of being criticized for doing so instead of just collecting facts.[46] His correspondence with the naturalist Henry Walter Bates (his companion in South America), his English friend George Silk, his agent Samuel Stevens, Charles Darwin, and others, along with his publications in British natural history journals, makes this a scientifically well-documented period of his life.

For Wallace, the significance of the geographical patterns that he observed, both local and global, was in their relation to his views on the origin of species. In this retelling of the genesis of Wallace's line from 1855 to 1863, two methodological themes are paramount. The first is his combination of features of physical geography with species change, a continuation of the kind of reconstruction of species origins and earth history he sought in his Amazonian research. The use of maps constitutes the second facet of his approach. Maps served Wallace as a conceptual framework, a metaphor, and a tool for synthesizing and communicating his results—they were the mental and actual space on which the processes of biological, geological, and geographical change formed a comprehensible pattern.[47]

The first public announcement of Wallace's evolutionary hypothesis was the so-called Sarawak paper, published in 1855: "On the Law which Has Regulated the Introduction of New Species." The article, also known as the "law" paper, has been carefully analyzed in relation to Wallace's zoological observations by several historians; only a few points relevant to his understanding of faunal regions need be made here. Wallace recognized the underlying importance of geographical and geological proximity of closely allied species for the problem of species origin. The propositions of his argument, listed as ten main facts of organic geography and ge-

[45] Charles Darwin and Alfred R. Wallace, "On the Tendency of Species to Form Varieties; and on the Perpetuation of Variation and Species by Natural Means of Selection," *Journal of the Proceedings of the Linnean Society of London* (*Zoology*), 1859, *3*:53–162. Wallace's sketch was mailed to Darwin from Ternate in Mar. 1858. The story of Wallace's sketch and its joint publication with Darwin's extracts is well-thrashed history: George, *Biologist Philosopher* (cit. n. 43); Barbara Beddall, "Darwin and Divergence: The Wallace Connection," *J. Hist. Biol.*, 1988, *21*:1–68; McKinney, *Wallace and Natural Selection;* Brackman, *Delicate Arrangement* (cit. n. 43); Fichman, *Alfred Russel Wallace* (cit. n. 7); Brooks, *Just Before the Origin;* and M. J. Kottler, "Charles Darwin and Alfred Russel Wallace: Two Decades of Debate over Natural Selection," in *The Darwinian Heritage,* ed. David Kohn (Princeton, N.J.: Princeton Univ. Press, 1985), pp. 367–432.

[46] In his autobiography Wallace records that soon after his 1855 "law" paper appeared, his agent wrote to him that he had heard several naturalists express regret that he was "theorizing" instead of collecting more facts: *My Life* (cit. n. 43), Vol. 1, p. 355. It does not seem to have discouraged Wallace from doing so; however, it probably contributed to his circumspect style in writing about common descent. Wallace's collecting activities are described in Wilma George, "Alfred Wallace, the Gentle Trader," *Journal of the Society for the History of Natural History,* 1979, *9*:503–514. Wallace's notebooks and journals are housed in the Linnean Society Library. The first notebook is referred to as the Wallace 1854 Notebook, the second as the Wallace Species Notebook (begun in 1855); the four journals are referred to by their consecutive dates. The species registers are notebooks containing primarily lists of species Wallace collected in the Malay, from 1855 to 1860, and are at the British Museum (Natural History) London. Letters to Samuel Stevens, Wallace's agent in London, are reproduced in Brooks, *Just Before the Origin,* pp. 22–26, 138–139, 140–143, 144–147, 174.

[47] Wallace's lifelong concern with maps and his use of other graphical forms of representation are discussed in Camerini, "Darwin, Wallace, and Maps" (cit. n. 2), pp. 136–188.

ology, were generalizations of known patterns of biological distribution. Wallace's argument about distributions in geographical space and geological time begins with large groups (as in the first excerpt below) and ends with species (the last excerpt). The numbers Wallace assigned to the propositions are included.

