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# C.R.Darwin and J.D.Hooker:
# Episodes in the History of Plant Geography, 1840-1860

by

Elizabeth Janet Browne

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## Abstract


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In the absence of any recent investigations into the study of plant and animal distribution in the early nineteenth century, I examine the themes which dominated this branch of natural inquiry. Using unpublished correspondence between Charles Darwin and Joseph Hooker, their published works, and treatises by other naturalists, I outline the establishment of biogeography from the twin roots of geology and biology.

I propose that there was a distinctive manner in which naturalists with a geological training or professional experience in that subject, such as Lyell, Edward Forbes and Darwin, regarded the topographical arrangements of today's living beings. There was an equally distinctive manner in which natural historians and systematists, such as Hooker, looked at the same phenomena. The parallelism is illustrated by a description of the way that each faction explained the problem of the origins of arctic and alpine floras, and the problem of geographically representative species.

Furthermore, I explain how naturalists, and particularly botanists, understood the study of distribution and the way in which they analysed their data. I trace the history and the characteristic features of 'botanical arithmetic' (or the statistics of distribution), and its transfer into related sciences, especially geology. These chapters reveal a hitherto unnoticed aspect of nineteenth century natural history.

I close with a full exposition of Charles Darwin's extensive botanical calculations on large genera and varieties which he used to vindicate his theory of organic evolution. This is based entirely on archival material, as yet unassessed by historians. I describe three stages in the development of Darwin's thought before the Origin of Species and discuss the discovery of a principle to account for diverging lines of evolution. This last I attribute to an alteration in Darwin's concepts following an enforced change in his arithmetical procedures in 1857.

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# Introduction

> "I know I shall live to see you the first authority in Europe on that grand subject, that almost key-stone of the laws of Creation, Geographical Distribution."[1]

Thus with an elegant compliment to his new friend Joseph Hooker, Charles Darwin praised the study of the distribution of animals and plants as a notable key to understanding nature. Recognising that this "grand subject" was more than a Baconian exercise in the gathering of facts, he roundly declared that it was, on the contrary, fundamental for determining the origins of living beings.

So Darwin certainly thought that biogeography was an important study, and recent historians have not neglected this aspect of his researches. Camille Limoges and Michael Ghiselin have outlined the significance of the facts of geographical distribution, which he encountered in the Galapagos archipelago and elsewhere, for the development of his ideas about organic change. Sir Gavin de Beer, Nora Barlow, R.C. Stauffer, P.J. Darlington, Martin Fichman and Malcolm Kottler have discussed particular topics which helped or hindered his investigations, whilst other critics have described his views in more general histories of biogeography and evolutionary biology.

Yet few scholars have attempted to assess the place of biogeography in nineteenth century science as a whole. Was it as important to Darwin's contemporaries as it was to him? Did they too regard it as a "key-stone" to the "laws of creation" and did they draw from the data theories and hypotheses of the same order as Darwin's proposals? I assert in this thesis that the answer to such questions is 'yes'.

I demonstrate that there was intense and widespread interest in biogeographical phenomena, and a fully articulated set of propositions and axioms with which naturalists could attempt to explain the distribution of life. This interest was manifested in a variety of ways, and I illustrate how and why dissimilar trends of thought were generated and gradually interlaced. Using unpublished correspondence between Charles Darwin and Joseph Hooker, their published works, and treatises by other nineteenth century naturalists, I therefore study the development of biogeography as a science.

Apart from the fact that no-one appears to have previously conducted such a survey, my work is necessary because there is some tendency on the part of modern commentators to dismiss this "grand subject" as one which was virtually non-existent or practically medieval in character before

Darwin and Alfred Russel Wallace introduced evolutionary biology. Even Ronald Good, a noted biogeographer of our own times who has a heightened appreciation of the history of his topic, refers to the pre-Darwinian period as one of mere exploration and discovery, from which the greatest achievement was only a gradual description of the world's living beings.[2] Others, such as F.R. Fosberg, elaborate on this view to state that early biogeographical attempts were "undirected", atheoretical, and confined to the collection of facts about the ranges and distribution patterns of organisms. Naturalists, it is said, found these phenomena "curious" and "mysterious" in the extreme and were unable to explain them until a theory of evolutionary change was proposed in 1858 and 1859.

This view makes little of the attainments of botanists, zoologists and paleontologists before and contemporary with Darwin. Of course the advent of evolutionary theory had a definite and far reaching effect on the course of distribution studies and I, for one, do not wish to minimise the importance of On the Origin of Species (1859) and The Geographical Distribution of Animals (1876) which set this science on the path which it was to follow for the next one hundred years. But the wish to glorify Darwin and Wallace has led to a somewhat unjust and inaccurate assessment of the history of biogeography.

It should be emphasised that there was a well developed discipline of plant and animal geography in existence before this intellectual landmark,a discipline which possessed clearly defined aims, a variety of methods of procedure and a number of conceptual and publishing conventions. In this thesis I describe how it had been gathering momentum since the turn of the eighteenth century when German scholars such as Karl Willdenow and Heinrich Link first outlined the requirements for a study of "Pflanzengeographie", and how, in the early years of the nineteenth century, other naturalists such as Alexander von Humboldt, Robert Brown and Augustin Decandolle set the high standards which later scholars were to emulate. These last included luminaries like Charles Lyell, Alphonse Decandolle, Joseph Hooker and Edward Forbes, all of whom made notable contributions to the subject before Darwin set out his suggestions. Together these 'pre-Darwinian' naturalists investigated the division of life into topographical regions and the successive changes over time which they had undergone. It was to this well furnished study that Darwin and Wallace added the notion that animals and plants could themselves change, and so gave the subject its modern tripartite constitution of space, time and organic modification.

In part these points determine the scope of my argument. Much of this thesis is devoted to a close examination of the content of biogeographical theories in the first half of the nineteenth century, with successive chapters given over to the various ways in which particular problems were analysed and explained, and to the methods and conventions which were brought into play to effect such explanations. As part of this examination two further chapters are specifically concerned with Darwin, where I consider in some detail how he used previously established biogeographical methods to further evolutionary theories.

But I should stress that the present thesis is not directed to a purely Darwinian goal. It surveys instead the study of distribution and points out two dominant elements which characterised this inquiry into nature.

I argue that there was a distinctive manner in which geologists such as Charles Lyell, Edward Forbes and Darwin regarded the topographical arrangements of plants and animals, and an equally distinctive manner in which natural historians like Joseph Hooker looked at the same phenomena.

These two approaches to nature were the outcome of the existence of the science of geology, on the one hand, and biology or natural history, on the other hand, as separate and in some respects markedly dissimilar subjects. Each discipline gave its practitioners a certain way of looking at things, a certain way of thinking about the evidence, and a set of axioms and assumptions which helped each man come to his own conclusions about the regularities to be discerned in the inorganic and organic worlds. When, in the nineteenth century, geologists came to study purely topographical phenomena and the distribution of today's animals and plants, they investigated these in the manner typical of their previous experience and training. In an analogous fashion, natural historians considered distribution patterns in the way to which they were accustomed. I call these two approaches to the distribution of existing organisms the 'geological' approach and the 'topographical' approach to nature respectively.

I do not, however, suggest that these lines of thought were in any sort of mutual opposition or antagonism, or even indeed that they were eventually fused together in the work of Charles Darwin. They are simply threads which reflect the composite nature of biogeography, for this subject is, after all, an amalgam of the sciences of geology and biology which allows the investigation of distribution through time and space. It is more valuable to think of them as different coloured

strands in the fabric of biological thought in this half-century, which were sometimes separated from each other and sometimes so closely interwoven that it would be futile to attempt to tease them apart. Hence in parts of my thesis it will be seen that geologists, for instance, borrowed methods from the so-called 'topographical' approach to nature, and that natural historians attempted to understand a 'geological' attitude to spatial phenomena.

To pause here for a moment, it might justly be remarked that the allocation of nineteenth century naturalists into categories like 'geologist' and 'natural historian' is inaccurate and anachronistic, in view of the comprehensive interests of men such as Lyell, Darwin or Hooker. These are severe charges for a historian to answer. Although my meaning will become clear to the reader as he proceeds through the following chapters, I should perhaps define my terms clearly at the outset. When I speak of Lyell as a 'geologist' in distinction to a 'natural historian' I mean only that he was familiar with the methods and practices of geological investigation; I do not mean that he deliberately confined his researches to purely inorganic and fossil phenomena, or that his explanations were couched in unilateral terms. Similarly when I write of Joseph Hooker as a 'natural historian' this appellation should be taken to signify the kind of practical experience and training which he had up till then enjoyed. My categories indicate the subjects within which polymathic naturalists such as these felt most at home.

Part one of this thesis is concerned with a detailed description of the 'geological' approach to the present arrangements of the animal and vegetable kingdoms. I juxtapose the theories proposed by Edward Forbes and Charles Darwin to account for the origins of the decidedly peculiar distribution patterns of arctic and alpine floras, and point out how they were based on their geological knowledge, in contrast to the suggestions proffered by Joseph Hooker. In chapter two I examine the problem of accounting for the existence of mutually exclusive yet closely allied 'representative' species through the eyes of Forbes and Hooker.

Part two is expressly concerned with a 'topographical' approach to nature. Chapter three deals with the study of the geographical subdivisions which are to be found in the distribution of living beings, and the way that natural historians devoted their time to the description and comparison of biological provinces. An important characteristic of this approach to biogeographical phenomena was the employment of the technique which went under the name of "botanical arithmetic", or as we

now understand it, the statistics of distribution, and it is with this technique that chapter four is involved.

The third and final section deals with Darwin's use of botanical arithmetic to further his ideas of evolutionary change. Using his private papers and his correspondence with Hooker, I outline successive stages in the development of these theories between 1844 and 1858, and three corresponding stages in his employment of statistical methods. An important part of chapter six is given over to a discussion of how an enforced change in the actual method of calculation which Darwin was using led to his so-called discovery of a "principle of divergence".

# Part I

# Prologue

"Geology" wrote William Whewell in 1840, "examines the existing appearance of the materials which form the earth, infers from them previous conditions, and speculates concerning the forces by which one condition has been made to succeed another."[1]

Such an attitude had not always been the case, as historians have pointed out.[2] Only since the Enlightenment had the earth taken on a 'life' or existence of its own, independent of an interventionist Deity, and intellectually removed from the history of mankind and its maker. Once allowed to be a separate body, no-one could deny that the earth had had a past and was about to experience a future. This sort of approach to the earth led scientists to see their existing surroundings as representing something more than just the present: because the lands and seas were now thought to be constantly recombining and restructuring themselves, students of the earth realised that everything which they saw was the product of time and process and that nothing was really 'new' or pristine. "The Past" declared Whewell again, "has been a series of events connected by /a/ historical causation, and the Present is the last term of this series."[3]

Such an obvious point is here underlined because it bears heavily on my arguments for the distinctive manner in which naturalists upon whom geological thought had left its mark actually regarded the distribution of existing organisms. Lyell, Forbes and Darwin all assumed that modern floras and faunas had had histories. Lyell, in particular, understood today's associations as a result of their past movements and habitations, and his volume two of the Principles of Geology[4] was entirely given over to a thorough examination of the changes which organic nature experienced at the hands of the inorganic. Others did exactly the same thing, and Louis Agassiz, the two Brongniarts in Paris, and the two Decandolles in Geneva, are only the most eminent names among the list of naturalists with a geological bias who thus gave all existing floras and faunas the benefit of a past. Darwin and Forbes, for example, struggled to understand how that past had regulated the arrangements of the present; in my first chapter it will be seen how they used the notion of historical biogeography to explain the existing patterns of arctic and alpine floras, and how easy it was for them to assume that these plants had enjoyed a fairly eventful history.

Geologists, moreover, appear to have brought more with them to the study of modern forms than this one special quality of historicism.

Intimately linked with such ideas about the way the arrangement of today's structures provided evidence of their past were notions pertaining to the stratified nature of the earth itself.

Without an awareness that the crust of the globe was differentiated into layers, it was hardly likely that scholars would infer that the earth had experienced changes from one state of affairs to another, and thence to a belief that it possessed a history. This awareness had been fundamental to the science even before the work of William 'Strata' Smith, and the development of stratigraphy proper merely codified what was already assumed about the need for geologists to describe and order dissimilar deposits. Nevertheless, after Smith's Strata identified by organised fossils (1816),[5] strata became the focus of practical and philosophical geology, and stratigraphy, coupled with a dramatic escalation in paleontological investigation, became an indispensable and favoured aspect of geological inquiry.

The most striking attribute of such an enthusiasm for stratigraphy was, I believe, the ability to visualise a continuation of beds or formations where none was apparent. Murchison, for instance, traced the Silurian and Devonian systems as far as he could in Europe and then proceeded to extend his observations in Russia where, inter alia, he discovered marine shells of Devonian age and specimens of fossil fish peculiar to the Old Red Sandstone in the same bed of rock, thus proving the identity between these deposits. This ability hinged on a remarkable grasp of the principle of continuity in nature, for it had not been easy to see any superficial similarity between the grey slates and shales of Devon and the red sandstones of Scotland. Murchison's interpretation rested, as did all stratigraphical theory, on the notion of a multi-layered earth whose regularities were interrupted by subsequent activity and displacement. Hence geologists were trained to recognise that two or more outcrops of rock which happened to be separated by the intervention of other beds (by intrusion, deposition or dislocation) were the remnants of a once continuous layer.

