Darwin's Botanical Arithmetic and the Principle of Divergence, 1854-1858

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The story of Charles Darwin's intellectual development during the years 1837 to 1859 is the most famous and extensively documented story in the history of biology. Yet despite continued interest in Darwin's papers, there are many problems and novel topics still to be explored that will indubitably add to such an account. It is the purpose of this paper to describe a little-known aspect of Darwin's researches during the pre-*Origin* period and to place this in the larger frame of his developing theories. The subject is what was then known as "botanical arithmetic" and its object, so far as Darwin was concerned, was to discover quantitative rules for the appearance of varieties in nature. These arithmetical exercises supplied the context in which Darwin discovered his "principle of divergence." I propose that Darwin's botanical arithmetic also provided a great deal of the content of that principle, or, to speak more precisely, provided the information that disclosed problems which could only be solved by the intervention of an extra "force" in evolutionary theory. On these grounds I make a case for Darwin's moment of discovery during the year 1857 – not, as is often suggested, in 1852.

That Darwin's botanical arithmetic has been neglected by historians is partly his own fault. In *On the Origin of Species*[1] he barely referred to his botanical statistics or the long sequence of calculations which he had undertaken from 1854 to 1858. He compressed and simplified these into a few meager paragraphs, giving his readers only six pages of statistical data to fill out the discussion of "variation under nature" in Chapter II.[2] By contrast, he had originally devoted over fifty tightly written folios, with further supplementary notes and tables, to the same theme in the "big species book," *Natural Selection.*[3] The topic must

1. Charles Darwin, *On the Origin of Species by Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life* (London: Murray, 1859); facsimile edition with an introduction by Ernst Mayr, Cambridge, Mass.: Harvard University Press, 1964.
2. *Origin*, pp. 53-59.
3. Robert Stauffer, ed., *Charles Darwin's Natural Selection, Being the Second*

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have been important at that time for the exposition of his theory, since the contents of *Natural Selection* provided the facts which Darwin intended to present to a predominantly scientific audience. Here were all his closely reasoned and intricate examples of selection at work, his expectations and qualifications, and his references to past and present authors. And here the "statistics of variation" play an important part in furthering evolutionary arguments.

There is still more to Darwin's statistics of variation than even this intended chapter for *Natural Selection*. Interpretations of this area of Darwinian thought can be additionally enlarged by considering the extant notes and jottings, the calculations themselves, and, in particular, by referring to Darwin's correspondence with his botanic friend Joseph Hooker. To appreciate the role which Darwin intended botanical arithmetic to play in his system, it is necessary to return to the original sheets of figures, the notes written to himself and to his advisors, and to his anxious correspondence with Hooker about the practical and philosophical considerations which could – and did – affect the inquiry. The Darwin archive is rich in such materials and furnishes an unexpected opportunity to look closely at how Darwin worked on a set of problems during the interregnum between the "Essay" of 1844 and the *Origin.*[4]

BOTANICAL ARITHMETIC

As a young man Darwin was certainly familiar with the basic tenets of that distributional procedure which went under the name of botanical arithmetic, although not perhaps with the command of statistical method that his contemporaries were then exhibiting. Botanical arithmetic was to biology what mathematics was to the study of electromagnetism, heat, or light; it promised great achievements in the organization and synthesis of intractable data, and successfully harnessed the growing enthusiasm for figures and numbers which was so much a part

Part of His Big Species Book Written from 1856 to 1858 (Cambridge: Cambridge University Press, 1975); subsequently referred to as *Natural Selection*. See pp. 134-164.

4. Darwin's papers on these subjects are contained in Cambridge University Library, Dar 15.1 and 15.2, Dar 16.1 and 16.2, Dar 45, and Dar 205.2 to 205.5, 205.9 to 205.10 inclusive (See Darwin Papers – Supplementary Handlist). His letters to Hooker of 1843-1858 are in Dar 114, and Hooker's replies in Dar 100, plus a few at the end of Dar 104. Owing to the forthcoming edition of Darwin's correspondence some of these manuscripts are subject to reorganization.

of nineteenth-century life. Mathematics in astronomy, for instance, had made that subject the queen of the sciences, and it offered the same kind of glory for other physical investigations. In a larger context, figures and probabilities were even then changing the face of economics, life insurance, medicine and medical policy, legislation, and philanthropy. Elsewhere, Laplace and Quetelet each in his own way had stimulated the development of modern statistics, and this was rapidly acquiring all the institutional trappings of a formal discipline. And at yet another level, figures were the source of great public interest and controversy – in the British Isles at least – in that the number of human inhabitants was the subject of fierce debate through the earlier years of the nineteenth-century. More than any other contemporary topic, arguments over population brought simple arithmetic into the lives and homes of the people. With this sort of background it is easy to see that arithmetical procedures in the biological sciences were part of a generalized push toward numbers at this time.[5]

Botanical arithmetic was a technique specifically designed to cope with biogeographical data, and, as the name given to it might imply, it was concerned with the numerical facts of distribution.[6] At its most basic level, botanical arithmetic (a term coined by Humboldt in 1815)[7] consisted merely of counting up all the species in area A and all those in area B, and itemizing how many were held in common. Certainly this was a useful tool because a country with a hundred species is quite clearly different from another with tens of hundreds, and regions with six or sixty species in common are evidently related in different degrees.

Yet it did not get naturalists very far, and so Humboldt,[8] followed

5. For a general survey see Michael Cullen, *The Statistical Movement in Early Victorian Britain* (London and New York, 1975), and Susan F. Cannon, "History in Depth: The Early Victorian Period", *Hist. Sci., 3* (1964), 20-38; this article is expanded in her *Science in Culture: The Early Victorian Period* (London and New York, 1978), pp. 225-262.

6. Janet Browne, "C. R. Darwin and J. D. Hooker: episodes in the History of Plant Geography, 1840-1860," Ph.D. diss. University of London, 1978, Chaps. 3 and 4; and forthcoming from Yale University Press.

7. Alexander von Humboldt, *Prolegomena* to his *Nova Genera et Species Plantarum Quas in Peregrinatione ad Plagam Eaquinoctiatem Orbis Novi* ... (Paris, 1815-1825), p. xiii.

8. Alexander von Humboldt, *Essai sur la géographie des plantes; accompagné d'un tableau physique des régions équinoxiales* (Paris, 1805), and facsimile edition of the first part only by Society for the Bibliography of Natural History, Sherborn Facsimile 1 (1959). Humboldt gave a more elaborate treatment to the same topic in *De Distributione Geographica Plantarum Secundum Coeli Temperiem et Altitudinem Montium, Prolegomena* (Paris, 1817).

closely by the elder Candolle,[9] and Robert Brown,[10] established the practice of converting such absolute numbers into statements of a proportional kind which could then be arranged with others in a table. Taking a model from human population surveys, all the naturalist had to do was to calculate the ratio of one group of plants (such as a family) to another (one of the major botanical kingdoms, or the whole flora of the region in question). These figures were then set down in such a way that the relative incidence of, say, grasses, could be traced through several geographical zones. In one of Humboldt's tables, for example, the ratio of Gramineae to the rest of the phanerogamous plants in equatorial America was stated to be 1:15, where in the Temperate Zone it was 1:12 and in arctic regions 1:10. Evidently this family played approximately the same role in floras belonging to all three latitudinal belts. With such tables in their hands, botanists could reflect on the causes of the patterns which they saw, and approach what was in their opinion a truly scientific study of distribution.

One ratio in particular became popular among geographical botanists and soon found its way into zoological and paleontological surveys. As introduced by Brown[11] in his analysis of the Australian flora in 1815, and popularized by Augustin de Candolle in his *Essai élèmentaire de gèographie botanique* (1820),[12] this was the calculation of the average number of species in a genus. It allowed the relative spread of species in any area to be discerned. For both Brown and Candolle this relationship between species and their genera had something to say about the distribution of "creative power" over the earth, although, it must be said, they held different views about the significance of the figures that they obtained.[13]

9. Augustin de Candolle, "Géographie botanique" in *Dictionnaire des sciences naturelles*, ed. F. C. Levrault, XVIII (1820), pp. 359-436, and reprinted as *Essai élèmentaire de géographie botanique* (Paris and Strasbourg, 1820). In one form or another this was an essential volume for the library of any self-respecting naturalist; both Darwin and Joseph Hooker owned well-thumbed copies. Gareth Nelson has recently published on Candolle; see "From Candolle to Croizat: Comments on the History of Biogeography," *J. Hist. Biol., 11* (1978), 269-305.

10. Robert Brown, *General Remarks, Geographical and Systematical, on the Botany of Terra Australis*, in Matthew Flinders, *A Voyage to Terra Australis, 1801-1803, in "HMS Investigator"* (London, 1814), and also issued separately the same year.

11. Brown, *General Remarks*, pp. 35-36, 55.

12. Candolle, "Géographie," pp. 400-410.

13. Brown, for instance, took an increase in the number of species per genus over some well-defined topographical space to indicate an increase in the action of

But whatever the metaphysical conclusions to be drawn from these simple calculations, the ratio of species to genus became an important tool for naturalists and a *sine qua non* of distributional essays by the early 1830s.

So, at Cambridge, John Henslow would not have neglected to teach his eager pupil the rudiments of this popular and versatile technique. If this were not enough, Darwin's youthful enthusiasm for Humboldt's works would have insured that he was made aware of the way in which at least one eminent scholar was discussing and displaying distributional data.[14] Moreover, even if he rejected his early experiences as old-fashioned, Darwin rapidly came up against the same technique used in an exciting variety of ways in Charles Lyell's *Principles of Geology*.[15] In notes made during the *Beagle* voyage, in the immediate postvoyage publications, and in the species notebooks of 1837-1839, Darwin made it clear that he was familiar with the scope and application of a statistical natural history.