1. Large groups, such as classes and orders, are generally spread over the whole earth, while smaller ones, such as families and genera, are frequently confined to one portion, often to a very limited district.
3. When a group is confined to one district, and is rich in species, it is almost invariably the case that the most closely allied species are found in the same locality or in closely adjoining localities, and that therefore the natural sequence of the species by affinity is also geographical.
6. Most of the larger and some small groups extend through several geological periods.
9. As generally in geography no species or genus occurs in two very distant localities without being also found in intermediate places, so in geology the life of a species or genus has not been interrupted. In other words, no group or species has come into existence twice.

The statements lead logically to his tenth and last proposition: "The following law may be deduced from these facts: —*Every species has come into existence coincident both in space and time with a pre-existing closely allied species.*"[48] As can be seen from these excerpts, Wallace carefully avoided a direct confrontation of creation and transmutation theories, although the article is rife with implications of evolutionary relationships. The thread that holds Wallace's law together is proximity: close phylogenetic affinity (Wallace's preexisting closely allied species) corresponds to proximity in geographical space and in geological time.

In the same paper, Wallace conjectured that the Galapagos Islands, an ancient volcanic group, had originally been populated by South American forms that had arrived there by winds and currents. The original species became extinct, being replaced by newly modified forms; Wallace's words—"differently modified prototypes were created"—left undefined the mechanism of creation. But the high degree of endemism of the Galapagos and the faunal and floral alliances with South America were explained by the great antiquity of the islands and the "descent" of their inhabitants from those of the nearest continent. Wallace compared these phenomena to patterns of faunal distribution he observed in the East Indian Archipelago. Among these islands, he hypothesized, a once-continuous fauna became disconnected by the isolating effects of volcanic activity, which separated formerly continuous land masses into islands. The effects of isolation were partial, with some species identical on neighboring islands and some closely allied but not identical. The numerous closely allied representative species on different islands reflected the substantial time that had elapsed since their separation. Wallace's explanation of the fauna of the western portion of the Malay Archipelago (Malacca, Java, Sumatra, and Borneo) took account of biological affinity, geographical proximity, and geologic history:

> The organic results we see in the very considerable number of species of animals common to some or all of these countries, while at the same time a number of closely allied

[48] Alfred R. Wallace, "On the Law which Has Regulated the Introduction of New Species," *Annals and Magazine of Natural History,* 2nd Ser., 1855, *16*:184–196, on pp. 185–186, 186. For discussions of this paper see Barbara Beddall, "Wallace, Darwin, and the Theory of Natural Selection, *J. Hist. Biol.,* 1968, *1*:273–280; McKinney, *Wallace and Natural Selection* (cit. n. 43), pp. 44–53; Fichman, *Alfred Russel Wallace,* (cit. n. 7), pp. 34–45; Browne, *Secular Ark* (cit. n. 7), pp. 171–174; and Brooks, *Just Before the Origin* (cit. n. 43), Ch. 5.

representative species exist peculiar to each, showing that a considerable period has elapsed since their separation. The facts of geographical distribution and of geology may thus mutually explain each other in doubtful cases, should the principles here advocated be clearly established.[49]

In spite of Wallace's circumspect style of addressing the issue of common descent, his intended meaning is clearly implied by a passage in the final paragraph: his law "claims a superiority over previous hypotheses, on the ground that it not merely explains, but necessitates what exists." What would be the necessity (or importance) of the "law" if species were the product of special creation? If Wallace did not believe that species evolved from one another, his law would be trivial. He later wrote that his law paper suggested the "when" and the "where" of evolution—that it could only occur through natural generation—but that the "how" remained unknown.[50]

In Wallace's notebook from this period we find an analogy that secures the notion that his understanding of the origins and distributions of organisms through space and time was in fact conceived of in map imagery: "System of Nature, compared to fragments of a dissected map—a picture or a mosaic—approximation of fragments shew that all gaps have been filled up."[51] What is interesting here is that the map, as a pictorial metaphor, served as a unifying framework for disparate bits of information about insect, bird, and mammalian forms at their respective locations. The conceptual gap (between affinities of closely related forms on different islands and the lack of affinity in species on geographically proximate islands) was closed by putting the pieces of the puzzle together as a map. Given that by this time Wallace believed in common descent, the map metaphor served as a means of combining evolutionary origins and distribution patterns in a single representation.