Such a point - perhaps self evident and trivial - is again basic to my present argument. When men with a geological training turned to examine biological phenomena of the present day they drew a parallel between existing distribution patterns and inorganic strata. Lyell and Forbes, for instance, applied the stratigraphical method to the study of floras and faunas and so thought in terms of their initial continuity and subsequent dislocation through the action of external causes. Hence, as will be discussed in a following chapter, Forbes supposed that the summit flora of the many mountains of Scotland was a set of remnants from a once

continuous population which had covered all the grounds between these sites. Biological associations were thus taken to be 'living' strata, and structures which could readily be understood with the aid of stratigraphical analogies.

Turning from these more general elements which were, I believe, common to all geologists in the second quarter of the nineteenth century, I would like to describe briefly two further points which emanated specifically from Charles Lyell and which affected the manner in which both Forbes and Darwin were to understand biological phenomena. Lyell gave to each of his followers, and in particular to Darwin and Forbes, a vision of a constantly fluctuating and moving earth, where all geological structures and events could be interpreted as the result of a rearrangement of the various bits and pieces of the globe. Nothing was absolutely 'new' for it could only be different from what had gone before; to him, the parts of the earth were ceaselessly reassembled and deployed to give rise to the changes of state which his contemporaries were pleased to call distinct epochs and eras. 'Uniformitarianism' was in this respect a markedly inappropriate label for Lyell's system of "endless variation".

So much has been written about Lyell's theories of a steady-state earth and his odd ideas about the fossil record that I do not need to rehearse them.[6] My point here is to emphasise the dynamism of his system which encouraged Forbes and Darwin to espouse the cause of motion in the inorganic and organic worlds. They attempted to understand geological events as the result of previous and continuing activity, as evidenced by Darwin's early papers to the Geological Society (over the period 1836 to 1843) which were every one a special effort to demonstrate "the infinite superiority of the Lyellian school of geology",[7] and by Forbes' dynamic account of the colonisation of the British Isles by plants and animals as and when land movements permitted.

They saw that the history of living beings was one of an active extension and withdrawal according to structural changes in the earth, of dislocation and connection of ranges, and of mixtures and isolations as localised sections of the earth's crust moved from one state of affairs to another. Forbes and Darwin therefore saw - though each to a different degree - movement and interrelated effects where other naturalists saw only stasis and non-dependence. Their descriptions of living populations were based on a dynamic flux of organic and inorganic forces.

Closely related to Lyell's concept of a dynamic earth was his emphasis on the continuity between apparently discrete formations. His steady-

state earth demanded that more stress be laid on sequence than was previously the case in geological theories. The historian, can, of course, show that his precursors and contemporaries were not at all unaware of this quality and had even used it to great effect in the description of the earth's past: Buffon, for instance, had pointed out that the progressive refrigeration of the globe had given the earth a sequential history, where each stage followed on from the next in a necessary manner; and at a period rather closer to Lyell's, Georges Cuvier had demonstrated the successive environments which the Paris basin had presented as Tertiary seas periodically innundated the area.

Yet Lyell's idea of sequence was something more than this. Uniformitarian thought enforced an understanding of the gradual step-like nature of all geological change, and he postulated that all geological structures represented artificial discontinuities in the history of the earth. There were, to him, no breaks in the geological table, and each stratum, formation or system had gradually blended into the next by the continuing action of forces proceeding at the same intensity as those of the present day. He therefore stated that everything to be seen in the geological record was in fact determined by what had gone before. Unlike Buffon, who had asserted that a relationship between epochs was necessary because the earth was experiencing a succession of states where (a) was followed in an orderly fashion by (b) and (c), Lyell stipulated that every geological event (and hence structure) was a rearrangement of the layers and the resources which were then in existence. In the same way as today is yesterday's tomorrow, Lyell assumed that every occurrence which had taken place in the history of the earth was at the same time both effect and cause: the effect of what preceded, and the cause of what was to follow it. That is, every stage in geological history was part of an unbroken series or sequence of continual activity.

Now this is plainly an important view for biological theories. Firstly, of course, this was the notion which inspired Darwin to think of the gradual change or transmutation of one species into another over time. It was, however, to prove notable in other respects and especially for the spirit in which Darwin and Forbes approached the study of distribution. By its very gradualism, Lyell's theory gave animals and plants time to disperse or retreat, in the face of favourable or unfavourable conditions, at an entirely natural pace. Certainly there was room in Lyell's system for major geological upheavals (he would not have denied that the throwing up of Monte Nuovo was an event of ~~catastrophic~~ dramatic proportions) so long as these events did not exert any intensity of action not

found in the present. But Darwin and Forbes took him to mean that the elevation and subsidence of continents and islands, for example, was usually gradual and slow enough for living beings to act in concert with these changes.

This last view allowed both Darwin and Forbes (following Lyell's example) to postulate that floras had spread naturally over wide areas which may not now be connected together. One such example of this supposition (described in chapter one) is in their virtually identical work on the origins of arctic and montane floras in the northern hemisphere, where it was assumed that arctic plants had moved from their usual latitudes to colonise southerly areas at a time when environmental conditions were appropriately cool and land masses suitably disposed. Forbes took this idea further to propose that all the plants of Britain were derived from different regions of Europe, and that they had migrated over lands now removed to occupy these islands. In turn these notions provided Forbes with the basis for his own idiosyncratic theory of nature, which is described in chapter two. Darwin was also to take these suggestions a little further to propose an elegant explanation for the origin of species, dependent on the isolation which islands provided and the dispersive power of organisms, coupled with ceaseless geological activity which upheaved or let down the earth's crust relative to sea level. Darwin's theory of combined organic and geological change is examined in chapter five.

The points which I have made in this short essay into Lyellian geology and the so-called 'geological' approach to nature will reappear in subsequent pages of this thesis. They are, as can be seen, a set of theoretical commitments induced from geological practice which were applied to the now living kingdom. Forbes and Darwin approached the study of the relations of today's plants and animals with several ideas in mind. They believed these organisms to have had a past which was subject to continual and gradual geological change, and that floras and faunas could have extended or retracted their boundaries according to prevailing conditions; they enjoyed a peculiarly geological interest in strata, which allowed them to draw some stimulating analogies between them and the organic world; and they asserted that every biological and geological occurrence be seen as a part of a dynamic and interrelated system in unceasing motion.

If the reader can imagine such an item to exist, I would therefore say that Forbes and Darwin wore 'geological' spectacles which coloured the way in which they perceived the facts of distribution. It is to

these geological spectacles that the two following chapters are devoted. The historical significance of this particularly 'geological' attitude to existing animals and plants is clear from our vantage point in the twentieth century, for biogeography as a modern subject owed its inception to geology and to the geologists of the first half of the nineteenth century. It was the science of geology which contributed the axioms and assumptions basic to today's subject, and it was geologists such as Lyell who constructed the first truly biogeographical explanations.

But why we might well ask, did geologists turn to study present living beings at all, when they had plenty to occupy themselves with under the ground, so to speak? What was it in the nineteenth century which encouraged geologically minded naturalists to investigate modern forms when these were already the subject of attention from natural historians? The answer lies in yet another important aspect of what I call the 'geological' approach to nature; Forbes and Darwin scrutinized existing organisms for the light which they might cast on the way in which successive beings were introduced to and removed from the fossil record, and they used information about topographical distribution to provide fuel for their theories about the history of life on this earth. Hence, in a properly actualistic fashion, geologists attempted to formulate laws about the distribution in space of animals and plants, to elucidate the structure of fossil populations and the changes from association to association which could be discerned in the 'testimony of the rocks'.

Therefore, Darwin and Forbes, following Lyell's example, were striving to produce explanations for life in all its diversity. Once Lyell had broken the virtual ban on speculation and theorising which was to be found in very early nineteenth century geology, by espousing a highly speculative and comprehensive system of the earth and her organised beings, his disciples (and, I might add, his opponents) took readily to the construction of grandiose schemes and theories. Darwin was not alone in formulating a scheme for nature which would explain the relationships between all living beings, modern and fossil. Edward Forbes' ideas, for example, are explained in some detail in the second chapter of the present thesis, and other naturalists such as Louis Agassiz and Richard Owen also attempted to answer the questions which Darwin eventually did. In short, the most notable point about the manner in which geologists of this second quarter of the century approached natural phenomena was that they possessed theories of the world to direct their researches into geographical distribution.

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## Chapter 1: The Problem of Arctic and Alpine Floras

When two people simultaneously discover the same theory or explanation, interest and enthusiasm are excited at any time, no matter what the subject.

Events such as these stimulate intense discussion at the time of their occurrence and questions of priority are often aired in no uncertain terms. Thus Newton and Leibniz disputed the other's claim to the discovery of the calculus, and Charles Darwin could not bear to relinquish all priority for the theory of natural selection to A.R. Wallace. And dual discoveries also inspire strong feelings in the breasts of the participants' followers, leading to curious issues such as the controversy sparked off by Tyndall and J.D. Forbes over the movement of glaciers, where each man uncovered a notable precursor for the opposing view.[1]

The fact that the history of science appears to be punctuated with many such instances has not gone unnoticed, and these events have excited equally intense discussion in historical circles. What can joint discoveries like these tell us about the nature of science and the intellectual context of the age in which they occur?

In this chapter I intend to examine one hypothesis which was proposed separately but virtually simultaneously by Charles Darwin and Edward Forbes in a series of papers ~~published~~ written between 1842 and 1846. They each set out detailed explanations for the origins of the decidedly peculiar distribution patterns of arctic and alpine floras which were firmly based on current geological theories.

Darwin, writing privately in a sketch expounding natural selection in 1842, and at greater length in 1844,[2] ~~and~~ proposed a neat and cogent account of the origins of arctic and alpine floras that antedated by only a few years an almost identical hypothesis put forward publicly by Forbes at the British Association meeting of 1845 and then expanded in a long memoir in 1846.[3]

Darwin was later to write up his views in full in 1856-58, and then to broadcast his own opinion in the Origin of Species (1859)[4] but always with due recognition that Forbes had here preceded him in print. There was thus no controversy over priority, nor any spirited defence of minutiae of the kind that litter the history of science. Yet the question loses none of its historical interest for existing as a half public, half private affair and indeed leads one to wonder how many other instances of a simultaneous discovery could be unearthed from archives less well known

than the Darwin papers.

The differences which existed between the two hypotheses (and that were recognised by Darwin to exist) can be attributed to the separate schemes of nature under which the two parties laboured and into which each theory was supposed to dovetail. The similarities, on the other hand, reflect the powerful and all-pervasive set of ideas about geology which were then current. In particular, the similarities between Forbes' and Darwin's proposals were due to their marked enthusiasm for Lyellian geology and for dynamic interpretations of the structure of the earth and the distribution of her organisms. This common interest induced Darwin and Forbes to select the same problem - one that had been outlined by Lyell in his Principles of Geology - and to provide approximately the same answer.

Yet I would not like to suggest that the possession of the same body of geological facts and fancies so restricted their thinking that they eventually brought forward an identical solution. To say this is only to begin to assess the richness and variety inherent in geological work of the years 1830 to 1850 or thereabouts. It belies the emphasis that I wish to assign to the science of geology in the construction of these twin proposals, for I believe that this vital and flexible science presented an assemblage of theories and concepts that could be disconnected and reassembled in an almost infinitely variable number of ways. With this view in mind I suggest that Darwin and Forbes independently chose from a plethora of alternative details those which seemed to bear most closely on the problem under consideration. Their choices were regulated not so much by the substantive content of each point but by their personal preferences and by their own philosophical inclinations. The fact that the two resultant theories were remarkably similar reflects, more than anything, the respect which both men felt for their mentor Charles Lyell and their dependence upon the set of geological ideas with which, at the start of their respective careers, he had furnished them.

To unpack these contentions a little further I intend to describe not only Forbes' and Darwin's views on the origins of alpine and arctic floras, but also those belonging to a third naturalist in the person of Joseph Hooker. He too had something to say on these groups of plants and had, at separate times, criticised both the theories which his friends had put forward. The significance of Hooker's opinion lies in the dual point that he could neither fully understand some of the more 'geologically' biased interpretations which were employed by Darwin and Forbes, nor could he persuade his own thoughts to coalesce into a third, independent, theory

with which he could refute or expand the others. In the event, and some time later in the 1860's, Hooker accepted Darwin's views on the derivation of alpine species and his more provocative suggestion of a trans-tropical migration of arctic plants to the southern hemisphere, but not without some qualifications over the manner in which this migration was actually effected.