There is much that could be said about Darwin's first use of botanical arithmetic and the ways in which it impinged on his ideas about transmutation, but it is, in my opinion, sufficient merely to point out that Darwin employed numerical arguments of this kind whenever and

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a creator. Each region, for him, possessed a "centre" or "focus" of creation where species were most plentiful, and from which center they had diminished (relative to genera) with distance. Candolle, by contrast, saw the incidence of genera to be the operative figure and suggested that the more genera there were relative to species, the more "creation" had taken place. He compared the number of genera in Tenerife with the number in France and found that islands were in this respect comparatively richer than continental land masses, although, of course, they were normally very poor in absolute terms. To him, islands like Tenerife were spots where creation had acted to produce greater diversity in the population and so, accordingly, these landforms constituted his "foci of creation." Candolle hence directed the attention of subsequent naturalists – and here we must not exclude the young Darwin – to islands and archipelagoes as objects of special interest for the study of creation.

14. Darwin cited Humboldt's *Personal Narrative of Travels to the Equinoctial Regions of the New Continent during the Years 1799-1804*, trans. Helen Williams (London, 1814-1829), with pleasure: Nora Barlow, ed., *The Autobiography of Charles Darwin, 1809-1882* (London, 1958), pp. 67-68.

15. Charles Lyell, *Principles of Geology, Being an Attempt to Explain the Former Changes of the Earth's Surface by Reference to Causes Now in Operation* (London: Murray, 1830-1833), III, 18-22, 31-32, 53-59. This work must be the most famous gift in the history of science, since Henslow pressed vol. I into Darwin's hands before his departure on the *Beagle*; Barlow, ed., *Autobiography*, pp. 77, 101.

wherever he felt that they might further his case or exemplify a problem. Readers of the notebooks will be able to recall several instances which establish that Darwin was not only *au fait* with current notions about the ratio between species and genera, but also able to produce competent mathematics when required to do so. In a recent paper Malcolm Kottler describes Darwin's reference to Leopold von Buch's giving the ratio of species to genera in the Canary archipelago, and his note to calculate his own cases of the Keeling Islands and the Galápagos.[16] David Kohn documents Darwin's attempts to work out the chance of one species being represented in populations some one or two thousand years hence.[17] Nor, of course, can one forget the use to which Darwin put the most famous ratio of all – that individuals increase in number in a geometric fashion when food supplies only do so arithmetically.

It is more appropriate to turn to a later period in Darwin's life, and to the manner in which he took up (in 1854) an arithmetical program of investigation that was based on calculating the average number of species to be found in selected genera. This was to metamorphose into a systematic examination of the relations between species and varieties, and of the genera to which they belonged, that was quite different in depth and scope from his previous excursions into statistics. Where before his calculations had been merely occasional and incidental to the central theory of transmutation, here he was to be occupied for the next four years with a topic which ultimately led to a substantive modification of his views about the workings of evolution.

BARNACLES AND ABERRANCE, 1854-1855

In a roundabout way it was the study of barnacles which stimulated Darwin to undertake numerical inquiries into nature. The cirripede study showed Darwin that, contrary to his written opinion of 1844, there *was* a great deal of variation to be found in the natural world. In

16. Malcolm J. Kottler, "Charles Darwin's Biological Species Concept and Theory of Geographical Speciation: The Transmutation Notebooks," *Ann. Sci.*, *35* (1978), 275-297, especially pp. 285-286, where he discusses Leopold von Buch's *Description physique des Isles Canaries, suivi d'une indication des principaux volcans du globe* . . . , trans. C. Boulanger (Paris, 1836). Darwin referred to this work in the B notebook, Dar 121, pp. 156-158.

17. David Kohn, "Charles Darwin's Path to Natural Selection," Ph.D. diss., University of Massachusetts, 1975, in the context of explaining Darwin's curious metaphor of a "fine family" of twelve brothers and sisters, in the B notebook, Dar 121, pp. 146-150.

the "Sketch" and "Essay" he had asserted that very little variation was seen in a "wild state," and had repeated over and over again that "most organic beings in a state of nature vary exceedingly little."[18] Consequently, he had relied on geological and geographical changes, either directly or indirectly (the latter by stimulating a reassociation of individuals into different patterns), to "unsettle the constitution" of wild animals and plants. These "unsettling" agents were presumed analogous to the supposed effects of domestication on the reproductive systems of organisms under any sort of cultivation. Now, however, by 1854, he was convinced that organisms in their natural state really did vary without any such "unsettling" forces.

Such a discovery weakened Darwin's arguments as put forward in the "Essay" where he drew a close analogy between selection in the wild and under domestication. A change in circumstances in both cases was assumed to lead to a "certain plasticity of form," and the reproductive system was stimulated to produce variant offspring upon which the selective forces operated. The crucial link was that variants, in this scheme, arose only when the reproductive system was disturbed. When armed with the knowledge that varieties pop up in the wild with no reason for their origination, Darwin saw that the central analogy of his thesis was invalid. At the very least he had to return to the "Essay" and examine his arguments in the light of this new information. So, in September 1854, just as soon as he had completed the final tasks related to barnacles, he did precisely that.

On September 9 he recorded in his journal that he "began sorting notes for species theory"[19] and turned to the biggest question that his revised version of the "Essay" would have to answer. That is, he took up the problem of how a superabundance of variation in the wild bore on his previous statements about the origination of species, and how speciation and extinction occurred when there were no geological or geographical changes necessarily invoked by the theory. Why, if there was a great deal of variation in nature, did species become extinct? Surely their variability ought to permit modifications to suit changing environments. Reopening the question of extinction, he moved to study forms which vividly represented a past history of extinguishing action. He took up the topic of aberrance.

18. Gavin de Beer, *Charles Darwin and Alfred Russel Wallace: Evolution by Natural Selection* [a transcript of the "Sketch" of 1842 and the "Essay" of 1844] (Cambridge: Cambridge University Press, 1958), pp. 95, 112-113, 114, 133-134.

19. Gavin de Beer, "Darwin's Journal," *Bull. Brit. Mus. (Nat. Hist.) Hist. Ser., 2* (1959), 1-21; see p. 13.

It was, he thought, the size of a genus which made it appear to be aberrant. The platypus or the penguin under this view should muster only a few – perhaps only two or three – species in every genus. Writing to Hooker at the end of 1854,[20] he described how he anticipated that a simple calculation of the number of species in several atypical genera should add up to an average which was considerably less than the usual number of species that might be expected – a figure normally taken as around seven or eight species per genus. Working from notes and lists supplied (via Hooker) by George Bentham[21] and George Waterhouse,[22] he found that this was indeed the case. Aberrant genera of weevils possessed about five species on average, where "normal" genera contained just over ten. So the aberrant groups were, in his eyes, plainly experiencing an extinguishing force that was removing species, one by one, from what must have once been a "normal" healthy complement of species.[23] Despite any variability which aberrant forms may

20. Francis Darwin and A. C. Seward, ed., *More Letters of Charles Darwin: A Record of His Work in a Series of Hitherto Unpublished Letters* (London: Murray, 1903), I, 86-87, where Francis Darwin gives only the year (1855) and I date as Dec. 11, 1854. This book is subsequently referred to as *More Letters*.

21. Dar 114, letter 156, and *More Letters*, I, 87. See also Dar 114, letter 159, and Hooker's reply, Dar 205.9.

22. *More Letters*, I, 82-84. These lists and notes are in Dar 205.9, relating to a catalogue of weevils: C. J. Schönherr, *Curculionidium Disposito Methodica cum Generum Characteribus* . . . (Leipzig, 1826), and republished as *Genera et Species Curculionidium* (Paris, 1833-1838). The edition Darwin used was cited by him as being edited by H. Jekel and published in 1849. I cannot, however, find any further details about this edition.

23. This purely arithmetical statement of aberrance was – albeit temporarily – of some significance for Darwin. Here he was demonstrating that, despite any amount of variability in nature, genera still tended to go extinct by the gradual depletion of their species. Accessory to this comforting conclusion was the added benefit that he might henceforth be able to talk about classification schemes in a solely quantitative, and not qualitative, manner. In an attempt to rebut the mystical quinarian system of W. S. MacLeay and his follower William Swainson, Darwin could show that there was no intrinsic property of "oddness" possessed by some forms and not by others. Furthermore, organisms could be grouped together in hierarchical (not circular) systems simply on the grounds of how much extinction had taken place to make the "gaps" between the branches of the tree of life more distinct. A short while later, however, Darwin was complaining to Hooker that this notion for aberrance would not do. Even if *Ornithorhynchus* or *Echidna* had a healthy complement of some dozen species or more, they would not be any less aberrant in classificatory terms. Hooker wrote that if one multiplied an anomalous form by 100 then one got a "normal" group in the eyes of taxonomists (Dar 205.9), to which Darwin responded that multiplying the monotremes by as few as twelve would not make them any less aberrant (*More Letters*, I, 86-87).

show in their structure, he concluded, they must eventually become extinct.