In the following year, 1856, Wallace visited Bali, Lombock, and Celebes, thus completing his first survey of the western islands of the archipelago. In traversing the narrow strait between Bali and Lombock (see Figure 5), he was impressed by dramatic changes in the distribution of birds; he wrote to Samuel Stevens, his agent in London, of the sharp discontinuity in the fauna of the archipelago: "The Islands of Baly and Lombock, for instance, though of nearly the same size, of the same soil, aspect, elevation and climate, and within sight of each other, yet differ considerably in their productions, and, in fact, belong to two quite distinct zoological provinces." Immediately, this crucial portion of what would become Wallace's line (identified by Darwin in unpublished notes) caught Wallace's attention and remained

[49] Wallace, "Law," pp. 188, 189. Wallace had read Darwin's *Journal of Researches,* probably both the first and second editions: Wallace, *My Life* (cit. n. 43), Vol. 1, p. 256. Wallace's notes about island speciation, with specific reference to the Galapagos, are found in his Species Notebook, and many passages from it are reproduced in McKinney, *Wallace and Natural Selection.*

[50] Wallace, "Law," and Wallace, *My Life,* Vol. 1, p. 355. Chambers made essentially the same point in 1846 in *Vestiges of the Natural History of Creation* (cit. n. 12): "That plan necessitates the facts of distribution, which the other hypothesis does not" (p. 289).

[51] Wallace, Species Notebook, 53r ("r" refers to the pages numbered 1–179 in this notebook; "v" refers to pages numbered 1–70 in the opposite direction of the same notebook). The entry is located after one dated 27 June 1855 and just before one dated Mar. 1856; the probable date of the "System of Nature" entry is Jan. or Feb. 1856. This entry ends a twenty-five-page section that includes a discussion of—more precisely, an argument with—Lyell's ideas on species change; this section of the notebook is discussed by McKinney, *Wallace and Natural Selection* (cit. n. 43), pp. 32–43; and Brooks, *Just Before the Origin* (cit. n. 43), pp. 68, 69.

a location of fundamental importance. In numerous subsequent descriptions of the boundary between the Malay and Australian faunal regions, Wallace expressed the significance of this faunal change by referring to a map. His frame of reference was a map that showed not only the proximity of Bali and Lombock, but the physical similarities of these islands as well. He was also struck shortly thereafter by the absence in Celebes of entire genera and families characteristic of the major islands of the western portion of the archipelago, promptly reporting his findings, along with a disappointing assortment of birds, shells, and insects, to Stevens.[52]

The significance of these findings—that is, the absence of certain groups in Celebes and the distinctiveness of the avifaunas of Bali and Lombock—is best understood when viewed in relation to the assertions of Wallace's 1855 paper. All other things being equal, one would have expected the faunas of Bali and Lombock to have been similar (see proposition 3). How can we understand his statement that these islands belonged to two distinct zoological provinces? We must assume that Wallace *saw* that the strait between these two islands had prevented the natural geographical sequence of closely related forms from developing.

He soon observed another piece of the Malayan faunal puzzle, on his extensive visit to the Aru Islands in 1857. Wallace reported on his observations of the natural history of the Aru Islands in a paper written during and after his six-month residence in the area.[53] He found what he considered to be an unusual degree of identity between the families, genera, and some species of birds and mammals of Aru and those of New Guinea, and similarities (but not identity) with those of Australia. Citing evidence from other regions, he argued that biological affinities between other similarly placed islands and continents (such as Ceylon in relation to India, or Sardinia in relation to Italy) were not as faunistically strong as those between Aru and New Guinea and Australia. Several species of marsupial mammals on the Aru Islands gave further evidence of a former connection with Australia.