Hence I here regard Hooker as a naturalist fully versed in the rules and problems of the study of distribution, who simply could not produce a Darwinian or Forbesian 'historical' explanation for himself, since he was so totally immersed in what one might call a 'topographical' approach to nature. The finer points of Darwin's suggestions escaped him until the whole theory of evolution had been put before him and the public, albeit in slightly different forms. Hooker's critique was founded on an incomprehension of what the notion of 'time' meant to geologists, and a refined sensitivity to the distribution of present day species which allowed him to find many many examples that did not seem to fit into his friends' grandiose schemes. So in a very broad sense we can see Hooker as representing one side of biogeographical practice - the concentration on the present-day arrangement of species - whilst Forbes and Darwin, ranged on the other side of the chamber, are presenting a thesis of the past changes which have given rise to a succession of floras. A mutual opposition is not however the case as I wish to present it, nor indeed was this the way in which the participants saw it. I hope to show only that these separate views of the 'geological' and the 'topographical' study of distribution ran their own course to the extent that sometimes one naturalist could not fully comprehend what it was the other was trying to do.

## The Problem

The problem of arctic and alpine floras was one that had escaped scientific attention before the eighteenth century. Then, with an increased interest in polar travel and exploration around the region of the supposed north-west passage, the Baltic and Behring straits, it had become evident that the association of plants which inhabited these areas was a coherent and consistently homogenous whole. The arctic flora showed little sub-division into great floral zones according to any regional proximity to the major continents, and hence the plants living in the boreal parts of North America, Europe and Asia were more closely related to each other than to the plants living in the respective continental areas more to the South. This was not simply a relationship of vegetal physiognomy, although naturally this too was very striking: stunted growth and dwarfish habits, increased hairiness of leaves and stems,

a general thickening of the green parts and the formation of cushions, tussocks, or rosettes were all characters which added to the conformable appearance of the flora. There was, in addition to this, the fact that these regions supported many species which were absolutely peculiar to the boreal zones, species furthermore, which were widely distributed throughout these latitudes. Consisting in the main of mosses, sedges, rushes, cotton grass and woody herbaceous plants, these species belonged to families which dominated the flora and therefore gave it a distinctive nature set apart from those of more temperate areas. Usually a poor flora in terms of species, the arctic zone was blessed with a correspondingly high number of individuals so that no area actually looked 'bare' except where the harshness and severity of the climate dictated otherwise.

In short, arctic latitudes and those which we now call boreal, ranging as far south as Oslo, Copenhagen, Newfoundland and the Aleutian Islands, were found to bear a flora that was typical and distinctive in the form of its plants, in the kind of families which lived there, and in the relative proportions of these families to each other.

In a similar way the tops of high mountains in the temperate regions of the northern hemisphere were systematically explored, and it was discovered that they too had dwarfed forms and typically hummocky growth patterns in the nether reaches of the snow line. The analogy on their physiognomy to that of arctic plants was correctly perceived and was assumed to be due to the severity of local conditions or the poverty of physical resources. But as collections increased through the sixteenth and seventeenth centuries at the hands of European botanists such as William Turner, Clusius, Gesner, Cesalpini, Pena and L'Obel, and more particularly with the production in the eighteenth century of numbers of local floras and regional lists, so botanists realised that many of the plant species found in the European mountains were identical with those of the arctic and sub-arctic regions, and yet others were closely related by generic or familial ties.

Mountain summits, however, were clearly separated from each other by low-lying lands in which no alpine or arctic plant could be expected to live, and over which no botanist would seriously suggest that they had migrated. Furthermore the montane species which were identical with those in high latitudes were divorced from their associates by some hundreds or thousands of miles which presented equally inhospitable conditions for their transfer. How then did they get where they were? Had the hand of God or some mysterious cosmic influence created plants in each region according to the conditions which prevailed, and so produced

two similar floras? The existence of, firstly, the same species on two adjacent mountains, and secondly, of the same sort of plants and the same sort of overall appearance for both alpine and arctic floras was to become in this manner a very crucial argument for the protagonists of special creation and for students of distribution in general.[5]

The first point, that the same species of plant lived on separate mountain summits, was one which did not become a problem for British naturalists until it was made apparent that Scottish mountains supported a great number of Scandinavian plants. With the instigation of botanical field excursions at Edinburgh and Glasgow in 1821 by their Professors of Botany (Robert Graham and William Hooker respectively) this was a fact that could not be long overlooked. These hardy forms were also to be collected in decreasing numbers along the mountain ridges of northern England and Wales, although here they were more likely to be accompanied by some few modified lowland species as the botanist moved in a southerly direction. Hewett Cottrell Watson, protégé of Robert Graham, was the first to make a note of this phenomenon as he stumbled through the mists of the Grampians in 1832, and he made the subject of Celtic botany very much his own by defying anyone to collect as much as he had whilst experiencing the same sort of adverse weather conditions.[6]

Not every boreal species lived also in the British Isles, but, as Watson pointed out, nearly every Scottish highland plant was to be found in the Scandinavian peninsula.

By contrast, the European Alps appeared to support what botanists of the nineteenth century began to call a "representative" flora in the wake of Humboldt's work to which I shall return in a moment. The plants of the uplands of the Pyrenees, Switzerland, Austria and Italy and, later, in 1841, the Carpathians,[7] were discovered to belong to the same genera or families as the species of arctic regions in the instances where they were not purely local or native to their own area. In such a way the southern floras mirrored or mimicked those of the north with an almost-but-not-quite identity. The phenomenon was not entirely a European one either: when taxonomists got to work on collections from the New World and particularly those parts which still remained under European rule (fortuitously for British naturalists, the more northern parts of the continent), or those obtained from the peregrinations of surveying ships in both hemispheres and from government out-stations in the various colonies, they found that these features of distribution were more or less consistent over the whole globe. Scandinavian plants were present in other countries not too far removed from that country; arctic-like plants were to be found in the

mountainous regions of north and south America, in Africa, the Himalayas and even New Zealand; and to some extent the Antarctic flora maintained a kind of "representation" of that which surrounded the north pole.

These peculiarities of distribution were not fully codified until after Alexander von Humbolt's great Essai sur la géographie des plantes (1807)[8] and his later work De distributione geographica plantarum (1817),[9] though they had undoubtedly been noted at several times during the preceding centuries. Nor did Humboldt himself attempt to explain the phenomena, but instead brought into focus all the points which directly and indirectly impinged on the topic of arctic-alpine plants. Humboldt described in an exhaustive and properly 'scientific' manner the physical conditions which regulated the distribution of all plants, and their collection into discrete associations or "assemblages" according to the temperature, rainfall, amount of sun and edaphic factors which each region possessed. He devoted a great deal of space in both these volumes to accounts of the zonation of mountains in which zones of elevation corresponded in their organic attributes to parallels of latitude, the higher regions of the mountain equating with the more northern or southern places of the globe. Thus on an imaginary equatorial mountain, and indeed in Humboldt's Tableau physique des régions équinoxiales added to the Essai, the full range of 'tropical' to 'arctic' floras would be encountered by the botanist as he moved from the base to the summit, representing in miniature the latitudinal belts of one or other hemisphere. These belts would naturally be compressed, distorted or eliminated according to where on the globe one's specimen mountain was assumed to exist: Humboldt gave a delightful plate with his treatise of 1817 of five mountains arranged together like a row of rock cakes according to latitude, and covered with different sorts of vegetation contingent on this topographical position and the height.

The parallel between elevation and latitude which Humboldt thus drew out attracted the attention which I believe it deserved, and, by the time of Lyell's Principles of Geology (1830-33), seems to have been something of an axiom of distribution. Lyell himself commented on the relationship and explained that any changes in climate would, under this rule, alter the distribution of living beings from ~~arctic~~ one to ~~temperate~~ another zones of latitude and similar zones up and down mountain-sides.[10]

So after Humboldt's Essai and the longer work of 1817 naturalists were doubly primed: at one level they were now ready and willing to take more notice of mountains than before; and at another, there was now a

distinct possibility that it might turn out that alpine floras were more than simply analogous to those of the arctic, and bore instead a metaphysical relationship of some inner symmetry (as Forbes was to propose) or that they were to all intents and purposes the very same flora which had been rendered separate at an earlier time (as Darwin suggested). The plants of alpine Europe provided substantive evidence for either view. On the one hand there were plenty of 'representative' species which gave these associations their distinctly 'arctic' air and which belonged to genera common in higher latitudes or closely related ones. Forbes was very impressed with such representation. And on the other hand, there was a positive identification of many alpine species with those existing in the north, which permitted an over-literal interpretation of Humboldt's analogy and the generalisation that these populations were essentially the same. Such was the position that Darwin was to take.

This was then a problem at the very heart of philosophical biogeography. The more a naturalist tried to draw up a coherent and all-embracing system of distribution based on his own ideas about creation and dispersal, the more he had to find a specific answer for the problem here described, since it could so easily be interpreted in a variety of ways and thus used against him. The stronger his answer, so the less likely were rival hypotheses to be. It therefore constituted something of a 'crunch' point on which distributional theories could stand or fall.

Certainly this was the manner in which both Forbes and Darwin approached the question.

Edward Forbes' explanation

Forbes (1815 - 1854) is now barely remembered by historians, and if he is it often appears to be for the 'wrong' reasons: as a correspondent of Charles Darwin; as a friend in need for T.H. Huxley when he arrived back from the Rattlesnake voyage without a job;[11] as the first paleontologist to the Geological Survey of Great Britain; as one of the founders of the Jermyn Street School of Economic Geology, which eventually formed the core institution of what is now Imperial College; as an expert marine biologist whose works and suggestions are still in regular use today;[12] and as a remarkable socialite who established the Red Lions Club of the British Association (still continuing) and who delighted his contemporaries with scientific songs and caricatures.[13] All of these points, true as they undoubtedly are and interesting for the light that they cast on Forbes' career and

engaging personality, seem to me to pass over the notable fact that Forbes was, in his time, a figure of considerable stature. In geological circles he stood on a par with men such as Lyell and Murchison.[14] His utterances were respected and his geology (i.e. the practice of it) was usually thought to be of an excellent quality. He was, in short, a force to be reckoned with.

Forbes' distributional studies were his major claim to contemporary scientific distinction, and he was noted by his colleagues chiefly for his explanation of the present-day patterns of animals and plants in Great Britain, and for the enunciation of two 'laws' of nature relating to distribution.[15]

Besides making his name known to British geologists through a series of papers on conchology given to the newly established British Association for the Advancement of Science in the late 1830's, he had been taken up by an enthusiastic Roderick Murchison whose brain-child the B.A.A.S. partly was. It was through his good offices that Forbes was enticed to London from Edinburgh where he was following a desultory career in medicine, and introduced to geological society as a "rising" naturalist. By now disappointed in his expectations of a comfortable inheritance which would allow him to pursue his interests as a gentleman naturalist, he sought to find a profession in science. In 1841 he was content to sail with Captain Thomas Graves to the Aegean where he could indulge his penchant for marine dredging, watercolour sketching and archaeological exploration among the ruins of Lycia. His extensive collections of marine invertebrata and the data on depths, substrates, water temperatures, currents and composition which accompanied them were acclaimed in his own time, and even now are justifiably said to be the foundation of European marine biology.

This surveying trip was cut short by Forbes' contracting malaria and an offer from his London friends of a position (albeit poorly paid) lecturing in botany at King's College. To supplement his income he managed to get appointed as Curator to the Geological Society's collections, again a post which he owed to the collective weight of influence wielded by his friends, of whom perhaps Lyell and Leonard Horner were most interested in his career.

During the next ten years Forbes went from strength to strength. In 1843 he presented the results of the Aegean survey in the Mollusca and Radiata of the Aegean Sea,[16] a title which belied the scope and intellectual depth of the work and in which he articulated his first major scientific statement about distribution. In the early months

of 1844 he gave a Friday evening discourse to the Royal Institution simplifying and expanding the former paper into The Light thrown on Geology by Submarine researches[17] which was praised by Leonard Horner in his presidential address to the Geological Society later that year,[18] and which ensured his appointment in 1845 to the newly formed Geological Survey of Great Britain under the direction of Henry De la Beche. In this position he published the long memoir for which he was noted by his contemporaries: On the connexion between the distribution of the existing Fauna and Flora of the British Isles and the Geological changes which have affected their Area...(1846), the most detailed attempt so far produced to correlate the present-day patterns of floras over Europe with the geological upheavals and submersions which had undoubtedly taken place as these were appearing and extending their ranges.

After this contribution, honours were heaped on Forbes as he continued to write, lecture and collate fossil collections, a rise to fame which culminated in the Presidency of the Geological Society in 1853 and, in 1854, election to the chair of Natural History in Edinburgh to succeed Robert Jameson his old teacher. For both these posts he was backed by the most eminent naturalists of the day.[19]

His removal from London for Edinburgh was mourned in geological circles, but his friends were even more distressed to learn of his death - from suspected kidney failure - only some few months later, and before he had even begun lecturing at the University.