Excited by this first encouraging essay into numerical assessment, Darwin also thought over the second and more important part of his new problem of unlimited variation in nature. Extinction did not seem to be greatly affected by the information, but what of speciation?[24] During November 1854 in a note to himself he reflected that there would be some symmetry in looking at speciation as the opposite of extinction: "Assuming species approximately constant, if extinction has fallen near and around the aberrant genera, then creation has fallen on the typical and larger genera. We can look far into future by looking to the larger groups."[25] Leaving the question of aberrance for these more novel pastures, Darwin devised a further arithmetical test to see whether "creation" had fallen on the larger groups in nature. Echoing the work done by Brown and Candolle in this respect, he calculated the ratio of species to their genus, but with a peculiarly Darwinian twist. He took species that presented varieties (and that could therefore be understood as evolving forms) and counted the number of each species' congeners. He expected to find that species with varieties appeared in genera that had many species. If the ratio of species to genus was low for forms suffering extinguishing action, then it ought to be high for actively speciating forms. Darwin's first calculations did indeed indicate something of this nature; drawing his computations on Hooker's *Flora Novae Zelandiae* to a close, he concluded that "the genera having one or more species presenting varieties marked by Greek letters, contain

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Nonetheless Darwin went on to further computations based on the aberrant genera in John Lindley's *Vegetable Kingdom* (3rd ed., 1853) with crosschecks on Bentham's and Waterhouse's material, being particularly interested to see whether the results still came out favorably if he removed monotypic genera from the sample. These papers are scattered through the various portfolios contained in Dar 205, the majority being in 205.9. Darwin did not confine himself just to the size of aberrant genera; he also attempted to work out if they ranged more or less widely than expected – an undertaking occasioned by his note on Swainson, Dar 205.5. To these ends he assessed how many "provinces" an aberrant genus ranged over when compared with the range of normal genera, as calculated from a list of provinces given by H. C. Watson in his *Cybele Britannica; or British Plants and Their Geographical Relations* [vol. I-III only] (London, 1847-1852).

24. I am here, and will continue to do so, using the term "speciation" in its loosest possible sense to convey merely the process of change by which new species come into existence. I do not wish to give the word its modern technical meaning of being a counterpart to divergent evolution.

25. Dar 205.5, unfoliated slip dated Nov. 1854.

rather more than twice the species on average, than do those genera with no varieties."[26]

Figures such as these were clearly going to be significant for Darwin. The autumn of 1854 had seen him anxiously reexamining the arguments of the "Essay" and turning over the problem of variation in the wild: he needed to find a mechanism for the origination of variant offspring, now that there was no requirement for the "unsettling" agency of geological change; he had to have something that would allow a transmission of biological change, now that he had relinquished the isolating factors of persistent elevation and depression of land relative to sea; and he had to decide in what manner his natural variants turned into species. Over the years that lay ahead Darwin found answers in, respectively, the need for cross fertilization between organisms at some stage in their life cycle, the mechanism of "pangenesis,"[27] and in his botanical arithmetic on the incidence of varieties. By studying varieties and, if possible, finding regularities in their appearance in certain genera or species, Darwin could approach a fuller understanding of the mode of evolutionary change. If there were any "rules" to variation and to the appearance of varieties he wanted to know about them, and this new line of investigation seemed to auger well.

VARIETIES AND LARGE GENERA, 1855-1857

From the summer months of 1855 through early 1857, in the interludes left to him from other projects and the composition of his "big species book," Darwin was occupied with the statistics of variation. His work revolved around the idea – often expressed in notes and letters – that varieties were simply "little" species. As mentioned above, he found that they seemed to appear in genera which had a large number of species. Continuing on from this discovery, Darwin attempted to determine if they also appeared in greater numbers in such genera – the correlation being important to him, for it showed that where there were

26. Dar 16.2, fol. 241, referring to J. D. Hooker, *Flora Novae Zelandiae* (London, 1853-1855), part 2 of *The Botany of the Antarctic Voyage of "HMS Erebus" and "Terror" . . . 1839-1843* (London, 1844-1860).

27. There is a sizable literature on Darwin's concept of variation, and its transmission: Peter Bowler, "Darwin's Concept of Variation," *J. Hist. Med., 29* (1974), 196-212; Gerald Geison, "Darwin and Heredity: The Evolution of His Hypothesis of Pangenesis," *J. Hist. Med., 24* (1969), 375-411; Peter Vorzimmer, "Darwin's Ecology and Its Influence upon His Theory," *Isis, 56* (1965), 148–155.

many species so there were correspondingly high frequencies of variation, and therefore the potential for further speciation.

In his calculations this line of thought took the form of demonstrating that large genera presented above the average number of varieties, or, alternatively, a great number of forms which ranked in between varieties and species. The proposition can be reconstructed as follows: if there were many variations in wild organisms (as the barnacle work showed to be the case) then there ought to be many varieties; if there were varieties, then he could expect to find some that were more strongly differentiated from the parent that constituted "incipient" species; and one step further on, he might also expect to find pairs or triplets of closely allied species which were neither varieties nor fully fledged species, but were somewhere in between. Not content to rest his case on a few and perhaps eccentric examples, Darwin set out to explore systematically the whole issue, twisting and turning to look at it from as many angles as possible, working his way through a pile of printed catalogues and an enviable richness of ideas. He calculated just about every relationship he could think of which included large genera and varieties somewhere in the proposition. He was gratified to find that the computations all pointed in the same direction: genera with many species were indeed groups in which more variations occurred, and in which "incipient" species and closely allied species could be found. In every one of the twelve or so volumes that Darwin examined this relationship held. He worked his way through the floras which he both knew and trusted, and which happened to be in his collection, such as Henslow's *Catalogue of British Plants* (second edition, 1835), Hooker's *Flora Antarctica* (1844-1847) and *Flora Novae Zelandiae* (1853-1855), and Hooker and Thomson's *Flora Indica* (1855), in addition to works given to him by his recent acquaintances the American botanist Asa Gray and the irascible British botanist Hewett Cottrell Watson. A typical calculation based on Gray's *Manual of the Botany of the Northern United States* (1848) ran as follows: "Now Asa Gray has marked for me 115 genera with 733 close species . . . these 115 genera have on average 115 [into] 733 [species] which equals *6.37* [species per genus], but the other genera with which this number is comparable, have on average *4.67*; hence the genera with "close species" have 1.7 on average more species."[28] That is, the genera with the closely allied forms among their species had more species per genus (6.37) than those

28. Dar 15.2, fol. 19. Fols. 17-19 are concerned with Darwin's earliest calculations on Gray.

genera which simply presented varieties (4.67). To Darwin these figures implied that of all the genera in the catalogue which could be assumed to be evolving – in that they possessed varieties – it was the larger ones which were doing so, as gauged by the occurrence of close species.

Under the influence of reading Alphonse de Candolle's substantial *Gèographie botanique raisonnèe* soon after its publication in August 1855, Darwin was led to expand his own survey of the incidence of varieties to include Candolle's ideas about geographical range and the frequency of individuals.[29] However, where Candolle used families (or what he called "natural orders") to calculate his points, Darwin preferred to use genera.[30] Genera with many species, he found, were often ones which were mundane and which also possessed many individuals in each constituent species. Such a correlation might perhaps have been arrived at by a priori reasoning, but because there were obvious pitfalls Darwin needed to establish the point to his own satisfaction. There were, he knew, contrary instances. There were cases of genera which had only one or two species being spread very widely over the earth, such as the tulip tree, and other instances of small genera with very abundant species, such as the earwig or penguin. Yet working through his floras, following the example of Candolle, Darwin confirmed a slight but consistent tendency for the two characters of a great geographical range and a multiplicity of individuals to appear in the larger genera. Writing on the latter point, for instance, Darwin considered the common species in Boreau's *Flore du centre de la France*: "With respect to

29. Darwin even acquired several of the floras used by Candolle for arithmetical purposes: Alexandre Boreau, *Flore du centre de la France, ou description des plantes qui croissent spontanément dans la région centrale de la France* (Paris, 1840); August E. Fürnrohr, *Flora Ratisbonensis oder Uebersicht der um Regensburg wildwachsenden Gewächse* (Regensburg, 1839); and F. A. W. Miquel, *Disquisitio Geographico-Botanica de Plantarum Regni Batavi Distributione* (Leiden, 1837). These were all used for various calculations by Alphonse de Candolle in his *Géographie botanique raisonnée, ou exposition des faits principaux et des lois concernant la distribution géographique des plantes de l'époque actuelle* (Paris and Geneva, 1855), pp. 463-471. See especially Darwin's copy of Candolle at the Cambridge University Library, and his manuscript index tipped in, inside the back cover of vol. II, where he listed these three works as being of particular interest.

30. Darwin's copy of Candolle, p. 528, Darwin slip pasted in. The full text reads: "I think if families are used, whole world or continent should be used as field of comparison. But I cannot say why I think so." He also wrote beside these tables, "It would be very curious to see what result would follow from *genera* calculated in this manner or by averages," ibid., p. 465. There are similar marginalia on pp. 465, 466, 467, and a further note reminding himself to skim over these pages "before making any calculations," ibid., p. 476.

plants marked C.C. as common, of the 413 genera, 180 have one or more species marked C.C. and these 180 genera include 736 species and therefore each genus has on average 180 [into] 736 [species] which equals *4.08* [species per genus]. Consequently the remaining genera (413-180=) 233 genera, including (1156-736=) 420 species, and each genus has on average 233 [into] 420 [species] which equals *1.80* [species per genus]."[31] These figures demonstrated that genera with common species (as denoted by the symbol C.C. in Boreau's catalogue) possessed an average of around 4 species per genus, whereas the remaining genera without such common species presented only 1.80. Clearly, 4 was more than 1.8, so the abundant species tended to occur in the larger genera.