At the same time, none of the families of birds and mammals characteristic of the western Malay Archipelago were found on Aru. In seeking the "full development of such interesting details," Wallace boldly contradicted previous hypotheses about zoogeographical relationships, specifically confronting what he saw as a fundamental contradiction in Lyell. He claimed that Lyell's description of the extinction of entire faunas in response to large-scale changes in the earth's environment (e.g., volcanism and mountain building), followed by the resettlement of an *entirely different* set of species suited to the new physical environment, simply did not fit the observed pattern in the Malay Archipelago. On the basis of water depths, physical geography, and, most important, animal distributions, he postulated that the islands had once been part of New Guinea, which itself had been connected to Australia. Some of the information Wallace used to formulate his reconstruction was collected by other

[52] Wallace to Samuel Stevens, 21 Aug. and 1 Dec. 1856, Lombock, in Brooks, *Just Before the Origin,* pp. 138–143. Wallace repeatedly referred to a nonspecific map of the region: "If we look at a map of the Archipelago, nothing seems more unlikely than that the closely connected chain of islands from Java to Timor should differ materially in their natural productions. . . . The remarkable change in natural productions which occurs at the Straits of Lombock, separating the island of that name from Bali; and which is at once so large in amount and of so fundamental a character, as to form an important feature in the zoological geography of our globe." Wallace, *Malay Archipelago* (1877) (cit. n. 19), p. 202. Wallace made a similar reference to this nonspecific map in his description of Lombock: Wallace to Henry Walter Bates, 4 Jan. 1858, in Wallace, *My Life* (cit. n. 43), Vol. 1, pp. 358–359.

[53] Alfred R. Wallace, "On the Natural History of the Aru Islands," *Ann. Mag. Nat. Hist.,* 2nd Ser., 1857, *20*(suppl.):473–485.

naturalists; he almost certainly had Earl's paper on the physical structure of the archipelago.[54] Wallace's resolution of the contradiction between Lyell's prediction and the observed faunas was to apply his own "law": if every new creation was closely allied to some species already existing in the same region, and if gradual extinction and introduction of new species were taken into consideration, then the faunal alliances between the Aru Islands and New Guinea and Australia would follow an expected pattern.

This extensive theorizing in what could have been a purely descriptive natural history of the Aru specimens sent to England demonstrates Wallace's need to seek explanations.[55] His hypotheses were built on the accrual of detailed studies of species distributions and the belief in the modification of species from preexisting ones. Geographical relationships provided the crucial link between biological processes (the production of new species from existing ones) and geological processes (the separation of New Guinea from Australia and a more recent separation of the Aru Islands from New Guinea). In the case of the Aru fauna, as in his other initial researches, he tried to comprehend the system driving his "law." By combining the physical history of the islands with the history of their faunas, he perceived their regional alliances.

Wallace saw another part of the boundary line separating the two major faunal regions by January 1858, nearly halfway through his stay in the region. After traveling to Bali, Lombock, and Celebes, he wrote of the boundary; his clear description reads as if he had seen a line on a map. This lucid account of "Wallace's line" occurs in a letter to his friend Bates from the island of Amboina, dated 4 January 1858. Several phrases are identical with those in his paper on the Aru Islands and with others in his notebook, demonstrating unquestionably the gradual synthesis of his findings:

> In this archipelago there are two distinct faunas rigidly circumscribed, which differ as much as do those of Africa and South America, and more than those of Europe and North America; yet there is nothing on the map or on the face of the islands to mark their limits. The boundary line passes between islands closer together than others belonging to the same group. I believe the western part to be a separated portion of continental Asia, while the eastern is a fragmentary prolongation of a former west Pacific continent. In mammalia and birds the distinction is marked by genera, families, and even orders confined to one region; in insects by a number of genera, and little groups of peculiar species, the families of insects having generally a very wide or universal distribution.

What is most remarkable about this passage is its context. In the same letter he wrote that he was gratified by Darwin's agreement with his 1855 law paper, and he described both his own and Darwin's plans for a fuller explication of the theory. Immediately before the passage just quoted, in regard to the boundary line between the two faunas, Wallace wrote: "Your collections and my own will furnish . . . material to illustrate and prove the universal applicability of the hypothesis. The connection between the succession of affinities and the geographical distribution of a group . . . has never yet been shown as we shall be able to show it."[56]

[54] *Ibid.*, p. 479; see also Earl, "Physical Structure and Arrangement" (cit. n. 37).
[55] See note 46.
[56] Wallace to Bates, 4 Jan. 1858, in Wallace, *My Life* (cit. n. 43), Vol. 1, pp. 358–359, 358.