Had Forbes lived I think he would have occupied such a respected place in the heart of British natural history that he must have offered a considerable threat, or counter-weight, to the theories that Darwin was to propose in 1859. Darwin certainly had recognised this possibility ever since he first read Forbes' distributional work, and he had suffered in two or perhaps three instances over a period of ten years from being "forestalled" by Forbes in one thing or another. Forbes carried enough weight and prestige to champion non-Darwinian theories of nature, as, in particular, he was an accomplished metaphysician and a well known proponent of that curious blend of Naturphilosophie and natural theology which was prevalent in British scientific circles at this time. He was one of a group of romantically inclined naturalists who believed in ineffable forces, symmetry, analogy and ideal types throughout nature (as did William Swainson, Richard Owen or, each in his own peculiar way, Louis Agassiz and the young T.H. Huxley) all of which were ultimately governed by a benign and non-interventionist God. If Forbes had indeed lived to contest natural selection he would have been a far more

persuasive - and hence more dangerous - opponent than the irascible and almost universally disliked Richard Owen.

I make these points because I suspect that some recent historians have succumbed to the temptation to try to understand Darwin's and Forbes' relationship through Darwin's eyes. The latter described it as a friendship which was at first close and which then, unfortunately, went sour as Forbes indulged in too much "rash speculation" for Darwin's taste. However, it is possible that Darwin may well have been attempting to explain away Forbes' evident success in the field of distribution by emphasising how very hasty some of his conclusions were. Darwin had been forestalled by Forbes over the interpretations of arctic and alpine floras; might he not put this down to the fact that he - the careful and meticulous scholar - had not wished to rush into print like Forbes? Again, Forbes constructed a history of organic life which was dependant on the dynamic movements of the earth's crust, and described spatial distribution as something which was also contingent on geological activity - two concepts that were at the heart of Darwin's hypotheses. Might the latter not attempt to banish these rival theories by consigning them to intellectual oblivion? Either way I suggest that we should not be too eager to take Darwin's opinion of Forbes as a reliable guide to what other people thought of him and his theories. Darwin was not a man of guile or brooding resentment by any means, but in his relationship with Forbes there are too many half-truths and hidden factors for historians to accept freely Darwin's own account or his opinions as expressed in letters to other contemporaries through these years.

Turning from these considerations to the main theme of this chapter, I should like to examine what it was that Forbes actually said about arctic and alpine floras and then to ask why it was that Darwin thought that during his life he had been anticipated in "only one important point" (Darwin was even elevating this above Wallace's contribution to natural selection theory), and why it was something which "my vanity has always made me regret".[20]

Forbes proposed his theory of arctic-alpine floras in 1846 in his paper On the connexion between the distribution of the existing fauna and flora of the British Isles and the Geological changes which have affected their Area, where it formed an accessory, but nevertheless important, argument for the existence of "specific centres". He believed that only one pair of individuals for each species had been originally created, and that from the single point that they may be assumed to have occupied they had extended their range concentrically as more and more individuals were produced by normal reproduction. This was, to Forbes,

plainly evident in the dispersion of organisms at the present day and, with his geological bias towards actualism, he supposed it to have been the case in the past. It was an idea that was commonplace at that time and which had been commonplace when Lyell wrote of it as an axiom in the Principles of Geology in 1830-1833, from whence Forbes, no doubt, picked it up.[21]

The only things which stopped this inexorable increase of individuals and the corresponding extension of their specific range were the existence of physical barriers (i.e. climatic or edaphic), geographical barriers (i.e. mountains, lakes, oceans) or the pre-occupation of land by another form. And ultimately, Forbes, like Lyell, thought that extinction would get them in the end, no matter how wide their range or great their numbers. Forbes called this enclosed region over which each species had spread a "specific centre", and generalised from this to a position where he called a whole flora by the same term.

In his paper of 1846 he particularly wanted to demonstrate that specific centres (in the sense of floras, or assemblages of a number of specific ranges) had contributed different parts of the British vegetation at different periods of geological time. This they had done by passing over lands which now formed barriers between sister floras, as England formed a barrier for plants destined for Ireland, or over lands which were now part of the sea-bed separating the British Isles from their nearest continental neighbours. So Forbes had to provide geological evidence that the parts of Europe now interposed between his sister floras had once been in a condition suitable to allow one specific centre or another to spread out and transmit its species to Britain. That is, he had to show that Cornwall was once connected to the north of France, southern England to central France, East Anglia to the Low Countries, south-western Ireland to the coast of Spain, and Scotland to Denmark and thence to the Scandinavian peninsula.

This, with some contrivance, he managed to do, although his proposal for a new 'Atlantis' in the Miocene to account for five or six Lusitanian species in Ireland generated much righteous criticism from more economically minded geologists.[22]

But his best and most striking example of the principle that he was here trying to establish was that of the arctic-alpine flora. Forbes went so far as to stake the whole point of his paper on this one

explanation:

> "The question of the general origin of alpine floras and faunas is, perhaps, the most important inquiry which such a position can affect, and may be regarded, in a great measure, as a fair test of its truth."[23]

He thought that if he could show how the plants of alpine Europe and highland Scotland were derived from a once more extensive arctic flora, then few naturalists could deny the validity of his thesis that all British plants had come from other regions in analogous ways.

Forbes proposed that the identity between the floras of Scotland and Scandinavia was a direct consequence of the subsidence and subsequent elevation of the whole of northern Europe during the period he called "glacial" or that of the "deposition of the northern drift". Following Lyell and in accordance with a great deal of confirmatory evidence, he believed that much of the northern part of the globe had experienced in the recent geological past very cold conditions and extensive subsidence of land, during which time glaciers occupied the remaining high ground while snow and ice more or less covered the rest, oceans etched out previous river valleys and 'rounded off' the sharp features of drowned continents while ice-bergs floated around in a "glacial" sea scratching rocks and depositing erratic boulders and piles of stones in odd places. This was Lyell's "Drift theory" and his alternative to an 'Ice-Age'[24] as Agassiz had suggested in 1840. This latter postulate dictated a universal Eiszeit which was formed from the extension of glaciers far beyond their existing limits to cover most of Europe, and which, on their retreat, were supposed to have gouged out or deposited all the features that we now associate with the Pleistocene age.[25] There were many points about Lyell's theory that were important for Forbes and I shall be returning to it and them in more detail below. Here I should only remark that Forbes described a typically Lyellian cool, oceanic and ice bound Europe:

> "This was the sea of the Glacial period, properly so styled, when the climate of the whole of northern and part of central Europe, was very different from what it is now, and far colder....This was the epoch of glaciers and icebergs, of boulders and groovings, and scratches. It exhibited conditions physical and zoological, similar - indeed, nearly identical - to those to be met with on the north-eastern coasts of America within the line of summer-floating ice."[26]

He suggested that the mountains of Scotland, parts of the Pennine chain, and Wales, all known to be considerably older than the "glacial" period, were for most of this geological epoch in the position of lowlying

islands, surrounded by a shallow glacial sea. In this particular topographical configuration the land received an arctic type flora that was created there and then (an important point to note), expressly suited for the local conditions. In fact, we may assume that, according to Forbes' doctrine of specific centres, this flora originated somewhere to the north of what was once Scotland and had simply spread south as the cold conditions of the glacial period and the subsidence of mountain tops into a collection of islands had allowed it to do.

Then, with a subsequent uplift of the sea bed and the alleviation of harsh and cold climates, Forbes asserted that the mountains were converted back to their original form and height, lifting the arctic flora on their slopes to three or four thousand feet. Only the plants which managed to remain in, or reach, a height which presented suitably cool environments would survive this elevation but, once there, there they would stay. Forbes wrote:

> "Now it was during this [glacial] epoch...that Scotland and Wales, and part of Ireland, then groups of islands in this ice-bound sea, received their alpine flora and a small portion of their fauna. Plants of sub-arctic character would flourish to the water's edge, but when a new state of things commenced, when the bed of the glacial sea was upheaved, its islands converted into mountains, its climate changed, and a suitable population of animals and vegetables diffused over its area, the plants of the colder epoch survived only on the mountain regions which had been so elevated as to retain climatal conditions similar to those which existed when those regions were low ridges or islands in the glacial sea."[27]

This was an elegant explanation which introduced nothing that naturalists did not know or take for a fact, and yet which quite notably synthesised these into something new. Forbes took Lyell's period of the northern "Drift", and the phenomena on which it was based, to posit the environment under which organisms were once living; he took Humboldt's rule of the zonation of mountains where the summits were in many respects physically analogous to true arctic regions; and he married with them the idea that floras spread and the earth moves up and down, to produce this pretty hypothesis.

Furthermore Forbes extended it to include not simply Scotland and other parts of Britain alone, but also to embrace central Europe and the Alps. Here, it will be remembered, on the sides of the Jura and other mountain ranges of central Europe there were species identical to those of the arctic circle, as well as some belonging to the same genera or families, yet being absolutely peculiar to these warmer regions. Taking initially only the first problem - that of identical forms in the Alps and the arctic circle - Forbes proposed that his glacial sea of the

Pleistocene had extended as far south as Switzerland, and that there was no reason to assume that subsidence had not taken place here also.[28] Thus the very same explanation would serve to account for this oddity of distribution:

> "Now I am prepared to maintain that the same means which introduced a subarctic (now mountain) flora into Britain, acting at the same epoch, originated the identity, so far as it goes, of the alpine floras of middle Europe and central Asia. For now that we know the vast area swept by the glacial sea...belted by land, since greatly uplifted, which then presented to the water's edge those climatal conditions for which a subarctic flora - destined to become Alpine - was specially organised, the difficulty of deriving such a flora from its parent north and of diffusing it over the snowy hills bounding this glacial ocean, vanishes, and the presence of identical species at such distant points remains no longer a mystery."[29]

And then Forbes launched into the second problem and into a discussion of representative forms, especially the representatives of arctic species which he found on European mountains. He posited that since there was a cool and semi-submerged topography in continental Europe as well as in Britain, and since the latter had received a flora especially suited for its particular conditions, there was no reason why the Alps had not too received a special flora of their own. He stated that this was indeed the case, and that the arctic regions and the Alps had both, whilst experiencing these very similar and severe conditions, been given two separate yet very similar floras. The one replaced the other in the same way that Humboldt's mountain summits represented the arctic.

Thus Forbes suggested that there had been a special creation of plants especially suited to the conditions presented by Switzerland and its environs whilst it was experiencing the geological changes of topography and climate that accompanied the Pleistocene. And although he did not say so, it seems to be the case that he believed <u>this</u> creation, this distinctive "specific centre" or floral assemblage, had been put on this earth with characters that emphatically mimicked the flora of other equally cold regions. The two floras were roughly the same because they were designed for the same conditions, yet they were different because they were sited in disjunct localities: in other words, they replaced or "represented" each other.

It is puzzling here to know why Forbes seemingly makes the Scotland-Scandinavia case so different from the Alps-Scandinavia case. If some of the alpine plants, though arctic-like, were specially created in that area why not the Scottish plants also? Forbes' choice of distribution

and survival in Scotland but special creation in the Alps seems entirely arbitrary. It is important, however, to note that he did postulate a creation for the true arctic plants: they had been created in Scandinavia during the cold period especially for those conditions, and had during that same cold period gradually spread out over a large area which included Scotland. Thus the one geographical region was one "specific centre" of creation. In the case of the Alps, other different species had been created which spread out over their region so forming another "specific centre" of creation. According to Forbes, God did not call the same being into existence twice so he postulated that these Alpine species had to be slightly different from those of the north.

And yet the facts of the matter indicated that there were also plants in Switzerland identical with those of the Arctic. It goes to show the strength of his belief in single as opposed to multiple creations that he suggested that these particular species had migrated from higher latitudes to colonise alpine lands when they were experiencing suitably cold conditions, when he could just as easily have postulated a double creation - one in the north and one in the south - to explain the occurence of identical forms in widely sundered localities.

For reasons best known to himself Forbes believed that nature exhibited both identity and resemblance or representation in a finely balanced system. I suggest that here he trimmed his sails to suit the wind and proposed a mixture of these two qualities to answer the one case where neither would suffice on their own. That is, the alpine plants of Switzerland were sometimes identical, sometimes analogous to those of the north, and so Forbes proffered an amalgam of his two explanations to account for the fact.

Further details on these views will be found in the appropriate chapter dealing with Forbes' vision of an all-embracing representation through space and time, and here I would only like to stress the mysticism which was implicit in this explanation of alpine floras. Forbes felt that if two, or even more, floras were created at the same time (i.e. if the original couples of individuals had been placed at what was to be the centre of their range) then for the sake of metaphysical ideals they ought to exhibit some sort of relationship. This he found in the morphological fact that species of one specific centre (viz. the Alps), though distinct forms, were actually members of the same genus or family as the species of another specific centre (viz. the arctic circle). There was a taxonomic closeness which to him was just as striking a fact

as the reappearance of identical forms in far removed areas.

So I suggest that Forbes thought that he had proved, or, at the very least, demonstrated the probability of a synchronous creation of analogous floras each in their own region. In his 1846 paper he showed how these separate floras could be mixed through the unremarkable processes of geological activity combined with a normal extension of ranges, which led to the arctic plants spreading south under particularly favourable geographical and climatic conditions to mountains which already had (or were in the process of acquiring) their own 'arctic-like' species.