In this extended survey of large genera and varieties there were several notable conclusions which Darwin could draw out to exemplify separate aspects of his current theories. His botanical arithmetic, for instance, explained much that was problematic in geographical distribution. Darwin made immediate use of these results in his chapter on geographical distribution for *Natural Selection*, composed during the earlier part of 1856 and revised occasionally thereafter to include new information, such as that derived from Asa Gray's "Statistics of the Flora of the Northern United States," published in September 1856.[32] Under the conviction that it was the big groups in nature that were more widely spread, Darwin could explain the origin of closely related yet geographically mutually exclusive "representative" species by asserting that as a species spreads out over a great area it will meet with different conditions, which stimulate local adaptations. He could also differentiate between genera that were small because of extinction among the ranks and genera that were small because they were at the start of their "life" by determining whether there were "discrete" or "close" species in them. The latter implied a "new" genus that was varying and producing more species, while the former indicated an "old" one that was gradually dying out through the extinction of first one and then another of its species, so rendering the existing forms rather distinct from one another. Furthermore, the same argument was applied to explain why some organisms were rare and others abundant, although here Darwin conceded that there were many additional factors which allowed, say, a plethora of individuals to be found in small (and

31. Dar 15.2, fol. 4.

32. *Amer. J. Sci.*, 2nd ser., *22* (1856), 204-232; *23* (1857), 62-84, 369-403. Noted in *Natural Selection*, p. 533.

supposedly "old") genera such as the earwig and platypus. Equally, he could explain the origin of markedly disjunct species by supposing them to be "remnants" left behind when a large and correspondingly widely spread genus died out.

Moreover, at a deeper cognitive level Darwin must have recognized that here were his "rules" of variation. From these arithmetical regularities which linked varieties to the larger and more widely dispersed genera, perhaps he could now reapproach the question of the mechanism of heredity. What was it that made these genera vary in such a consistent manner? Here was a query which positively demanded an answer, and one to which Darwin was giving his special attention at the end of 1856 when he was struggling to write up material on the "possibility of all organisms crossing: on susceptibility of reproduction to change," for Chapter III of *Natural Selection*. In these pages he attempted to demonstrate that all animals and plants cross-fertilized one another at some stage in their life cycle, and that *this* process was the cause of subsequent variation. Cross fertilization therefore replaced his earlier views about physical changes in the environment which ultimately unsettled the reproductive system. But he still had no real evidence to deploy in order to answer the question: Why vary? No evidence, that is, beyond the clues which emerged from his work on large genera.

These clues must have been tantalizing. It seemed to Darwin that the properties of large genera that he had isolated by arithmetical considerations indicated that these forms were "best adapted" to their countries. Variation, it will be remembered, was the raw stuff of speciation for Darwin. It was on variants that natural selection worked to produce forms that were well adapted to their surroundings, and an accumulation of such adaptations "made" a species. If, therefore, most varieties occurred in the larger genera, then these taxa should be the "best adapted" to their local environment, and small genera should be less adapted.

Darwin tried to explain this idea by relating the quality of adaptation to some physical attribute that genera might possess, such as the capacity to range widely over diverse terrains. Writing in 1855 of widely spread species and noting that they seemed to exist through geological time for a longer period than most species, he pointed out that this fact could be explained by linking wide range with "high" adaptive powers: "It is" he wrote, "that wide spread [range] shows that [form is] best adapted and therefore survives longest."[33] And again, thinking on the

33. Dar 205.9, unfoliated slip dated Dec. 1855.

reverse case of small genera which were strictly local in geographical extension: "Genera with few species show that those peculiarities which the species have in common *are not so well adapted* to the country [being] inhabited, as those genera with many species; and hence they do not range so far."[34] So Darwin was associating the size of a genus with its potential and actual adaptation, measured in this particular instance by geographical range but just as easily gauged by any of the parameters which he had introduced into his botanical arithmetic – the number of varieties, for example, or the abundance of individuals would have done just as well here. Adaptation was the factor which linked all these things together.

Darwin used this notion of adaptation to explain how his numerically large genera eventually turned into smaller ones, and vice versa. He called this the "coming in and out" of genera in the history of life, and it signified the process of the "birth" of a "new" genus out of an existing group of species, and the latter's subsequent decline into an "old" genus. For Darwin in 1855 and 1856 this process was not so much a splitting up of one great spectrum of species – as in his principle of divergence – as it was a process of breaking off, where one or perhaps two well-adapted species devolved from the parent genus. This latter set of species was thought to die out as the "break-away" forms flourished and grew. Such notions are markedly different from those which he was to put forward in the *Origin* under the label of "Divergence," and it is therefore important to understand precisely what it was that Darwin meant at this point in time, during 1855 and 1856.

It seems that Darwin envisaged that a large genus, and consequently one which spread widely, would have some species at the edge of its range which were exposed to "many conditions and several aggregations of species." They were exposed to the elements that encouraged struggle and competition. Should such a species vary, as species belonging to large genera were likely to do, he continued, in a note to himself: "it may be selected to fill some new office, and mere chance would determine the origin in a large genus of some new and good modification."[35] To paraphrase, the introduction of a new and good adaptation to a satellite species at the edge of a large geographical range would lead

34. Dar 205.5, unfoliated slip dated Feb. 1855. My italics.

35. Dar 205.5, unfoliated slip dated Nov. 1854. Darwin was still holding to this view in May 1856, as is evidenced by a page headed "Classification" and beginning, "As only few individuals of species survive and propagate, so it seems only a few species in a group survive and propagate: simply because in struggle only few get right variations," ibid., unfoliated slip dated and headed as above.

to the formation of a new line of development and, ultimately, to the rise of a new genus and the demise of the old.

Certainly this was how Darwin explained such ideas to Charles Lyell, when pressed to give details of his theory of transmutation in 1856. Lyell recorded the conversation in his "Scientific Journals": "Genera differ in the variability of the species, but all extensive genera have species in them which have a tendency to vary. When the conditions alter, those individuals which vary so as to adapt them to the new circumstances, flourish and survive while the others are cut off."[36]

This view, of course, was not unfamiliar to Darwin. He had used such an explanation as early as the notebooks, and consistently ever since that time. Ernst Mayr and others have rightly emphasized the significance of geographical isolation in this respect and how Darwin used it as the process by which divergence of character could take place. But here it can be seen how deftly Darwin wove new findings – such as the statistical evidence for variation – into the fabric of his earlier thought, and how he expanded and embroidered his ideas as fresh information was made available through his own researches. In 1856 he seems to have had a fully integrated and workable scheme to account for the origination of new genera from the old.

To weave everything together was now imperative for Darwin. Lyell had encouraged him to begin writing up his theories in the spring of 1856, and by the autumn of that year he had already finished two of the less complicated chapters – those on variation under domestication and on geographical distribution. But difficult chapters were in the offing. Would his ideas about the size of genera and the number of varieties hold up under the critical examination which he gave to all his written materials? More significant – since they were concerned with the very heart of his arguments – would his suggestions for the growth of genera and their inevitable fragmentation into smaller genera explain the way in which groups of species increased in number, diverged from each other, and eventually died out as others took their place? Could he explain the history of life?

DIVERGENCE WITHOUT A "PRINCIPLE"

The crux of Darwin's principle of divergence in 1859 was an increasing differentiation between individuals. This accounted for the

36. Leonard G. Wilson, *Sir Charles Lyell's Scientific Journals on the Species Question* (New Haven and London: Yale University Press, 1970), p. 54.

divergence of varieties, one from another, and the same process, in turn, led to a divergence between species and other higher taxa. In the *Origin* and elsewhere Darwin stated that it was the most *diverse* offspring which managed to live and contribute successfully to the next generation: "The more diversified the descendents from any one species become in structure, constitution and habits, by so much will they be better enabled to seize on many and widely diversified places in the polity of nature, and so be enabled to increase in numbers."[37] In short, the most different variety in any bunch would be the one favored by natural selection.

To make this idea perfectly distinct in the *Origin*, Darwin then invoked the well-known notion of the benefits of a division of labor between the various parts of an association. In Darwin's eyes this meant that more forms of life could be supported in any one area, since they all performed different tasks, or, more properly, different functions in the overall drama of existence. The division of labor allowed many varieties to live together, but only when they were all of a widely diversified nature and deviated enough from their parent species and from one another to permit a coexistence for all.

In a word, then, it was diversify or be done for. The crucial point behind Darwin's 1859 ideas on divergence was that selection favored a differentiation from the norm, and that the most distinct offspring would also be the luckiest.

This assertion was accompanied by an important corollary and by many pages of explanatory detail in both the *Origin* and *Natural Selection*: Darwin stated that divergence could be seen most often – was most likely to occur – in the larger groups in nature, and particularly in the larger genera, for these were the very forms which presented the most varieties and hence "fuelled" the process. To convey these ideas in a visual manner Darwin prepared first a draft, and then a complete diagram, of the process of growth and divergence in genera, which were appended to *Natural Selection* and the *Origin*, respectively.

Without spending further space on this topic it ought to be possible to summarize the three main elements of Darwin's views on divergence in its finished state. First and foremost was, of course, the notion that life was readily subdivided into different classes, orders, and families, which indicated a hierarchy of relationships that evolutionary theory had to explain. Life was for Darwin a branching affair. The second element of the three which went toward his principle, and the one which

37. *Origin*, p. 112.

has been noted most often by historians for evident reasons, was the so-called rule of the division of labor. And the final element of the triptych was that concerned with large genera and the incidence of varieties, the "boiler-house" of the whole machine. To it briefly, there was the phenomenon of divergent lines, the mode by which they were formed, and the cause and effect attributable to them.

However, despite the fact that these elements were evidently closely intertwined and mutually supporting constructs in Darwin's finished theory, they were more or less separate concepts in Darwin's mind at least until the end of 1856. Each one carried its own panoply of Darwinian explanation and seems to have existed in a relatively autonomous state.