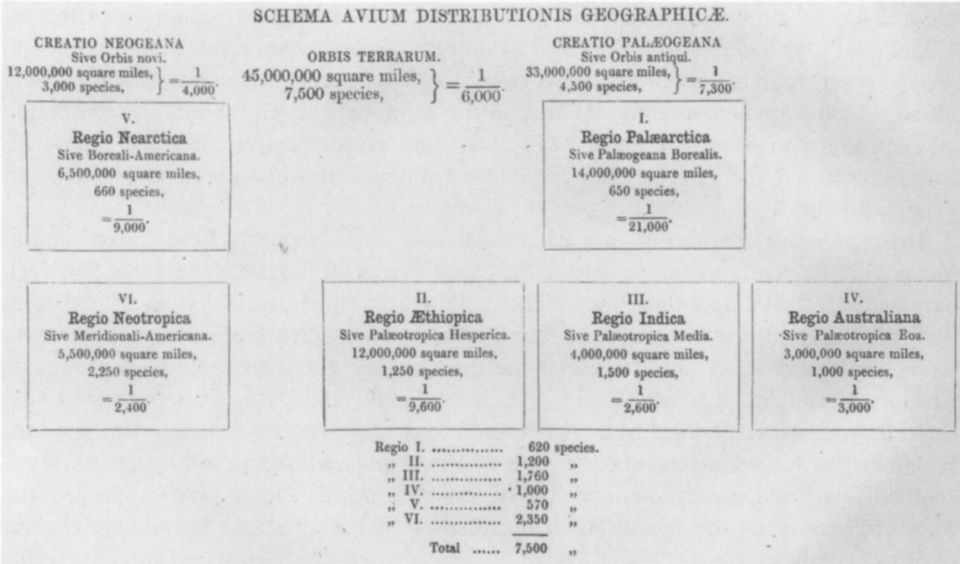

Figure 7. *Diagram from Philip L. Sclater's "On the General Geographical Distribution of the Members of the Class Aves," published in the* Journal of the Proceedings of the Linnean Society (Zoology) *in 1858.*

It is not a coincidence that less than two months after this, Wallace pieced together his famous feverish account of natural selection. Here is a clear connection between the faunal boundary line, Wallace's ideas about evolution (the succession of affinities), and his pivotal theoretical paper of 1858. Apparently, when Wallace wrote in January 1858 "the connection between the succession of affinities and the geographical distribution of a group," he was referring to his evolutionary insight into the phylogenetic relationship of closely allied Asian forms whose ancestry was distinctly different from that of the Australian forms in the eastern portion of the archipelago. Wallace's "law," his line, and his theory of evolution by natural selection were all pieces of the same puzzle and were essentially in place by February 1858.

After writing his natural selection paper, a more confident Wallace turned his attention to extending his biogeographical findings in an evolutionary framework. In a letter written in March 1859 to the journal *Ibis,* he described his views on patterns of distribution in response to the publication of Philip Sclater's paper on zoological provinces of the globe. Sclater described verbally and diagrammatically six regions determined by bird distributions (Figure 7) but did not delineate boundaries between the regions on a map. Sclater could not define precisely the boundary between the Indian and Australian faunas, naming only a few islands that could be allied to one or the other region with some certainty. Wallace's letter corrected and delimited Sclater's regional scheme and extended it to include the whole of the plant and animal kingdoms. He also gave a clear description of his line in presenting the limits of the Asian (i.e., Indian) faunal region: "Its south-eastern limits I draw between the islands of Bali and Lombock, and between Celebes and Borneo, and the Moluccas and the Philippines."[57]

He remarked that the boundary between the Indian and Australian regions was most extraordinary and seemingly inexplicable, dividing as it did an apparently homogeneous region into two provinces that had less in common than any other two upon the earth. The key to this "inexplicable" problem was to understand that the ancestry of Asian forms was largely separate from that of Australian forms—which, however, Wallace did not openly aver—and then to look at a map and consider the number of groups in common for each pair of islands; former land connections would then become clear.