Unfortunately for Forbes, however, it was the strictly actualistic explanation of this intermingling of floras and not his explicit statements of analogous creations which received contemporary praise. Geologists such as Leonard Horner, Roderick Murchison and Charles Lyell were delighted with his elegant combination of geological dynamics and biological movement, and envisaged a new science of geographical distribution based on motion. At the British Association meeting of 1846 at Southampton, Murchison claimed that "these views" of Forbes', "will introduce a new class of inquiries into natural history, which will link it on more closely than ever to geology and geography," and went on to describe his "theory of the origin of Alpine Floras distributed far apart".[30] Horner told the Geological Society of the merits of this "admirable example" in what he believed to be an "interesting and attractive" memoir full of "suggestive" and "great views".[31] And Lyell was so extremely gratified by such an extended usage of his own theories of local climatic changes, geological elevation and subsidence, and the dynamic movements of floras and faunas which he postulated in the Principles, that he did not even seem to mind that Forbes had blatantly omitted to cite Lyell's own priority in these fields.[32]

This then, was Forbes' theory of the origin of mountainous plants throughout Europe. Despite his own philosophical suggestions about 'representation', the hypothesis was taken up for the new wave of geological dynamism which it furthered and for the very neat explanation of the way plants and animals spread and were rendered disjunct by continuing geological processes.

What did Darwin think of it? He too was part of this new-wave geological set which circled around Lyell and which preferred to work with a constantly shifting earthly crust. He was, in fact, rather disappointed because he had independently come to very much the same conclusion about the introduction of Scottish and Alpine plants. Writing to Hooker a few days after Forbes had first spoken of these

notions at the British Association meeting of 1845 (in a preliminary sketch of the 1846 paper[33]), Darwin complained:

> "Forbes is doing apparently very good work about the introduction and distribution of plants. He has forestalled me in what I had hoped would have been an interesting discussion - viz. on the relation between the present alpine and Arctic floras, with connection to the last change of climate from Arctic to temperate, when the then Arctic lowland plants must have been driven up the mountains."[34]

And, if one turns to Darwin's own writings on this question in his species sketch of 1842 and the Essay of 1844, it can be seen that he was quite right. Forbes had forestalled him, for Darwin's theory was remarkably the same as the one that Forbes put forward. There were minor differences which I shall discuss in a moment, and there was one major extension of the proposal which Darwin developed under his own steam, but nevertheless in most respects these two accounts were identical.

Charles Darwin's explanation.

In the same way as Forbes' explanation of arctic and alpine floras was a deployment and demonstration of his ideas about specific centres and 'representation', so too was Darwin's account steeped in his own philosophy of nature. The issue was one that had to be described in terms of natural selection and "descent with modification", and, like Forbes, Darwin saw that whatever theory he produced it would be a critical one for larger, more general interpretations of biogeography. If this one particular question could be answered in Darwinian terms, then so could other distributional patterns be drawn into an evolutionary scheme.

In the first sketch of his theories of natural selection and evolution, drafted in 1842 and consisting of little more than a series of aide-mémoires, Darwin introduced the arctic-alpine problem into a discussion of general geographical distribution where he was anxious to show that changes in climate or altitude could affect the ranges of species. He needed to show that there were plenty of alterations in the physical configuration of land to fuel all the rearrangements of species which he thought might "unsettle" the "constitution" of some of them and make them vary. Thus he wrote:

> "Subsidence of a continent in which free means of dispersal, would drive the lowland plants up to the mountains, now converted to islands, and the semi-alpine plants would take the place of alpine, and alpine be destroyed, if mountains originally not of great height. So we may see, during gradual changes of climate on a continent, the propagation of species would vary and adapt themselves to small changes causing much extermination."[35]

He was here concerned with the fluctuations of level which would cause some species to climb up or down mountains to remain in a suitable climatic zone, and the effect that this might have on the poor plants which lived right at the top. These would not survive at all if the land subsided to any great extent, for there was nowhere higher for them to go to maintain appropriately cool conditions. Quite evidently basing his view on Humboldt's law or rule of the zonation of mountains, Darwin thus envisaged these zones moving higher or lower up and down the sides of hills as the land itself subsided or was elevated by geological activity. And again quite plainly basing his ideas on Humboldt's parallel between areas of elevation and latitude, Darwin suggested in the later parts of this passage that these shifts in a mountain flora would be mimicked by similar changes of climate over a continent. The rearrangement and extinction of plants as seen on a mountain that was undergoing changes of level, would also be found on a continent which was undergoing changes of climate.

All these points and more were to be read in volume two of Lyell's Principles.[36] Here in the middle of a long exposé of how frequently physical conditions were changing, Lyell told his readers that alterations in the level of mountainous lands would result in the movement of plants up and down their slopes, and that analogous changes in climate on the 'flat' would lead to the extension or retreat of arctic or temperate floras into different latitudes. Lyell was here interested in showing that extinction was part of the regular order of things, and that species were subject to ceaseless changes in their stations and so rendered liable to be extinguished.[37] But it seems to me very probable that Darwin took these remarks and applied them for his own thesis that much change led to an unsettled "constitution" and thus to variation.

And I believe that it was Lyell's comments and those which followed in the next few pages of the Principles that gave Darwin the basis of his theory of alpine-arctic floras. Lyell illustrated the alterations in distribution that would result from changes in elevation or climate, and he then went on to suggest that in an analogous fashion so would major belts of vegetation migrate from north to south (or vice versa) if the earth itself became cooler (or warmer). "If the earth is cooling down", he wrote, "there will be a migratory movement from the poles to the equator", and conversely, if the earth heats up the movement will be from the equator to the poles.[38] Likewise, in the case of arctic plants which inhabited the mountain summits of Scotland there would be a general flow of these species from the heights to low lying

land if cooler conditions set in:

> "If the climate, therefore, of the polar regions were transferred to our own latitudes, the species in question would immediately descend from these elevated stations to overrun the low grounds."[39]

In these words lay the source of Darwin's theory, and, I am quite sure, that of Forbes as well. Darwin proposed in 1842 that during the period of snow and ice which was then more or less acknowledged as a certainty, the climate of Europe was such that arctic plants could move southwards from their usual haunts to colonise the land available. With a later change in temperature for the better, these species would be forced to retreat either back to the arctic circle or upwards, up mountains, in pursuit of cooler conditions. The forms thus left on elevated lands would, in effect, be little islands of arctic species marooned in a sea of temperate and lowland plants. He noted:

> "The mountains of Europe were quite lately covered with ice, and the lowlands probably partaking of the arctic climate and fauna. Then as climate changed, arctic fauna would take place of ice, and an innundation of plants from temperate countries seize the lowlands, leaving islands of arctic forms."[40]

And only two years later in 1844 he presented his meaning more fully in the Essay:

> "Now we may with confidence affirm, from the number of the then floating icebergs and low descent of the glaciers, that within a period so near [to the present] that species of shells have remained the same, the whole of Central Europe and of North America (and perhaps of Eastern Asia) possessed a very cold climate; and therefore it is probable that the floras of these districts were the same as the present arctic one...At this period the mountains must have been covered with ice of which we have evidence in the surfaces polished and scored by glaciers. What then would be the natural and almost inevitable effects of the gradual change into the present more temperate climate? The ice and snow would disappear from the mountains, and as the new plants from the more temperate regions of the south migrated northward, replacing the arctic plants, these latter would crawl up the now uncovered mountains, and likewise be driven northward to the present arctic shores."[41]

So taking Humboldt's analogy between height and latitude, Darwin reasoned that arctic plants were just as likely to move up as they were to return north under the pressures of changing climate. And he took Lyell's suggestion that changes in climate would be accompanied by changes in the characteristic vegetation, to suggest that when Europe was undergoing very cool conditions it would support a flora suited to the snow and ice. Barely having to reverse Lyell's point that summit floras would descend to the lowlands under a decreased temperature, Darwin asserted

that an increase in temperatures would cause them to "crawl up" the recently ice-bound mountain slopes until they found an appropriate home.

Like Forbes, he assumed that there was a sort of double flux or movement of plants and climate, simultaneous with the activity of geological processes. But, and this is a notable point, Darwin did not suggest that Europe was necessarily subject to elevation and subsidence of land relative to sea level. His theory as given above did not mention the hydrographical configuration that Forbes had insisted on: that is, Forbes asserted that European mountains were left sticking up out of a shallow "glacial" sea as the only available land for plants to colonise. And nor did Darwin talk of plants "flourishing to the water's edge" as did Forbes. For the major difference between Forbes' and Darwin's theories was that Darwin had no need of the sea or the watery configuration of drowned continents which all contributed to the isolation of Forbes' arctic plants. Darwin's boreal species were active colonists and they spread wherever there was land for them as yet uncovered by snow or ice, for they moved themselves across Europe and, when the time came, up mountains. Darwin's plants were not lifted by the elevation of their habitat (i.e. the remains of submerged mountains); they got there under their own steam in the face of pressure from encroaching temperate species. Forbes' plants were passive, at first isolated by the act of colonising islands in a glacial sea and then elevated to the heights in which they were eventually to live.

Nevertheless the similarities between the two theories are striking. Both men supposed a change in climate which allowed plants of other latitudes to overrun what was left of Europe, and Darwin depended on ice and snow as a limiting factor where Forbes preferred a sea. With a subsequent change in temperature, both theories posited that the arctic species would follow their native climates, and return to northerly latitudes or elevations which would support them best. And the most striking similarity of all was the fact that these proposals were both put forward to answer exactly the same question: why were there identical species on the heights of temperate zone mountains and in the polar regions. Darwin and Forbes saw this question in a light which agreed in every respect, and both suggested that the identity was due to a former extension of one flora which was subsequently disunited and segregated through geological activity and changes in climate. They both claimed that the plants left on the tops of mountains in Europe were the remnants of a once widely spread association of northern species, so that their similarity to plants isolated on other mountains and to those of the

arctic circle was not at all mysterious but a simple result of continuing natural processes.

With these more general tenets in common it is clear that any differences between Darwin's and Forbes' theories are indeed minor. Yet there was one further difference which I hold to be rather more significant and to reflect the individual philosophies of nature which each naturalist held dear to his heart. Forbes had explained the existence of similar but not identical arctic-alpine species in the north and in central Europe in terms of a "representation" which his metaphysical principles required. Darwin, on the other hand, was to account for the same phenomenon on the alternative footing of natural selection.

Darwin postulated that the appearance of species closely related (but not identical) to those of polar regions in Switzerland and elsewhere on the globe (even as far away as Tierra del Fuego) was a result of the same sort of combined organic and geological processes, with a bit of natural selection and consequent modification thrown in. In his Essay of 1844 he set out in detail the far flung distribution of arctic forms and their congeners and pointed out that his theory would account for all these "apparently anomalous" cases. He suggested that during the same cold period the snow line of the mountainous backbone of north and south America could have been much lower. He continued by asking whether it would be possible that arctic plants of high latitudes could have migrated down along this "broad high-road" brought on by the low descent of the snow line, and so reached the austral hemisphere and even perhaps the Antarctic. He wrote:

> "In this case the alpine plants of the long chain of the Cordillera would have descended much lower and there would have been a broad high-road connecting those parts of North and South America which were then frigid. As the present climate supervened, the plants occupying the districts which now are become in both hemispheres temperate and even semi-tropical must have been driven to the arctic and antarctic regions; and only a few of the loftiest points of the Cordillera can have retained their former connecting flora. The transverse chain of Chiquitos might perhaps in a similar manner during the ice-action period have served as a connecting road (though a broken one) for alpine plants to become dispersed from the Cordillera to the highlands of Brazil."[42]

In other words, the plants which Darwin here called "alpine" (meaning mountainous and characteristically 'arctic' in character) were provided with suitable conditions all the way from one pole to another, along which "high-road' they spread and migrated until warmer conditions forced them, as in his previous example, to retreat to cooler latitudes

or elevations. Only the highest peaks of the Cordillera would be high enough to supply conditions which approximated to those of the arctic circle, and here, on these few peaks, would be found remnants of their "former connecting flora".

And these species would, by necessity, be juxtaposed with others native to the Cordillera so that some would be rendered extinct whilst others changed and adapted to local circumstances. So he could explain the apparently odd case of the "mountains of Europe, of some mountains in the United States...and of the summits of the Himalaya having many identical species in common conjointly with the arctic regions, and many species, though not identical, closely allied."

This last hypothesis was worked up to a very sophisticated degree for Darwin's 1856 to 1858 "big Species book" which he had begun to write at Lyell's recommendation.[43] The principles of the theory did not change, but Darwin added considerable detail - much of it gleaned from his botanical adviser Joseph Hooker - and expanded his ideas to full literary exegesis. By now, of course, he was quite aware that he had been forestalled in print by Forbes and he took care to cite Forbes in all the appropriate places. Indeed Darwin was so scrupulous in this affair that it might even seem that he did not recognise <u>any</u> differences between the two theories.[44]

Thus in 1856 Darwin continued with the same ideas about the origins of mountain floras in Europe and wrote of these and the similar species of north America and Asia as if they were, once again, the remnants of a formerly more extensive arctic assemblage:

> "I can see no great difficulty in supposing that all the organic beings now common to the two worlds, inhabited the long line of shore-land from eastern America to Lapland. As the glacial epoch came on, the species in common, associated with some not in common, would have migrated southward, and subsequently as the warmth returned they would have remigrated northward to their present homes. ...Hence we might expect to find in favourable situations, both on the southern highlands and in their latest northern homes, nests of species occuring elsewhere but not in the country immediately adjoining on either hand."[45]

He pointed out that all the plants of the arctic circle were very similar and that they encircled the pole from eastern America right round to Lapland, via Alaska and Siberia. These moved in accordance with climatic changes, and parts of the original flora were left stranded on high land throughout the northern hemisphere.