To begin with the first element, an awareness of divergent lines of modification had been with Darwin ever since he first questioned the immutability of species. He had always been conscious of the hierarchical arrangement of nature and had, moreover, always known that this was a feature that had to be made intelligible in any theory offered to the public. Even in his earliest notebook in 1837, he sketched out the various lines of modification which could arise from a single form.[38] After he had finished working on barnacles, one of the first things he turned to was a detailed study of what it was that made classification schemes the way they were. In this respect he even occasionally used the word "divergence" to describe the phenomenon of branching modification: "Nov. 1854 . . . for otherwise we cannot show that there is a tendency to diverge (if it may be so expressed) in offspring of every class, and so to give the diverging treelike appearance to the natural genealogy of the organised world."[39]

Here the significant point to note is that Darwin was using the word *divergence* as a descriptive label for the overall patterns he could see in nature. From his various notes and jottings, and in particular from the memoranda contained in his portfolio marked "Divergence,"[40] there is no evidence to suggest that Darwin as yet envisaged a special mechanism for this phenomenon other than natural selection. He appears to have thought that natural selection would preserve new – and hence different – modifications that would, in turn, give rise to a cluster of species and genera that were markedly distinct from the parent form.

38. B notebook, Dar 121, p. 36.
39. Dar 205.5, unfoliated slip dated Nov. 1854.
40. Dar 205.5, but marked in Francis Darwin's hand(?).

The process was effected by the geographical scheme described in 1855 and 1856. Darwin thought that a new genus arose from the introduction of some favorable adaptation to a satellite species at the edge of the geographical range covered by any one large genus.

The second element which was important for the construction of Darwin's principle was, as has been emphasized, the division of labor. Camille Limoges has recently described the route by which Darwin was first made aware of this concept within the biological context,[41] as has Sylvan S. Schweber even more recently with regard to the economic context.[42] So Darwin was certainly not ignorant of this notion after about 1851 or 1852. But he tried at first, and especially in 1855 when the idea of a division of labor appeared often in his notes, to relate this evidently "beneficial" diversification to a combined cause of competition and the absolute abundance of resources in any one area. A division of labor was not applied to the question of divergence of character, for Darwin already had an explanation for that in peripheral differentiation. It was applied instead to the problem of accounting for the difference in the amount of life which regions could support.

Consequently, in a difficult but rich passage written during January 1855, Darwin linked "resources" with "struggle" to give diversity or monotony in a flora or fauna, as the case may be:

> Now in considering amount of life supported in given area, besides size as an element, as in trees and elephants, besides period of non-action during winter in cold climates, I think some such element as amount of chemical change should if possible be taken as measure of life, viz. amount of carbonic acid expired or oxygen in plants. I have been led to this by looking at a heath thickly clothed by heather, and a fertile meadow, both crowded, yet one cannot doubt more life supported in second than in first; and hence (in part) more animals are supported. This is not final cause but mere result from struggle (I must think out last proposition).[43]

41. Camille Limoges, "Darwin, Milne-Edwards et le principe de divergence," *Actes XII^e Cong. Int. Hist. Sci.*, *8* (1968), 111-115, where he suggests that Darwin thought of the principle of divergence in 1852 after reading Henri Milne-Edwards' *Introduction à la zoologie générale* of 1851.

42. Sylvan S. Schweber, "Darwin and the Political Economists: Divergence of Character," *J. Hist. Biol.*, in press. I am grateful for being allowed to read and comment on this paper before publication.

43. Dar 205.5, unfoliated slip dated Jan. 30, 1855.

In short, although this was clearly a passage elaborating on the phenomenon of a division of labor and the diversity of associations, there was here no talk of selection favoring the most distinct variety which might appear. Nor did Darwin at this time put these thoughts about diversity into a temporal context to illuminate how he saw the branches of the "tree" of life sprout and grow away from the root stock. Instead, the division of labor was explained in terms of natural selection and served, in turn, to explain what we might call the "biomass" of an area. He went on to argue in the closing sentences of this piece that poor regions encouraged little interspecific competition and therefore tended to support remarkably uniform floras and faunas, such as heathlands, conifer forests, or freshwater biotas. The "fertile meadow," by contrast, supported "more life," not because this was how God or anyone else had envisaged it, but because there had been a great deal of "struggle." Hence competition and the idea of "resources" between themselves accounted for the "amount of life supported in a given area."

So it appears that the division of labor, useful as it undoubtedly was, was brought into the embrace of natural selection theory as it then stood. It did not stimulate a reconstruction of that theory, as is often assumed to have been the case. Although introduced into Darwin's thoughts in 1852, it did not then or subsequently (for a few years at least) mean the same thing as it represented in the final principle of divergence. It was, we might say, adapted to its immediate context.

To pass on now to the third and final element of the three that were to go toward Darwin's theory of divergence, it is clear from the earlier parts of this paper that he had been studying the occurrence of varieties since the beginning of 1855. From that time through to the middle months of 1857 Darwin had been exercising his thoughts and pencil over the issue of where he might expect to find varieties – and thus variation – in nature. Mayr,[44] Sulloway,[45] and Schweber[46] independently suggest that this interest in *varieties* attracted Darwin's attention away from individual *variations*, leading him into difficulties he could well do without. It seems to me, however, that in this context Darwin did not consciously distinguish individual variants from groups of

44. Personal communication, and in "Darwin and Isolation," in Ernst Mayr, *Evolution and the Diversity of Life: Selected Essays* (Cambridge, Mass.: Belknap Press of Harvard University Press, 1976), pp. 120-128.

45. F. J. Sulloway, "Geographic Isolation in Darwin's Thinking: The Vicissitudes of a Crucial Idea," *Stud. Hist. Biol.*, *3* (1979), 23-65. I am grateful for being able to read this before publication.

46. Schweber, "Darwin and the Political Economists."

individuals with a common variation. It was, after all, the problem of individual variation in the Cirripedia which provoked an investigation into varieties, and the conclusions he drew from the latter study implied that where there were groups called varieties there was also variation at the individual level. Armed with natural selection, the formation of classificatory taxa was not a problem for Darwin: selection acted on individual variants to produce varieties, which then increased in strength to become first "marked varieties" and then "incipient" and "close" species, until at last they passed over some metaphysical dividing line and could be called species. The same forces also served to explain the divergence of higher taxa.

Although this was a process of accumulated differentiation or divergence from the original stock, Darwin did not – before mid-1857 – invoke a principle of divergence to explain such an action. Instead he believed, as already indicated, that natural selection alone took care of the process of increasing divergence from the norm. Natural selection "made" species by picking out those variations which were well adapted to the prevailing circumstances, and pushed them on and on in some one direction. Once again, there was no talk of selection actually favoring the most diverse variety which happened to appear in any series.

In all three cases cited, Darwin did not introduce the core concept of his mature principle of divergence. Instead he explained and applied the notions of a branching history of life, an ecological division of labor, and a superabundance of variation in the larger genera, in terms which implied that he believed the problems were accounted for. Darwin therefore invested each topic with a meaning and an explanatory framework that was somewhat different from his later notion, and that was here neatly interlocked with current considerations. These are indeed the elements which went toward Darwin's idea of divergence, but here in his notes before 1856 or so they were not interrelated in any concrete fashion.

DIVERGENCE IN THE NATURAL SELECTION MANUSCRIPT

On May 14, 1856, Darwin noted that he "began by Lyell's advice writing Species sketch,"[47] and he then methodically worked his way through subject after subject, chapter after chapter, more or less as the reader was supposed to do. It is clear from the arrangement of material, as the editor points out, that Darwin added a section on the "Principle

47. De Beer, "Darwin's Journal," p. 14.

of Divergence" to one of his completed chapters. This addition was finished in the early summer of 1858 and inserted into Chapter VI, "On Natural Selection," which had originally been considered complete on March 31, 1857. The most obvious explanation for this action is that Darwin was in some way ignorant of – or at least uncertain or uneasy about – the subject matter of his interpolation.[48] It is my suggestion that Darwin discovered the need for a proper principle of divergence between these two dates. Consequently, we should expect to find in the first draft of this Chapter VI all his ideas about the formation of species and the hierarchical arrangement of living beings *without* the explanatory tool of a principle. And this I think we do find.

The most telling feature of any comparison between Darwin's initial chapter on speciation and its ultimate form (which included the principle of divergence) is that the first draft is obscure and woolly on points where the second bears a certain clarity of expression. In this sixth chapter Darwin was intent on treating the vexed question of how he supposed forms to gather enough differences to "turn into" species, genera, and even families, as his theory required. He therefore attempted to explain his conviction that selection could produce distinct lines of modification and that it was the cause of an apparently "directional" evolution.

Without any explanation of divergence, Darwin did two things. He emphasized the role of competition, and described the availability of suitable "places" in the "polity of nature" for every step from varietal to specific rank. Competition for these "places" insured that only a "well-adapted" variety succeeded in occupying them, and that one form was always replaced (or rather, ousted) by another that was even more "well-adapted" or "better" organized. This process of replacement appeared to move in or tend toward certain directions, a phenomenon which Darwin had difficulty in explaining. Here he fell back

48. Or, perhaps, he originally intended the piece to go into another chapter. Darwin had, however, completed all his chapters by then, and written out detailed tables of contents for each. The "principle of divergence" does not appear in these lists. One would expect on this argument to find a cancelled entry. One further possibility remains: that Darwin wrote the section intending it to go in an unwritten Chapter XII. The only subject left for him to cover was an expansion of the discussion on geographical distribution to include representative species (*Natural Selection*, pp. 534, 577-581). Such an intention would certainly have brought him to reconsider mechanisms for divergence. But there are no manuscript pages that could be understood as opening pages for this potential chapter, and the piece itself has been foliated by Darwin to fit into Chapter VI – running from fol. 26a to 26nn.

on the phrase "expression of variation in a right direction" to indicate – in an unintentionally teleological manner – such a movement. It was a convenient if cumbersome phrase for the trends which he was later to call divergence of character.