With a solution to the problem of the boundary basically in hand, Wallace elaborated on these ideas in an 1860 paper entitled "On the Zoological Geography of the Malay Archipelago," considering in greater detail the characteristics of the Australian and Asian faunal regions. Although he again agreed with Sclater's general scheme, he sought to refine the boundaries of the two regions "and to call attention to some inferences of great general importance as regards the study of the laws of organic distribution." These inferences dealt with vast changes in the surface of the earth and the hypothesis of evolution. Wallace based his analysis on the presence or absence of a variety of species, including insects, birds, and mammals. He compared the Indian and Australian faunal elements of the eastern and western portions of the archipelago and defined a boundary line only where the two regions are closest: "the Strait of Lombock (only 15 miles wide) marks the limits and abruptly separates two of the great Zoological regions of the globe."[58]

In his efforts to extend the boundary line in a precise manner, Wallace found that the Philippine Islands and Celebes posed difficulties. Later, in 1863, he placed the Philippines in the Indian region despite the lack of some characteristic features, such as mammals. He resolved this problem by assuming a more ancient separation from the Asian continent for the Philippines than for the other eastern Malayan islands. The situation was further confused in 1868, when T. H. Huxley referred to "Wallace's line" but drew a line passing to the west of the Philippines.[59]

Celebes was far more difficult to interpret because of its peculiar mix of Asian and Australian animals and the presence of genera having little or no affinity with those of adjacent islands. This fact suggested that this island was more ancient than the others, but its marked affinities with Africa made it particularly anomalous. Wallace hypothesized that the Celebes group represented the eastern fragment of a former Indian Ocean continent, but he did not commit himself in 1860 as to which faunal region it belonged to, although he had done so in 1859 in the letter to *Ibis* and would do so again in 1863, only to reverse his opinion much later. The faunistic evidence from Celebes led him to conclude in later work that "it will perhaps ever remain a mere matter of opinion" whether it should be considered part of the Asian or Australian region, remarking that "there is no other example on the globe of an island so closely surrounded by other islands on every side, yet preserving such a marked

[57] Alfred R. Wallace, "Letter on the Geographical Distribution of Birds," *Ibis*, 1859, *1*:449–454, on p. 450. Wallace was responding to Philip L. Sclater, "On the General Geographical Distribution of the Members of the Class Aves," *J. Proc. Linn. Soc. Lond.* (*Zool.*), 1858, *2*:130–145.

[58] Alfred R. Wallace, "On the Zoological Geography of the Malay Archipelago," *J. Proc. Linn. Soc. Lond.* (*Zool.*), 1860, *4*:172–184, on pp. 172, 173–174; this paper was communicated to the Linnean Society by Charles Darwin, 3 Nov. 1859.

[59] George, "Wallace and His Line" (cit. n. 1), p. 4.

individuality in its forms of life; while, as regards the special features which characterize its insects, it is, so far as yet known, absolutely unique."[60]

For Wallace, zoological regions reflected patterns of faunal similarity and dissimilarity because of the "fact" of evolution. Given common descent, the proximity of closely allied species could be of great utility in making inferences about geological history. Although his results were inextricably tied to his evolutionary perspective, Wallace did not mention natural selection, evolution, or his own or Darwin's theory in the 1860 article. He stated simply that those who viewed island productions as inexplicable or anomalous were wrong:

> We really require no speculative hypothesis, no new theory, to explain these phenomena; they are the logical results of well-known laws of nature. The regular and unceasing extinction of species, and their replacement by allied forms, is now no hypothesis, but an established fact, and it necessarily produces such peculiar fauna and flora in all but recently formed or newly disrupted islands, subject of course to more or less modification according to the facilities for the transmission of fresh species from adjacent continents.[61]