In many cases too, he supposed, there would be native floras in such regions and these would mingle with the transported species if they could

survive the cold conditions. For example, he thought that the Alps and Pyrenees (which had been standing for several epochs before this time) must have had some plants covering their slopes before the cool period set in, and that these plants would join the others and act in concert with them:

> "Previously to the glacial epoch these mountains must have had their alpine species, such as Gentians etc. which do not inhabit the arctic regions, and these on the returning warmth, after having, as it would appear, spread over the surrounding country would together with the arctic species have reascended the mountains."[46]

But this was an aside. Darwin pressed on with his main point that the processes here in action presented "all the elements...which tend to modify species". That was, a "considerable lapse of time, isolation, and especially association with somewhat different sets of organic beings." He resumed his discussion with an elaboration of how arctic-alpine floras were especially likely to become modified:

> "As soon as this southern movement had taken place, the several existing floras and faunas of the northern hemisphere would have been separated from each other, as at present, would have been differently associated together and exposed to somewhat different conditions. And as we are now dealing with comparatively ancient times, we might expect, according to the principles which we are testing in this work, that only a few species of those originally in common would have remained absolutely identical, but we still might expect plainly to see in the productions...of temperate Europe, N. America, and Eastern Asia, evidence of their descent from a common home and common parentage; and this, I believe we do see, in the many representative species of these now quite separated countries."[47]

In other words, the outliers or remnants of arctic floras would be liable to vary, be selected and change in some slight degree to become what Darwin called "representative species", or forms very closely related to their sibling species. Hence he could explain why many of the plants of the Alps, or indeed the Himalayas or Cordillera, were allied, but not identical with those of high latitudes. Natural selection and evolution were here replacing Forbesian ideas of mystical analogies or representations; Darwin could account for all ranks of differentiation from the 'norm' of existing arctic species by calling in selective processes to a greater or lesser degree, where Forbes had relied on a diminishing force of "representation". The further an alpine flora was from the north pole, the greater the discrepancies between it and its source, increasing from specific differences to those of generic or familial rank. Forbes answered this fact by pointing out how very symmetrical it was to

have "generic correspondences, specific representations and specific identities" varying with distance. Darwin countered by postulating that here selection was acting under different conditions for varying lengths of time, and so of course the products would be taxonomically increasingly removed from any aboriginal stock in common.

Now Darwin pushed this last notion to its logical extreme, as foreshadowed in his earlier Essay of 1844. He proposed the theory that arctic and temperate plants had migrated through the tropics at some previously colder period to colonise the mountains and lowlands of South America and Australasia. Citing all the evidence he could muster to prove that the whole globe must have been cooler during the Pleistocene (though not necessarily all cold all at the same time), he suggested that the tropical plants were thus under some strain and less likely to ward off invading temperate and arctic plants.[48] Naturally arctic species could only cross the equator where there was high land such as the Cordillera or Himalaya, but he thought that there was every possibility that temperate species could have penetrated and held their own in the lower lands between the tropics. He wrote that he thought this view would explain why there were European temperate plants in Australia or the Cape, northerly forms like birches and brambles in the hinterlands and foothills of the Himalayas, and species belonging to genera confined to the arctic circle in mountainous New Zealand. Everything was due to a trans-tropical migration when the earth was once cooler, and subsequent modification under the influence of changed associations and prolonged isolation from the parent flora. It was a vision of breathtaking grandeur (not without its problems however, which Darwin had the good sense to itemise and solve to the best of his ability), and it was perhaps the first pan-global theory of distribution ever to be articulated. And it was entirely his own creation. There was nothing like this in either Forbes or Lyell.

* * * * *

It was, in fact, this last hypothesis which proved to be very difficult for Joseph Hooker to swallow, even though it was he who had supplied Darwin with much of the botanical information used to buttress it. He thought the doctrine a "startling one", and confessed that "I can hardly stomach keeping the tropical genera alive in so very cool a greenhouse."[49]

Since his - Hooker's - problems with Darwin's theory of trans-tropical migration and other points which he put forward pertaining to

arctic-alpine floras, were freely discussed among the two friends, they are well worth further study. They illustrate in an effective manner what it was that Darwin and Hooker thought that he was doing.

Rather than continue now with an analysis of Darwin's opinions on this and other issues relating to arctic and mountain plants as here discussed, I turn to examine the difficulties which Hooker found in Darwin's proposals. Whilst he read Darwin's manuscript about the distribution of floras he also remembered problems that he had had with Edward Forbes' theory, and these too were drawn into his discussions with Darwin. We can find in Hooker's notes and letters something approaching a full and informed contemporary critique of the whole business.

Joseph Hooker and the geological approach to nature.

Although Darwin's friends were rarely asked to read his preliminary sketches of natural selection, Hooker was one of the chosen few, and the naturalist to whom Darwin most frequently turned for advice and criticism. He was invited in 1856 to comment on Darwin's case for arctic-alpine floras, a piece which had been written out for his big "species book" under the rubric of "Geographical Distribution". It was the first sample of his work directly related to natural selection that Hooker had read since he had gone over the short Essay of 1844 at Darwin's request,[50] and, no doubt, he was flattered to be singled out in this way. On Darwin's part, he knew Hooker to be the most suitable "sounding-board" for a botanical and distributional hypothesis of this order and lost little time in notifying him that he would want Hooker to read his paper as soon as it was finished. He called it a theory of "alpine floras and faunas and the supposed cold mundane period."[51] In practice, however, as we have already seen, it was almost totally devoted to plants and their dispersion, although Darwin did throw in a few references to marine shells following in the footsteps of the snow and ice in an equivalent manner.[52]

By July 30th 1856 Darwin's manuscript was still not copied out and so he had to curb his impatience for Hooker's verdict until the latter's return from a summer walking tour in late September. When the manuscript (amounting to some forty pages) eventually reached its destination Hooker found that Darwin had appended a note instructing him in what spirit he was to peruse it. He was exhorted not to be "too severe", nor "yet too indulgent", so that, reading between the lines, it was evident that Darwin was anxious for Hooker's approval.[53] Indeed, as he had said a little earlier in the year, this subject was

important for him since he was trying to answer all the points which appeared at first glance to be against his theory, and this section was primary material for showing that "multiple creation is a fallacy".

By November 4th Hooker had dispatched an encouraging note to which Darwin gratefully replied, and, on the 9th he gave his considered verdict:

> "I have finished the reading of your MS, and have been very much delighted and instructed. Your case is a most strong one, and gives me a much higher idea of change than I had previously entertained; and though, as you know, never very stubborn about unalterability of specific type, I never felt so shaky about species before."[54]

And he remarked that he had added comments to the text and had also "a page or two of notes for discussion".

It is these comments and notes that here deserve observation. Many were concerned with minor details, as might be expected, and others with more substantial aspects of Darwin's proposals. Of the latter there are two recurrent themes which represented the major difficulties that Hooker was to experience, and it is to these alone that I intend to direct attention for reasons which will shortly become apparent. Starting at the point where I left off in the previous section, I shall look at Hooker's commentary on Darwin's theory of a trans-tropical migration, and then, to round off this chapter, at Hooker's scepticism about the transportation of plants by icebergs. The bulk of Hooker's criticism illustrates the differences between Hooker's assumptions about nature and those of Darwin and Forbes.

Certainly Hooker was perplexed by Darwin's doctrine of a migration of arctic and temperate plants through the tropics to appropriately cool regions in the southern hemisphere. Why were not all tropical species killed off? And since temperate regions were closer to the equator than were polar latitudes, surely the temperate forms would have begun to move earlier in geological time than those of the arctic, and thus would have had a longer time in which to colonise the southern parts of the globe? But the numbers of such/australe temperate species were few. How did Darwin "wriggle" out of that?

Unfortunately these queries are not now extant, but Darwin's reply of 15th November makes the questions quite clear by the sort of answers which he provided. "I have not been able to stop myself meditating on your powerful objection to the mundane cold period" he wrote, and attempted to explain why he did not believe that "many-fold more of the warm-temperate species ought to have crossed the Tropics than of the

sub-arctic forms".[55] He agreed that temperate species would, in fact, begin to penetrate the tropics long before the arctic or sub-arctic forms reached these very warm regions, but, he asserted, they would thus be exposed to new conditions for a far longer time than any boreal species and so - according to his views - would be subject to variation, natural selection and change in identity. Therefore, he wrote, there would be few absolutely identical species in the temperate floras of the north and south but rather more representative species.

> "But according to the notions which I am testing...in such change, I think, the result would be as follows. Some of the warm-temperate forms would penetrate the Tropics long before the sub-arctic, and some might get across the equator long before the sub-arctic forms could do so (i.e. always supposing that the cold came on slowly), and that therefore these must have been exposed to new associates and new conditions much longer than the sub-arctic. Hence I infer that we ought to have in the warm-temperate S. hemisphere more representative or modified forms, and fewer identical species than in comparing the colder regions of the N. and S."[56]

The answer to Hooker's query thus lay in the suggestion that temperate plants would move as soon as the cold came on ("always supposing that the cold came on slowly") and would indeed penetrate the tropics long before the arctic forms managed to do so. Yet on the theory of natural selection these first movers were inevitably exposed to "new associates and new conditions", and hence were subject to change, so that most of his migrants would now exhibit a different but still "representative" constitution. Here we can see the importance of representative species to Darwin's theory of natural selection. And, by implication, because the migration was a continuing movement, the species which were in Darwin's terms the 'last' to cross the tropics were also the forms which were thus exposed to new conditions for the least length of time and so likely to remain identical.

In short, according to Darwin it all depended on time: if long periods elapsed then species in a new environment ought to change; and if altered circumstances have existed for only a short while then no change can be expected. "Time" he told Hooker, "is a most important element".

And this sentiment was taken to heart by Hooker. But he spotted a flaw in Darwin's argument which laid everything at the door of time, and riposted in no uncertain terms. If it was time that was the crucial element why had not the arctic forms changed more than the temperate ones? They had twice as far to go and took twice as long to do so; surely

Darwin ought to let them become modified?

> "I write only to say that I entirely appreciate your answer to my objection...You certainly have wriggled out of it by getting them [temperate plants] more time to change, but as you must admit that the distance traversed is not so great as the arctics have to travel, and the extremes of modifying cause not so great as the arctics undergo, the result should be considerably modified thereby. Thus: the sub-arctics have (I) to travel twice as far, (2) taking twice the time, (3) undergoing many more disturbing influences."[57]

And only a few days later he repeated the point that Darwin's hypothesis failed to account for the fact that in their global peregrinations arctic plants were exposed to more changes than most plants ever experienced. "You expose them to more extreme conditions than any other plants can ever be subjected to". Ought not they to be "proportionally altered"?[58] As Hooker saw it, Darwin was arguing on the one hand that time gave altered conditions and new associations which led to changes in species for temperate plants, and on the other hand, that the same elements led to no modification in the case of arctic plants. Darwin was lacking in consistency, and Hooker volunteered the opinion that "I think this will hardly hold water".

Besides this, Hooker asked in a bewildered manner whether Darwin perhaps assumed some kind of "latent" arctic property which was "masked ...in the tropical part of their course"? This property might thus restrict the amount of change which any arctic plant could undergo, and so the southern individuals remained more or less the same as those of the north. Such a suggestion was equivalent to asking Darwin to dine with the Devil, and he replied at length within twenty-four hours to disabuse Hooker of this notion. It was natural selection which explained everything and he was only sorry that he had not sent Hooker some preliminary notes on the "theory of causes of variation" and a proper account of how variability was, in his eyes, different to the formation of new races or species.[59]

He therefore claimed that variations may well have occurred as all these plants - arctic and temperate alike - had moved around the globe, but that he did not expect any stable varieties or races to have arisen until each form was more or less settled in its new surroundings and among its new companions. That is, the conditions were changing too rapidly and fluctuating from one extreme to another so that selective activity had nothing steady to work against. Selection undoubtedly took place, but Darwin thought that its results were continually being cancelled out. Only when relatively stable conditions were prevalent did Darwin's variations manage to accumulate minute changes.

And with this letter Darwin closed the debate. Perhaps he suddenly realised how little Hooker knew of his ideas and thought that it was futile to continue any further until Hooker had read other parts of his big "species book". Or perhaps the two met at the Philosophical Club as they had been attempting to arrange to do and thus had resolved the issue verbally. In any event their correspondence on this topic ceased abruptly at the end of November, and by December 1st the two men were deeply immersed in a discussion over the sexes of trees.

But despite the brevity of this sequence of letters there are some notable general points to be made. In particular, the notions which both parties seem to hold about the nature of geological time deserve a closer look for it was this single theme of 'time' that I believe constituted the major stumbling block in Darwin's theory of a trans-tropical migration with which Hooker had to contend. And because their ideas about 'time' were different they were led to express themselves in different ways.