To emphasize, however, that there was plainly some sort of directional selection, he contrasted the results of natural selection with the unstructured and nondirectional variations of polymorphic species: "the variation must be in the right direction to profit the individual, otherwise it will not be selected . . . I am inclined to believe that in the polymorphous or protean groups of species, as they have been called, mentioned in our chapter IV, which we meet with in every great class, we see more fluctuating variability – perhaps the very tendency to vary being inherited – the variation being of no use in any one direction to the being in question, and therefore with no one character steadily selected, augmented and rendered nearly constant."[49] As he said, there was a world of difference between the accretion of advantageous characters in a "right" direction, which would profit the individual, and the fluctuating variability of polymorphic forms where the variation was "of no use in any one direction." In order to expand on his point Darwin continued: "The expression of variation in a right direction implies that there is a place in the polity of nature, which could be better filled by one of the inhabitants after it has undergone some modification: the existence therefore of an unoccupied or not perfectly occupied place is an all important element in the action of natural selection."[50] This was certainly an effective argument: the process of transmutation could be considered as a stream of raw varieties flowing into a millpond, where the miller (natural selection) could channel water over a series of weirs and filters (the availability of "places"). Every hole in the filter was a "place" for which varieties competed; those which got through contributed to the continuing flow of water in one particular direction.

Darwin consequently devoted a longish section of this first draft of Chapter VI to describing all the possible ways in which "niches" could be vacated or made "not perfectly occupied" by their owners. Under the rubric "Causes favourable and unfavourable to natural selection" he worked his way through all the changes imaginable which could affect or increase the number of ecological nooks and crannies into which a modified variant could slip.[51] This was the only manner in which he

49. *Natural Selection*, p. 252.
50. Ibid.
51. Ibid., pp. 251-261.

could account for the facility with which one advantageous modification could be added onto another, and could start the ball rolling in "any given direction."

With a principle of divergence, which we know he possessed by the spring of 1858 (for it was at this time that he added the section with this title to Chapter VI), Darwin could transcend these arguments. He could state that it was not "niches" or "places" that determined which variety should survive. The forms which escaped extinction did so because they were the most different. Twelve months after he had composed the passages above, he returned to the same problem to describe what he now believed: "Here in one way comes in the importance of our so-called principle of divergence: as in the long run, more descendents from a common parent will survive, the more widely they become diversified in habits, constitution and structure so as to fill as many places as possible in the polity of nature, the extreme varieties... will have a better chance of surviving or escaping extinction, than the intermediate and less modified varieties and species."[52]

It can be seen in this later passage, composed in 1858, that Darwin did not have to talk of there being a readymade number of ecological niches waiting for the newly modified variants to come along and occupy them. On the contrary, he could claim that modified forms were so different from those previously in existence that they automatically created their own "places," where none had been before, on the rare occasions when they could not simply oust a lesser variant from its home. Since it was the most *extreme* variety which survived, the overall construction of the population would tend to become more diversified and, under the rule of the division of labor, several lines of modification would be encouraged. Hence the "amount of life" supported by any one region would become ever more diverse and complex.

In summary then, Darwin's initial attempt at this sixth chapter (completed March 1857) was focused on the question of explaining diverging lines of evolution – a "right direction" – without any idea of a principle which might invoke selectional advantages for those forms which happened to be most different from the ancestral stock.

It must be emphasized that the composition of Chapter VI set the scene for Darwin's discovery of this principle. Throughout the period of writing he was ever alive to the possibilities of clarifying ideas and drawing in new correlations or more effective arguments. The "big species

52. Ibid., p. 238. As an aside, note the way in which Darwin used the same words in the *Origin*, quoted earlier in the present paper, note 37.

book" was an unparalleled opportunity for him to test his own ideas *in extenso* and to uncover flaws in his reasoning or evidence. When writing out some sixty or seventy pages on the question of natural selection and its apparently directional results, Darwin must have reflected deeply on what he was trying to say, whether it could be said more effectively, and – most of all – whether what he said truly described the manner in which he supposed natural selection to work. There is nothing in intellectual life which demands so much attention to detail and so much concern with overarching themes as literary exposition for one's peers. Darwin was brought to the point where his ideas – once so clear in his mind – were now clouded by doubts. He must have seen that the "expression of variation in a right direction" was ineffective and even misleading, and must then have begun casting around for the solution. We can with some degree of certainty assert that Darwin was primed for a major reformulation of his thoughts.

THE "TRIGGER"

For the "trigger" which sparked off Darwin's sudden formulation of the principle of divergence, it is necessary to return to his botanical arithmetic, which had been proceeding in an orderly fashion throughout the writing period. On July 14, 1857 – just three months after completing Chapter VI for the first time – Darwin discovered that he had made an elementary error in his mode of calculation. He wrote an impassioned letter to his young friend John Lubbock, who had pointed out this distressing fact: "You have done me the greatest possible service in helping me to clarify my brains. If I am as muzzy on all subjects as I am on proportion and chance – what a book I shall produce! . . . I am quite shocked to find how easily I am muddled, for I had before thought over the subject much, and concluded my way was fair. It is dreadfully erroneous. What a disgraceful blunder you have saved me from . . . But oh! if you knew how thankful I am to you!"[53]

He simultaneously criticized his own foolish statistics and praised Lubbock's skill in detecting the faults in his method of computation. Now although Darwin openly encouraged Lubbock in all scientific

53. Francis Darwin, *The Life and Letters of Charles Darwin, Including an Autobiographical Chapter* (London: Murray, 1887), II, 104. This letter has, of course, been noted by historians, although no-one has as yet decided what it meant to either Lubbock or Darwin. See, for example, Fred Somkin, "The Contributions of Sir John Lubbock FRS to the *Origin of Species*," *Notes & Recs. Roy. Soc.*, *17* (1962), 183-191.

matters and often indulged in innocent flattery, such uninhibited enthusiasm was quite unlike the even tenor of his usual correspondence with this friend and protégé, and perhaps mirrored a deep sense of shock on Darwin's part. For his remarks were a just assessment of the situation: Darwin had indeed been too simplistic in his protracted analysis of species, genera, and varieties. As if to spread the burden of this sudden and painful revelation, Darwin fired off a similar letter to Hooker on the same day, complaining that he was the "most miserable, bemuddled, stupid dog in all England" and that he was ready to "cry with vexation at my blindness and presumption."[54] Historians can only be thankful that he did not carry out his extravagant threat to tear up his manuscripts and "give up in despair."

In a nutshell, the reformulated method of computation required that the entire flora or list of plants be divided into two groups according to the size of genera *before* any calculations were carried out. Moreover, instead of using averages Darwin was encouraged to work out a prediction for his variable which he could then compare with reality. He told Lubbock: "I have divided the New Zealand Flora as you suggested. There are 339 species in genera of 4 and upwards, and 323 in genera of 3 and less. The 339 species have 51 species presenting one or more varieties. The 323 species have only 37. Proportionately (339:323::51:48.5) they ought to have had 48½ species presenting varieties."[55] In other words, Darwin separated his initial population into two roughly equal parts, with all the genera that possessed four species or more in one group, and those with three species or less in the other. The advantage of so doing was that now any quotient simply had to be expressed in terms of belonging to either group, thus being either "large" or "small" in species number. Then, proceeding along lines normal in contemporary botanical arithmetic, although not those he himself had previously followed in this context, Darwin estimated from one set of ratios what he should expect to find in the other. By following the "rule of three," an elementary proportional device which gave the fourth term of a statement from the other three, he arrived at a figure (in this case the number of varieties) which ought to be found in nature if she was consistent. In comparing predicate with reality – 48.5 with 37 – he discovered that the small genera had fewer varieties than they should. This in turn implied that there was less "creation" going on in these small groups, a conclusion which was in no way counter to Darwin's previous results.

54. F. Darwin, *Life and Letters*, II, 103-104.
55. Ibid., p. 104.

But the technique *was* markedly different. Where before Darwin had asked the question whether genera which possessed his desired quality (such as many varieties, or a wide range, or whatever) also presented large numbers of species, he now looked at the problem the other way around and calculated whether some predetermined "large" genus had more of whatever was under discussion than correspondingly "small" genera.

In all previous computations he had divided his sample – a catalogue of plants – into two groups of genera, one of which contained the variable and the other of which did not. Occasionally he also used a third category, which was the whole population. From these he derived the average number of species per genus for each category, and then compared the results. Whichever group showed a higher average was considered to be the "larger." This was exactly the same technique he had used for his first calculations on aberrant forms: Darwin had used it consistently since 1854 without change or reexamination, assuming that if the results came out "right," the method was serving its purpose well enough.

But what was suited for aberrance was not necessarily the best method for calculations on the incidence of varieties. Such a method used to calculate in the second context did not, strictly speaking, prove what Darwin thought it did. Even if genera with species that vary had, on the average, more species per genus than those without species that vary, it was possible that varying species occurred most frequently in small (or in middle-sized) genera.[56]

Furthermore, although it was not categorically incorrect, Darwin's use of the final figures was wide of the mark he was attempting to hit. He compared one average with another, and thought he had proved his point if one was larger than its pair. Since this was only a *relative* estimation of generic size, Darwin's results often show fluctuation between one calculation and the next over the questions: "How large is large?" and "What sort of difference makes one genus larger than an other?" Writing of the average number of species per genus in Boreau's *Flore du centre de la France*, for instance, Darwin demonstrated that the section which carried varieties had 5.36 species per genus, where the

56. That is, the group of genera having varying species might consist of a number of small genera (in each of which there are very many species which present varieties) and a few large genera (in each of which there are only a few varying species). This group of genera might prove, on average, to have more species per genus than the group of genera without varying species, but it would be wrong to conclude from this that varying species and large genera go together.

other section presented only 1.97. He asserted that varieties were therefore to be found in the "large" genera, when his results merely indicated that they appeared in the *larger* genera. To his contemporaries, five species in a genus was not by any means "large." Hooker considered any genus with over ten species to be very large, and others thought seven or eight species a reasonable figure for a large genus.[57]

Darwin's idea of "large" was throughout his earlier statistics in reality simply a statement of "bigger than." He seemed to have no concept of any absolute largeness or bigness. Lubbock undoubtedly seized on these discrepancies and pointed out that Darwin was calculating relative largeness when his conclusions spoke of some real difference in size. Lubbock therefore abolished all connotations of relativity and substituted a division of the given population into two halves, one containing all the truly large genera and one the small. Now, even if people quibbled with Darwin over his definition of "large," at least he had defined it in unequivocal terms. The central question therefore remained the same one that Darwin had posed in earlier computations: Do varieties (or commonness or wide range) occur in the larger genera? But it was rephrased by Lubbock to insure that it was rigorously answered.