Shortly after his return to England in 1862, Wallace drew the map delineating his division of the Australian and Indian faunas. He presented the map (see Figure 1) when he read his paper "On the Physical Geography of the Malay Archipelago" to the Royal Geographical Society in June 1863. After describing and delimiting the area, he considered the major geographic features of the archipelago—volcanism, vegetation, climate, bathymetry (water depths), and geological and zoological relations to Asia and Australia. Wallace drew together several lines of evidence in reconstructing the most likely evolutionary history of the region and its inhabitants. As in previous accounts, he called attention to the unusual fact that the striking disparity in the organisms of the two regions did not correspond to their physical or climatic features.

Following Lyell in citing contradictions to the old doctrine that animals and plants are directly dependent on the physical conditions of their environment, Wallace argued strongly that both biological and geological history are necessary to account for observed patterns in the geographical distribution of plants and animals. Just as geological and physical features provide clues to biological evolution, the evolutionary relationships and geographical distribution of animals provide essential clues to former land connections. On this point, however, we find in 1863 a shift from the reliance on major continental movements to a belief in the permanence of the major continental land masses. This shift did not appreciably alter Wallace's reconstruction of past changes in the gradual fragmenting of land from Asia and Australia to form the islands of the East Indian Archipelago. The pro-permanence view provided solid ground for his subsequent treatises on geographical distribution and earned him the full support of Lyell and Darwin. According to Darwin, Wallace's 1863 paper epitomized "the whole theory of geographical distribution."[62]

[60] *Ibid.*, pp. 4–5 (see also note 36 on Darwin and Celebes); and Alfred R. Wallace, *Island Life* (London: Macmillan, 1880), pp. 432, 434.

[61] Wallace, "Zoological Geography of the Malay Archipelago" (cit. n. 58), p. 182.

[62] Darwin to Wallace, 29 Jan. 1865, in Marchant, *Alfred Russel Wallace* (cit. n. 39), p. 132. Martin Fichman describes changes in Wallace's views about the permanence of continents in "Wallace: Zoogeography and the Problem of Land Bridges," *J. Hist. Biol.*, 1977, *10*:45–63.

CONCLUSION

Although the idea of faunal regions existed well before Darwin and Wallace came on the scene, it was Wallace's placement of his line *on a map* that forged evolutionary meaning onto the notion of regions. This meaning does not inhere solely in the line—the map has to be seen in the context of the text in which it appears. The same is true of Darwin's mental maps of faunal regions—they are part of a larger text. I have argued that Darwin and Wallace engaged in a strikingly similar process of evolutionary theorizing about the origins of East Indian fauna, leading to the delineation of a boundary line. Wallace's map served as a conceptual framework, as well as a means of argumentation and, when published, of persuasion.

The tenacious and controversial legacy of Wallace's line becomes clearer when its development is viewed in its close relation to the development of Darwin's and Wallace's evolutionary theories. The East Indian Archipelago is of interest both as a case study in the formulation of Darwin's theory and as an emblem of his sensitivity to the faunal complexities of a region that later became famous in Wallace's and subsequent zoogeographic analyses. Darwin described an approximate boundary between the two major faunal regions in the Malay Archipelago, anticipating one of the critical portions of Wallace's line between Bali and Lombock. The passages relating to the region in the *Origin of Species* make more sense when viewed against the background of his more extensive and earlier notes.

Wallace is less well known for his lifelong insistence on the necessity for precise species distribution maps than he is for his much-disputed line. Detailed knowledge of species distribution was the basis for Wallace's efforts to formulate a general scheme of faunal regions. In one image, Wallace's map redefined and unified the various notions of biological regions current in the first half of the nineteenth century, embodied the evolutionary history of the diverse biota of the East Indian Archipelago, and participated in a genre of visual representation extending into the contemporary culture.

Darwin's and Wallace's mental and actual maps were the table on which the evolutionary scheme was played out, comparable in importance to the geological time scale. The enduring program of drawing boundary lines is a concrete manifestation of the extent to which cartographic constructs provided a framework for the development of the two men's theories and for the subsequent development of evolutionary biogeography.