Darwin was able to think of time's flow as being in some way independent of the organic and inorganic changes by which it is usually measured. Neither the physical constitution of species nor the physiographical construction of the earth were, for him, necessary indicators of the passage of time. Thus he appeared to hold that the hands of a clock were a mere convenience to give men some idea of the passing of an another absolute time.

I could here point out that Darwin's idea is of course Newton's. In the Scholium to definition VIII of the Principia Newton distinguished what he called natural time from relative or apparent time, and pointed out that there may not be any regular motion by which man can truly estimate the "flowing of absolute time".

Hooker, by contrast, thought that the onward movement of time was marked or characterised only by a succession of alterations in the geological conditions of the earth and, if Darwin's theories were true, by a succession of alterations in the organic kingdom. A change from (a) to (b) was the only way in which Hooker could visualise time as a dimension.

With a confidence born of this belief, Hooker asserted in one of his November letters:

> "You cannot but allow of Time and altered conditions and altered associations...that all these are more or less convertible terms."[60]

To put it another way, were not time and change in the inorganic and organic worlds synonymous? Hooker could not comprehend a change in time without any physical changes to denote it.

Thus it seems to me that Hooker elaborated on Lyell's dreadful warning in the Principles that geological periods were invented, just like the rank of genus or order in zoology and botany, and that the time scale was merely an artificial construction based on the differences that each set of formations presented to those which lay above or below.[61]

Hooker took geological time to be indicated by the changes from one formation to another, and so understood Darwin's theory of the transformation of species as something which proceeded along analogous lines. In this way he must have thought that species, genera and families were terms applied by naturalists to denote the degree of change which each form had undergone through time. Or at least this is how he interpreted Darwin's theory. "Time" and "altered conditions" and "altered associations" were, to him, inter-convertible terms, so that the concept of time implied a change both in physical conditions and organic distribution patterns. This last, under Darwin's view, was assumed by Hooker to lead automatically to change in specific identity.

Yet Darwin's response to this brief but telling assertion was, in a word, "No".[52] Such a correlation between time and change was not what he meant, for evolution was established on natural selection not time. "Time", he wrote, was "important only so far as giving scope to selection". And he recognised the differences between his view and Hooker's by lamenting "God knows whether you will perceive at what I am driving".[63]

My suggestion here is that Hooker applied his own understanding of geological time to a thesis where time was something rather different. Darwin's time ran independently of any organic or inorganic 'markers' and simply allowed by its passage "scope for selection". This latter view, I contend, was if not typical at least characteristic of a geological approach to natural phenomena. Contemporaries of Darwin's such as Lyell, Edward Forbes and Leonard Horner, were well aware of the range of pitfalls and advantages to be derived from separating or amalgamating a succession of geological periods with something which was an independent chronology.

Forbes, for instance, in his individualistic manner, was all for a clear demarcation to be drawn between geological time and that separate time scale which formed "no part or essence of the Divine scheme of organised nature", and he asserted that time was merely an "attribute with which man's mind invests Creation."[64]

Leonard Horner saw things slightly differently and exhibited a firm grasp of what we might now call 'geological relativism'. He tried to explain to the Geological Society how epochs were 'parcels' of time and that they could therefore be arranged relative to each other and to the present without any need to correlate them with an absolute chronological scale (such as might be provided nowadays by carbon dating ~~or pollen analysis~~). He pointed out in 1847 that geological periods meant "measures of past time" and that "at the time pliocene deposits were forming in Europe, it was pliocene time all over the world".[65] This was a statement necessary in view of the contention that had been, and was still then arising over the contemporaneity of certain deposits - not necessarily pliocene - at far removed localities.[66]

Lyell too had tried to demonstrate exactly this point that periods were 'parcels' or "measures" of time, albeit with no firm boundaries, by his espousal of a purely arithmetical way to characterise formations. Instead of relying on the kind of species which each deposit might bear, or on analogies between these forms and the fossils of its neighbours in time and space, Lyell had claimed that miocene and pliocene, for instance, could be demarcated by the proportions of living to extinct species. The proportions of every fossil assemblage were assumed to be the same wherever they appeared on the globe, and so the ratio of extinct to extant forms in pliocene America was the same as the ratio of pliocene Europe.[67] Therefore, as Horner pointed out, any slight differences in morphology would not obscure the fact that these deposits had been laid down under one "pliocene time" that reigned over the entire world.[68]

So Lyell and Horner were agreed that geological time was relative and based entirely on the degree of change which could be discerned from formation to formation, and from epoch to epoch. Yet neither would, I think, have denied that there was also absolute time of a sort which the post-Einstein world might like to retrieve. And it was this time that Darwin was talking about when he claimed that long periods were significant in that they gave "scope to selection". The passage of many centuries rendered it more and more probable that varieties should occur and that selection should act.

Hooker, on the other hand, however much he realised that geological time was based on relativism, was still unable to relinquish the notion that time was something which could only be gauged by a change from one state of affairs to another. No wonder then that the two men were at odds over how Darwin's theory of migration, which involved time and change but with such a fine distinction between them, should be interpreted.

Hooker despite his attempt to understand Darwin's meaning could only show his inability to grasp the niceties of the dual time that geologists spoke of. He was not fully versed in the ways of geological thought, and, quite naturally, took Darwin's remarks to relate to the sort of time with which he was familiar. In short he had difficulty with the geological approach to nature.

To expand on this assertion a little further, but in a slightly different context, I should like to turn now from Hooker's lack of comprehension of Darwin's time notions to look at his other comments on this theory of arctic-alpine plants, which also reveal yet more incomprehension of the 'geological' method.

Hooker could not see how either Darwin or Forbes proposed to get their floras moving from point (a) to point (b).

The suggestions which both naturalists had put forward seemed to Hooker to be patently inadequate and in some cases entirely against the facts of distribution. To characterise each position briefly, Forbes had presented a scheme in which the 'island in a glacial sea' constituted the major theme and so he had been forced to rely on transporting his arctic flora from the polar regions by icebergs; Darwin did not speak of seas or islands but he insisted that the outline of Europe had remained roughly the same, though prone to changes of level throughout the pleistocene, and so he too had to call in icebergs to supplement overland dispersal; what Hooker would have liked was a big elevated continent over which arctic plants could have migrated south with no such accessory aids.

I suggest that Hooker's reasons for preferring continental extension or land bridges of this nature were entirely negative and founded on the difficulties that he could so easily discern in any alternative view, such as those he found in a dependence on icebergs and a more or less random and accidental dispersal mechanism. And as I shall point out shortly, these difficulties were as nothing to Forbes or Darwin for they looked at the question through different eyes.

Firstly, there were for Hooker many practical reasons for rejecting iceberg transportation . He had spent years circumnavigating the southern ice pack with Captain Ross, and he had rarely seen ice floes carrying sticks, soil or plants. He had, nevertheless, been looking for precisely that phenomenon, as he told his family back home and his mentor the father of Charles Lyell.[69]

More than this, he wondered if Forbes had made his glacial period too cold so that it was impossible to believe that "the northern land

was warm enough for any plants at all". Perhaps, he asked Darwin, Forbes had really meant that these species were created in southerly regions when they were cooler, instead of their marching down from the north?[70]

And again, if icebergs were to be used, then Forbes and Darwin alike did not use them properly. Both naturalists had concentrated on a North-South movement to the exclusion of any East-West transfusion of plants, and Hooker suggested that there was a possibility that the flora of Greenland (remarkably poor in arctic species) might be explained by a latitudinal dispersion rather than a longitudinal one. Furthermore would Forbes, he asked Darwin, "suppose that the presence of the S.Shetland Anas antartica [an antarctic species of duck] on the Falklands was due to iceberg transportation North?"[71] If Forbes and Darwin were to propose moving ice as a dispersal mechanism then they must be prepared to explain why most species seemed to have diffused from the north pole, when it was quite plainly the case that icebergs moved around the southern hemisphere in a direction from south to north.

But more than any of these empirical arguments Hooker noted that such irregular methods of dispersal would give rise to a typically 'insular' set of floral relationships, which arctic and alpine floras did not now exhibit. That is, because islands were usually colonised by an odd assortment of species, one from one family and one from another, their proportions of species to genera was notably extreme. Teneriffe, for example, possessed only one species for every genus on the island: the ratio was I:I. Coral islets were particularly remarkable in this respect, and although poor in plants they usually exhibited a very high diversity, or many different families on the one island.[72]

Now to Hooker iceberg transport was as random and accidental as the means by which true oceanic islands were colonised. But existing arctic and arctic-like floras did not exhibit these characteristic proportions, and so, he reasoned, they must have diffused over dry land, for this was the only way in which they could retain the original associations of plants. "There is much in the distribution of Artic plants", he wrote, "wholly opposed to the idea of ice transport being an active agent in dispersion".[73]

And here Hooker suggested that a simple change in isotherms would sufficiently alter the climate of Europe to render it something like Labrador's:

> "A lowering of IO degrees of mean temperature would render the greater part of Britain suitable to the growth of Arctic plants; it would give it the climate of Labrador, situated in the same

> latitude on the opposite side of the Atlantic. Britain is the warmest spot in its latitude, and a very slight geological change would lower its mean temperature many degrees."[74]

He sent Darwin a sketch map illustrating his meaning, and hazarded a guess that perhaps there had once been elevated land between eastern America and northern Europe - "an intermediate sunk area".[75] In so doing he was admirably conforming to Lyell's theory of climate, by which the latter postulated that changes in the ratio of land to sea would alter local climates from equable (insular) conditions to extremely seasonal (continental) conditions, or vice versa.[76] Thus Hooker suggested that a "very slight geological change" would lower the temperature of the British Isles to virtually arctic levels and modestly proferred an "intermediate sunk area" as his agent for this change. A large continent being elevated to the north of Britain would, in Lyellian terms, render the climate more extreme and hence the mean temperatures lower than before. In this way Hooker would have no need of Forbes' insular topography or his glacial sea, and thus could dispense with iceberg transportation. Moreover he could 'fill in' the oceanic area which Darwin postulated had remained in roughly the same place during the cool period, and so give arctic plants firm and dry land over which they could diffuse from the arctic circle to western Europe and beyond.

But, and this I must emphasise, Hooker was here only making scattered remarks and putting forward a very tentative suggestion. In all its elements, however, the proposal tallied point for point with some former suggestions which he had made to account for the antarctic plants in New Zealand. There he had rejected iceberg transport and criticised Forbes' idea of islands when all could be explained by a change in local relationships between land and sea that gave altered temperatures. To assist antarctic plants to get to New Zealand Hooker gave them a large, now submerged, southern land mass which connected the high latitudes of the south with Australasia (and at some other time, the southern regions with Chile and Tierra del Fuego), and over which they had migrated when conditions were suitably cold. The very elevation of this continent would, according to his Lyellian views, provide exactly this change in climate, and its eventual submersion would correspondingly provide a 'warming-up' period as temperatures returned to 'normal'.[77]

Yet Hooker never pressed his point home or attempted to devise a more fully articulated theory of arctic-alpine or even antarctic-New Zealand floras, at least not until he proposed these opinions in 1860 as Outlines of the distribution of Arctic plants.[78] But here, in 1856

and well before he was conversant with the whole range of natural selection and evolution theory, Hooker was more hesitant and reluctant to generalise about a combined geologico-biological distributional history. He saw himself at this time as a useful "worrier of poor theorists" such as Darwin or Forbes, and not as the protagonist for some alternative view. Furthermore, I suggest that Hooker would not have been able to develop a theory of the scope exhibited by those belonging to his two friends even if he had wanted to. Hooker's approach to the issues of distribution which the arctic-alpine case brought into focus was different from that of either Forbes or Darwin. His obvious dislike of random colonisation, where the facts seemed to weigh against it, illustrates in one more respect Hooker's inability to grasp essentially geological assumptions.

This inability hinged on what I called in a previous section the comprehension of the stratified nature of the earth. I there pointed out that a feature of geological study in this second quarter of the century was the more or less unconscious acceptance of an idea that strata were arranged in layers like the skin of an onion, and that these layers could be traced over the surface of the earth to a greater or lesser extent by their visible outcrops. Hence several isolated localities could be linked in the imagination as one extensive bed which had been dislocated, eroded or covered up in the passage of many ages. The essential point was the geologists could visualise outcrops as part of a whole layer that was once, or still remained, continuous in topographical space.

Now when men such as Darwin or Forbes attuned to this way of thinking turned their eyes towards plant or animal distribution patterns on the existing surface of the earth, they quite naturally assumed that 'outcrops' of particular floras or faunas were once part of a single whole - a layer - of organic beings. They drew an analogy between strata and floras and understood the latter just as if they were things that were subject to continuous geological activity which might render them disjunct, dislocated and perhaps confined to very small outliers or 'pools' of characteristic species. Thus a flora scattered over a series of islands or mountains and surrounded by entirely different plants presented them with few intellectual problems: they were simply outcrops of one once-continuous whole which had subsequently been separated.

Even Forbes' curious notion of a special creation of "representative species" at different centres conforms to this stratigraphical analogy.