Darwin, however, was reluctant to acknowledge the superiority of Lubbock's suggestions, even when he found that the new method did give the same sort of result that had been forthcoming from earlier calculations. He confessed that "the case goes as I want it, but not strong enough, without it be general, for me to have much confidence in."[58] This was only one example where previously he had drawn up hundreds, so why should he unreservedly accept its results? So much is perhaps understandable when a long investigative program is overthrown. Be this as it may, after his letter to Lubbock Darwin turned to a more extended examination of this novel method.

His rough notes for a calculation of the incidence of varieties in Hooker's *Flora Novae Zelandiae* show that he estimated not only the number of varieties he should expect to find in small genera (and about which he had written to Lubbock), but also that he tried the proposition around the other way to see if larger genera had more varieties than proportion would dictate.[59] Such appeared to be the case; so, with

57. Hooker, for instance, wrote to Darwin in the spring of 1844 detailing a calculation he had made to discern whether the larger genera were also mundane; in it he took large genera to number over six species, and small under four. Dar 100, letter 4, and Darwin's reply in *More Letters*, I, 402-403.

58. F. Darwin, *Life and Letters*, II, 103-104.

59. Dar 16.2, fol. 243 verso.

gathering confidence, he settled down to rework some of his previous statistics.

Only five days after the news from Lubbock, Darwin had gone through his old calculations on Babington's *Manual of British Botany* (third edition, 1851), correcting and marking these as "useless" and drawing new conclusions dated July 18. By August he was soliciting Hooker's aid in obtaining for him the floras which he had borrowed previously ("I am at a dead-lock till I have these books to go over again"), and was asking his advice for further floras to so calculate ("I wish much you would think of any well-worked Floras with from 1000-2000 species with the varieties marked").[60] And some time soon after this he engaged the services of a willing and numerically skilled associate who was able to do the preliminary and time-consuming sorting of the data for him. The man he fixed on was a Mr. Norman, the village schoolmaster from Downe, who is now an obscure individual known only for this relationship with Darwin.[61]

For by now it is evident that Darwin was determined to rework everything which he had done before. He may have gathered extra confidence and renewed vigor from the fact that he had been experimenting with Lubbock's method, until he had found an alternative and more immediately striking mode of presenting results. Instead of going to the trouble of working out (by proportionality) an expectation which then had to be compared with reality, Darwin seems to have preferred working out his real figures as parts of a thousand, which were then compared with one another. This slight modification can have been nothing more than a personal preference for simple and immediately recognizable statements, and historians need lay no more weight on it than this.

What is more notable is Darwin's determination to rework this extensive body of data in the knowledge that his "big book" was more than half completed. He was, in 1857, prepared to sacrifice whatever time it would take to go through an exercise which had already occupied

60. F. Darwin, *Life and Letters*, II, 105.

61. Mr. Norman received a small payment for his work, which must have amounted to a considerable sum to judge from the pile of papers in his hand, in Dar 15.2, Dar 16.1, and Dar 16.2. Darwin even had the gall to offer Norman's services to Hooker, saying, "is it not a pity that you should waste time in tabulating varieties? for I can get the Down[e] schoolmaster to do it on my return, and can tell you all the results" (F. Darwin, *Life and Letters*, II, 128). For Darwin's notes and instructions to Norman, see Dar 15.2, fols. 77-82, 90A, 95, and Dar 16.1, fols. 133A, 136A, 145 verso, 174A, 184A.

his spare time for some twenty months. This resolve is indubitably a measure of the significance with which Darwin now invested the subject of variation and the characters of large genera. Now he implicitly committed himself to an unspecified period of revision and addition in the future. "The subject," he told Hooker, "is in many ways so very important for me."[62]

The subject was indeed important for him. It still provided central evidence for variation and speciation in nature, and it still demonstrated an important correlation between the size, topographical range, and individual abundance of genera. All this provided material for his chapters on variation under nature and geographical distribution. But I suggest there was now an extra dimension which made it even more significant for Darwin, even more necessary than before. In conjunction with correcting his calculations he had hit upon the "principle of divergence."

THE DISCOVERY OF A "PRINCIPLE"

The only contemporary evidence relating to Darwin's discovery of divergence is to be found in his correspondence.[63] He wrote to Hooker in August 1857 describing a few botanical calculations, and added some words on the "principle of divergence" as it bore on his general theory: "If it will all hold good [his botanical arithmetic] it is very important

62. F. Darwin, *Life and Letters*, II, 105.

63. There is of course the famous autobiographical account, in which no year is given: Barlow, *Autobiography*, pp. 120-121. Another recollection of the discovery of divergence comes in a letter to George Bentham in 1863. "I believe," wrote Darwin, "it was fifteen years after I began before I saw the meaning and cause of the divergence of the descendents of any one pair." If we take Darwin at his word – even though he was here speaking loosely about an event that occurred some ten years previously – the implication of this statement is that he thought of the principle of divergence in 1852. That is, add Darwin's term of fifteen years to the date 1837, when he first opened a notebook on the transmutation of species, and we come up with the year 1852. But who is to say, in the absence of accessory evidence, that Darwin understood 1837 as a beginning? Might he not as easily have meant 1842, when he first began writing up his ideas in extended form? If we add fifteen years to *1842* the discovery of divergence could have taken place in 1857. The ease with which these figures can be manipulated indicates that caution is required when we are dealing with a moot point like the disclosure of divergence. There seems to be no good reason either to accept or to reject Darwin's testimony, but it should be borne in mind that he did not *claim* the year of his revelation to be that of 1852. He only suggested that it was fifteen years after some other – unspecified – time. See F. Darwin, *Life and Letters*, III, 26.

for me; for it explains, as I think, all classification, i.e. the quasi-branching and sub-branching of forms, as if from one root, big genera increasing and splitting up, etc. as you will perceive. But then comes in, also, what I call a principle of divergence, which I think I can explain but which is too long, and perhaps you would not care to hear."[64]

That was all he said on the matter. Further corroborative evidence can be derived from a letter written one month later in September 1857 to Asa Gray, in which Darwin effortlessly epitomized the whole theory of evolution by natural selection (eventually put forward as part of Darwin's contribution to the Linnean Society paper of July 1858), and in which he included a closely argued paragraph on "one other principle" which "may be called the principle of divergence." Yet to Gray Darwin preferred to describe the notion not as one which explained large genera increasing in size and breaking up into smaller ones, but as an idea founded in the division of labor. He told Gray:

> The varying offspring of each species will try (only few will succeed) to seize on as many and as diverse places in the economy of nature as possible. Each new variety or species when formed will generally take the place of, and so exterminate its less well-fitted parent. This I believe to be the origin of the classification or arrangement of all organic beings at all times. These always *seem* to branch and sub-branch like a tree from a common trunk; the flourishing twigs destroying the less vigorous – the dead and lost branches rudely representing extinct genera and families.[65]

Both these letters clearly described divergence as it was to appear in both the *Natural Selection* manuscript (in the addition of 1858) and in the *Origin*. Evidently Darwin knew of it in August and September 1857. But of course it would be naive to imagine that these two letters necessarily reflect a recent or contemporaneous discovery of the notion, since Darwin could have known all about divergence in his cradle yet not thought to tell anyone about it before this time. All we can say with certainty is that whereas he did not speak of a principle of divergence in his "Essay" of 1844, he did mention it in the late summer of 1857.

There is one further aid for historians in this matter. As Robert Stauffer has brought out in his edition of Darwin's "big species book,"

64. *More Letters*, I, 99, dated Aug. 22 [1857].
65. *Life and Letters*, II, 125, dated Sept. 5 [1857].

it appears that Darwin referred to "Divergence" in his outline "Table of Contents" for the first draft of Chapter VI. The latter was completed, according to his journal, on March 31, 1857. So, on the face of it, it would seem that attention should be directed to the pre-1857 period for the discovery of this principle. However, this neglects the very real possibility that Darwin here meant to describe divergence of character in terms that were not precisely the same as his final understanding of the concept. The suggestion is substantiated by Darwin's subsequent cancellation of the table of contents. He then replaced it by one that included a *principle* of divergence.[66] Again, the implication is that he had thought of something in the interval.

Briefly, then, the story line runs as follows. Despite an early awareness of the phenomenon, Darwin did not see the need for a principle to explain divergence until some time between composing the "Essay" and the *Origin*. The recent publication of *Natural Selection* shows that Darwin possessed precisely the same concept of divergence in the spring of 1858 as he had in 1859, because he added a long section on this topic to his original Chapter VI, "On Natural Selection." From internal analysis of the first draft of this chapter, completed in March 1857, it appears that Darwin did not at this earlier time have any fixed notion of a "principle" per se, although he was trying to account for the same phenomena by using only natural selection. However, as demonstrated earlier, he did possess all the elements of a "principle" in his intellectual repertoire, although these too were correlated with natural selection. Therefore, he did not have the principle in March 1857, and he did have it in the spring of 1858. We can make a further refinement of this statement by drawing in the two letters which Darwin wrote to Hooker and Gray, describing his "principle of divergence" in scant detail, during the late summer of 1857. These were dated August and September, respectively.

It appears then that we should look to the summer months of 1857, and more precisely to the period of April to July, for something which allowed Darwin to juxtapose the elements of his principle and to see that they were intimately related and mutually explanatory ideas; something that led Darwin to discover a "gap" in his theory and to formulate the answer.

On July 14 Lubbock introduced Darwin to a new way of doing his botanical calculations and caused Darwin to reject all that had gone before as "the grossest blunder." Momentarily startled and dismayed

66. *Natural Selection*, pp. 22-23, 28, 213.

Table 1. The composition of *Natural Selection* and events relating to divergence

Year	Mo./day	Activity	Chapter
1854	Sept. 9	"Finished packing up all my Cirripedes"	
		"Began sorting notes for Species theory"	
	Nov.	Took up topic of aberrance and "creation"	
1855	Jan.	Began investigation into large genera	
1856	May 14	"Began by Lyell's advice writing Species Sketch"	
	Oct. 13	Finished whole of "Variation under Domestication"	Chap. II
		Finished first part of "Geographical Distribution"	Chap. XI
	Dec. 16	Finished whole of "Crossing"	Chap. III
1857	Jan. 26	Finished first part of "Variation under Nature"	Chap. IV
	March 3	Finished whole of "Struggle for Existence"	Chap. V
	March 31	Finished first draft "On Natural Selection"	Chap. VI
		Listed "Divergence" in Table of Contents	
	July 5	Finished whole of "Laws of Variation"	Chap. VII
	July 14	Letter to John Lubbock	
		Began correction of botanical arithmetic	
	August	Decided to repeat all calculations	
	Aug. 22	Letter to Hooker describing "Principle of Divergence"	
	Sept. 5	Letter to Asa Gray describing "Principle of Divergence"	
	Sept. 29	Finished whole of "Difficulties on the Theory"	Chap. VIII
	Dec. 29	Finished whole of "Hybridism"	Chap. IX
1858	March 9	Finished whole of "Mental Powers and Instincts"	Chap. X
	April	Finished revising botanical arithmetic	
	April 14	Began writing "Discussion on large genera & small, & on Divergence and correcting chapter VI"	
	June 12	"Finished" above; added section on large genera to chapter IV and section on divergence to chapter VI	
	June 18	Interrupted by letter from A. R. Wallace	

by this unwelcome revelation, Darwin refused to relinquish the conclusions which he had come by so conscientiously and prepared to start again. The changes which Lubbock encouraged him to make forced him to look not at the *relative* size of genera but at the *absolute* "bigness" or "smallness" that each presented. He had formerly been content to put forward results where "large" was merely a question of being bigger than the standard – as four was bigger than two – and so he called any genus large as long as it possessed more species than the control. Now, however, in July, Lubbock made him contrast absolutely large genera of a predetermined size with correspondingly small ones.

This change in emphasis made Darwin shift his gaze to focus on the *success* which large genera so evidently enjoyed. He suddenly saw that it was not just variation and the fortuitous production of "good" adaptations which induced large genera to produce yet more and more species, but it was also their *potency*. Large genera really were more successful than the small. They were, in fact, the very acme of success, being more widespread and more abundant in individuals than their smaller confrères, and also turning out more varieties within which more "good" adaptations were likely to emerge. Large genera were the winners, and their size was a definite statement about their superior position in life. In a biblical turn of phrase, Darwin asserted that "in the great scheme of nature, to that which has much, much will be given."

It was this notion of success and its corollary of "winner takes all" which allowed Darwin to collect and fuse together points that had up till then been separate entities in his mind. All at once things fell into place.

Insofar as we can decide what may have been going on in anyone's mind, this reassortment of details can be reconstructed as follows. Through Lubbock's ministrations, Darwin suddenly recognized that large genera had more advantages than most. This was why they were widespread and numerous in individuals. Where before he had spoken only of forms being "better" adapted to their surroundings, here he had *real* advantages to deal with. The varieties which were produced in such numbers from the larger genera should also be superior, if his ideas about the inheritance of characters were true. Moreover, natural selection told him that "good" variations were preserved, so what happened to this wealth of superior variants? Here, he invoked the division of labor, which permitted any number of individuals to coexist as long as they were more or less distinct from one another.

He was therefore confronted with a vision of many superior variants vying with each other for "places" in the economy of nature, and with the rule that only the most diversified set of individuals would manage to live together; from this state of affairs he could ascend easily to the proposal that it was the most distinct or extreme variety which was favored by natural selection.

Once he had an association between the notions of "advantage" (that is, success) and "diversification," everything else followed. If selection was tending to push varieties away from one another in morphological or behavioral terms, then it must also be forcing species to develop along lines of modification that diverged from one another. Darwin could now quite clearly see that a large genus would eventually fragment into several smaller groups of species by a splitting action, and not from the pronounced superiority of a single species which then eliminated its congeners. A large genus broke into two or three sets of species, each one of which was characterized by a markedly distinct modification. But in the course of time, as he must have been aware, this sequence of growth, splitting, and growth would gradually add to the number of genera on the earth unless there was some extinction going on. The power of extinction was thus called in to maintain a semblance of balance in the history of living beings, and he reasoned that forms which were not sufficiently extreme or different must fail to reproduce their kind. Hence, by a circuitous route, Darwin arrived back at the same proposition with which he had started: that it was the most distinct form of life that was favored by natural selection. Such a revisitation may have reinforced the truth of this maxim in his own mind, for had he not reached exactly the same point from two directions – the preservation of "good" varieties and the elimination of the "bad"?

Moreover, if this was the route along which Darwin's thoughts proceeded, it is clear that he would now – in July 1857 – have strong reasons for correcting his botanical arithmetic. Here were striking new concepts which depended to a large degree on the conclusions derived from arithmetical statements about the appearance of varieties and the properties of large genera. After mid-1857 it was the principle of divergence that made the subject "so important" for him. Furthermore, this link between Darwin's arithmetic and divergence explains why Darwin did not manage to put his new thoughts on paper until all the botanical calculations had been completed for the second time. He could not write the "Principle of Divergence" for Chapter VI until he was confident in its statistical base. It was not until the spring of 1858 that he was satisfied with his data, and then he returned immediately to this taxing question. Indeed, Darwin noted in his journal that the weeks between April 14 and June 12, 1858, were devoted to a double writing up: he drew up a "discussion on large genera & small" to be added to Chapter IV ("Variation under Nature"), and at the same time he wrote on "Divergence & correcting chapter VI."[67] The implication is that each discussion depended on the other. The interdependence of these additions is emphasized by Darwin's concluding note that, on June 12, he "finished [the] above" – effectively lumping the two subjects together in practical terms if not in intellectual ones. It seems entirely possible that the correction of Darwin's arithmetic acted as a trigger which stimulated a reassortment of the various elements of the theory

67. De Beer, "Darwin's Journal," p. 14.

of transmutation, and which, in the process, generated his "principle of divergence."

Under this interpretation of Darwin's work before the *Origin*, the emergence of a principle of divergence can be seen as the last leg of a long inquiry into the general issue of divergent evolution. Over this period Darwin approached the question from a number of angles: at times he thought the problem was solved; at others it ballooned out in a disturbing and temporarily uncontrollable fashion, forcing him to reevaluate previous arguments, to gather new information or reinterpret the old, and to provide reformulated explanations. It was a see-saw existence. Many of the phenomena of divergent evolution noted by Darwin through the years 1837-1840 found an explanation in the sketches of 1842 and 1844. Having dealt with these facts to the best of his ability, Darwin turned to a study of barnacles, no doubt to corroborate his writings in various ways. There, a whole new range of evidence was disclosed, obliging him to return to the thesis of 1844 in order to expand and alter his lines of reasoning. Divergent evolution surfaced as one of the more significant difficulties in need of a solution. In the immediate postbarnacle years he may well have explained divergence through using the concept of a division of labor, as many historians believe. But the issue was not closed. In the light of unlimited variation in nature Darwin undertook numerical studies of varieties, species, and genera, to determine the "source" of new species. Over a period of months (from 1854 to the end of 1856) this botanical arithmetic indicated that large genera were more "fertile" than the small. Darwin, never one to leave a fact unexplained or a question unasked, noted that if a "fertile" genus produces more and more species, these species will merely remain variations on a single theme unless divergence intervenes. How could the genus split into several genera? At first, before the beginning of 1857, he answered this question with a somewhat hazily formulated scheme of geographical isolation, depending for the most part on results drawn from his arithmetical calculations bearing on the wide geographical areas covered by species-rich and variable genera. Yet when he came to order these thoughts into a written synopsis for the "big species book," then firmly under way, the argument failed him. The "expression of variation in a right direction" still lacked an adequate explanation. As he was endlessly turning the problem over during the first six months of 1857, a relatively trivial event, not immediately concerned with divergence although intimately connected with his numerical studies, caused Darwin to stop in his tracks. The reorganization of his arithmetic stimulated a reorganization of the issue of divergence. The various pieces of the puzzle were reassociated and reassembled in mid-1857, producing the much-vaunted "principle." Its explanatory power was great and Darwin was eager to provide proper substantiation; he delayed the revision of the long manuscript until the arithmetical basis of the concept was fully examined, and then hurriedly wrote up his ideas. The "principle of divergence" was emphatically part of Darwin's theory by early 1858.

If there is any message from this sequence of events, it is that Darwin's theories changed and evolved as he himself grew older and more mature, and that the "Essay" and *Natural Selection* – and indeed, the *Origin* as well – represent only his considered opinion on the problem of species at a given point in time. There is no good reason to believe that Darwin's ideas were static from the "Essay" onward, and no good reason to reject the possibility that the meaning of certain key concepts changed and developed during the following years. The interval between the end of the barnacle work and the time when the "big book" was interrupted by A. R. Wallace ranks as one of the most interesting and rich fields yet to be explored.

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