There was nothing to prevent, and a great deal to encourage, his considering separate "centres" as if they were independent deposits laid down at the same time which happened to possess slightly different forms of life, in the same way as Lyell had demonstrated this to be a common feature of contemporaneous Tertiary beds. In modern terms we would call these different sets ecological variants, as in the case where the fossils found in the London basin are not quite the same as those found in the Paris basin.

To Darwin and Forbes such a stratigraphical analogy would have been so usual that it could only be relinquished with difficulty. Indeed it is hard for modern commentators to believe that there might have been naturalists who did not see disjunct populations of animals or plants as 'living strata' so to speak. But Hooker was one of these men, and (although for other reasons) so were most of the early nineteenth century naturalists who believed in multiple creations.

I argue that Darwin and Forbes on the one hand, and Hooker on the other, had fundamentally different ideas about the distribution of floras. The two former were prepared to overlook what might seem like inadequate methods of transport to shift their floras from one area to the next, because it was so evident to them that the flora had really been spread out over the whole area.[79] The ways and means of migration were thus purely incidental - though interesting and necessary to explain - to the grand concept that the plants had once been a continuous whole that had blanketed the area. Indeed, reasoning backwards, both Forbes and Darwin claimed that if disunited populations like arctic species on mountain summits were found, then it could safely be inferred that conditions had once been such that these forms had been spread out over the available land. But Hooker, who had no similar vision of layers of strata or any geological analogy to fall back on, found the lack of any adequate dispersal mechanism to be a glaring omission. No grand theorising could alleviate a situation where, to his eyes, the transportation of floras was so patently ignored. He was so immersed in topographical botany, and knew so much more about the distribution of plants then either Forbes or Darwin, that he was especially sensitive to a side of the hypothesis which was relatively unimportant to its two proponents. Thus his critique of the arctic-alpine theory focussed on the absence of proper explanations of the movement of plants from one region to another, and in huffings and puffings over proposals for ice-borne dispersal. In a second line of attack he tentatively offered an alternative which seemed to him more satisfactory, that is, he suggested some former

continent over which plants could migrate to the regions that they now inhabited.

So I think that once again Hooker demonstrated in his response to Darwin's and Forbes' theories a certain incomprehension of the geological approach to nature, and especially to the geological way of looking at distributional phenomena. Yet I am not here trying to categorise Hooker as misunderstanding something that was eventually to be proved 'right' or 'better'. He was, instead, primed by his own extensive knowledge and interests to regard these suggestions in one particular way. He considered transport to be the crucial issue of any theory of arctic-alpine floras, whereas Darwin and Forbes thought the interaction between geological processes and organic life to be the crux of their proposals. The topographical botanist and the distributional geologists were proceeding in parallel tracks and failed to see each other's point of view.

## Conclusions

In this examination of the theory of arctic-alpine floras many themes current in early nineteenth century geology have been touched on, and the most notable point which emerges from such a general survey is that the subject was then rich and complex and enjoyed a wide range of hypotheses from which further ideas could be extracted. In passing, it has been demonstrated that the so called dual 'discovery' of an answer for the distribution patterns of arctic and alpine plants emanated from Forbes' and Darwin's common background and, in particular, from their mutual adherence to Lyellian views. Moreover, Hooker's comments on these theories were conducted under his own interpretation of Lyell's geology, and so, in an odd way, one gets a glimpse of how easy it was to use Lyellian principles to criticise proposals themselves established on Lyellian precepts. Much of the history of this period thus seems to depend in quite a significant manner on personal factors such as how questions and answers were understood by each individual.

In turn, these personal factors illustrate a polarisation in contemporary thought about distribution. Hooker picked up features of Darwin's and Forbes' doctrines which the two latter found relatively unimportant, and tried to use his comprehension of post-Lyellian geology to present a possible alternative. Darwin and Forbes focussed on something entirely different which required an appreciation of geological methods and concepts to an extent that Hooker seemed unable to grasp. Things that Hooker found important such as transportation hardly featured

in Darwin's and Forbes' theory; concepts such as a separation of geological time from absolute time were, on the other hand, vital for Darwin and difficult for Hooker to understand. The one naturalist was thus steeped in a topographical attitude to nature which, when applied to historical or chronological theories, led him to home in on non-essential points or to demonstrate an incomplete understanding of geological concepts. The other two, though presenting slightly different theories, were united in their appreciation of the finer points of geology and in the niceties of a geological approach to natural phenomena such as distribution. It was not that either side did not try to understand each other for they were, after all, ranged together in an attack on the same problem. I believe that they simply did not realise that the statements which were being put forward came from different backgrounds (viz. the geological or the topographical), and so they felt that there were no distinguishing marks to be accounted for. In other words, Hooker, Darwin and Forbes all thought that they were engaged in the same pursuit with the same theoretical background and that they could each contribute an equal part to the debate. But the discrepancies which I have here brought out indicate that this was perhaps not the case. There were, instead, two ways of looking at and theorising about nature. One was the geological, and the other was the topographical approach to the study of distribution.

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## Chapter 2: The Problem of Representative Species

'Representative' species came to occupy a special place in the construction of biogeographical theories in the earlier half of the nineteenth century. The phenomenon itself was by no means easy to interpret yet it could not be ignored for, as I shall point out, more and more examples of species 'pairs' and of ecological replacements were being brought to the attention of naturalists as the work of collection and cataloguing progressed. The fact that such analogous forms actually existed had to be incorporated into and explained by current hypotheses about the origins and distribution of life. This was an activity which led in some instances to the proposal of individualistic and eccentric theories of nature's "Laws". Alternatively, men such as Asa Gray or Joseph Hooker declared that this problem was insoluble until more facts were known about distribution.

In 1859, of course, Charles Darwin was to propose an acceptable account of the origins and continuance of representative forms based on his theory of competition and natural selection, and it has been argued on several occasions (correctly in my opinion) that it was to this problem alone, as manifested for instance in the bird life of the Galapagos archipelago, that Darwin owed the outlines of a concept of evolution. Darwin defined 'representative' species as very closely related forms which are geographically mutually exclusive.[1] In his view, which coincides with modern opinion, they are species assumed to have possessed a common ancestor from which each has diverged to some small extent under the influence of competition and continued adaptation to different environments. Thus every species of tortoise in the Galapagos archipelago is dissimilar to others belonging to the same genus, and is peculiar to its own islet. In today's terminology these forms are called 'representative' species where the differences are strongly marked, like those of the tortoises, or 'geographical races' where the differences are of a lesser degree. In either case it is clear that the beings themselves replace each other in separate areas.[2]

Though I shall have much more to say about this particular phenomenon of geographical replacement - which is after all the most important element in any discussion of 'representative' species - I think it is necessary to point out that there are other manifestations of representation and replacement in nature.

The first that springs to mind is the so-called 'ecological' replacement of one species by another, where, for instance, the marsupial mole takes the place of its placental analogue in Australia, or European oak trees are represented in Africa by brachystegia woodland. There are also more general instances of this sort of replacement as in the fact that every major land mass has local forms of cattle, sheep or goats, and many have separate families fulfilling the same role in nature, as, say, kangaroos and llamas act as the largest herbivorous creatures of Australia and South America in the absence of any native cows or horses.

Another type of representation is to be seen in the way bats, for example, are the mammalian counterpart to birds, and seals to fish. And pressing this last statement a little further, it could be said that all vertebrates 'represent' some common plan which is reflected to various degrees in their structure, so that every animal with a backbone could be considered as a variation on one theme. Hence the study of analogous or homologous organs and the classificatory relationships which connect all living beings, legitimately come within the purview of students of representation.

Facts such as these which we can now separate and categorise as different phenomena peculiar to the evolutionary heritage and background of each organism were not at all separated by nineteenth century naturalists. They were all subsumed under the rubric of 'representation'. Thus in 1859 the American botanist Asa Gray itemised five categories of "representative species" which he believed to exist in the vegetable kingdom, and these ranged from purely geographical varieties to an order of magnitude parallel to the case of marsupial and placental mammals cited above.

William Swainson, of whom I shall have occasion to speak more fully, developed an all-embracing system of nature entirely based on his notion of representation as a quality which linked all living beings together, in the same way as we now understand evolution and a common ancestry to draw all organisms into the same plan or scheme of things. George Waterhouse, a multi-talented zoologist and close friend of Darwin's, thought that representative forms were somehow the most typical or 'normal' of any family or group, and Edward Forbes saw representation not only through topographical space but through the fossil record as well. Even the Compte de Buffon in his Histoire Naturelle of 1749-84 saw no good reason to distinguish between the representation which was to be found in the arctic and rufous forms of the fox, and that found in the

European mole and its marsupial cousin in the Antipodes. To him these phenomena were part of the same single natural consistency and hence virtually indistinguishable.

Thus when naturalists spoke of 'representative' species they did not necessarily mean the living beings which we call 'representative' species. Such an elementary point needs to be made because all recent accounts that touch on this topic appear to have ignored the possibility that previous explanations might have been constructed to answer the whole range of biological evidence. Two modern historians in particular have dealt with this subject in some detail and yet describe those theories only which accounted for a purely geographical replacement of species by species such as that exhibited by the Galapagos tortoises.[3] Such a tendency on the part of historians may well be dubbed the Galapagos syndrome, for they have allowed a modern (i.e. Darwinian) definition of 'representative' species to dictate their choice of ideas to be examined in this particular section of pre-Darwinian biology, and have thus relegated a spectrum of ideas about these and associated phenomena to the background.

A linear - Darwinian - perspective therefore makes little of the existence of a wider notion of representation by concentrating solely on explanations offered for the fact of geographical replacement. Here, by contrast, I hope to illustrate something of the scope of early nineteenth century ideas about representation and hence to show how suggestions about the nature of the forms such as the Galapagos finches or tortoises were frequently, and usually inextricably, mixed up with attempts to explain the more general problem of ecological and even morphological "representation". To do this I have chosen to examine in some detail the theory of nature proposed by Edward Forbes which depended to a great degree on the notion of a replacement of species through space and time, and thus helped him to understand (at least to his own satisfaction) the appearance of geographical variants and proper 'representative' species. This is followed by Joseph Hooker's attempts to explain the same phenomenon and a description of the manner in which his efforts were bedevilled by wider issues which stipulated that representatives were part of some greater metaphysical consistency. By concentrating on the way in which particular naturalists answered current problems of their time this chapter will highlight noteworthy features of pre-Darwinian biology.

The problem

Because 'representative' species (that is, closely allied species) appeared in separate geographical areas and each in association with dissimilar groups of animals and plants, they were at once the most striking and the most perplexing features of any attempts to divide the world into faunal or floral provinces. The European Royal fern Osmunda regalis, for example, had its place taken in America by its close relative Osmunda spectabilis, and the rhinoceros of Africa was replaced by slightly differing species of the same animal in India and Java. Why, when America and Europe were sufficiently different to support diverse populations, was there also a pair of ferns which signalled some affinity or deeper relationship between these areas? Why again, in the case of India and Java, should there be two different sorts of rhinoceros when most of the other species were identical and the environmental conditions were hardly dissimilar? Representative species could clearly either distinguish or relate biological regions.

Naturalists of the first half of the nineteenth century were not quite sure which of these two points was the more significant. Some such as Edward Forbes produced an explanation based on an uneasy compromise, whilst others like Louis Agassiz held an unshaken conviction that representative species were forms which defined and separated provinces one from another. They were all quite sure that the species themselves were dissimilar because they lived in different regions and that one therefore had to look to the physical conditions of the areas (in the first instance) and then to the history and creation of living beings to discover the reason why. The Parisian entomologist Theodore Lacordaire explained that the naturalist had to "revert to external circumstances first" and if these were insufficient to answer the question "why species inhabit such and such a locality, rather than others?", he must go to higher causes.[4] Agassiz, it must be said, paid only passing attention to these external circumstances since the existence of representative forms was for him a dramatic and conclusive proof of the existence of a divine Creator. He had no need of environmental differences to explain these beings when he had a far more majestic and powerful agent in God. In his Essay on Classification from the Contributions to the Natural History of the United States of America (1857) he asked why two forms of one species should live in the same geographical regions as did other more widely dispersed forms which possessed no representative species:

> "By way of example, I would mention the European and American Widgeon...or the American and European Red-headed Ducks...which inhabit respectively the northern parts of the Old and New World in summer, and migrate further south in these same continents during winter, while the Mallard...and the Scaup Duck ...are as common in North America as in Europe. What do these facts tell: that all these birds originated together somewhere, where they no longer occur, to establish themselves in the end within the limits they now occupy? - or that they originated either in Europe or America, where it is true, they do not live all together, but at least a part of them? - or that they really originated within the natural boundaries they occupy? I suppose with sensible readers I need only argue the conclusions flowing from the last supposition. If so, the American Widgeon and the American Red-headed Duck originated in America, and the European Widgeon and the European Red-headed Duck in Europe...The details of the geographical distribution of animals exhibit, indeed, too much discrimination to admit for a moment that it could be the result of accident, that is, the result of the accidental migrations of the animals or of the accidental dispersal of the seeds of plants...It was this, ...which led me to distrust the belief, then almost universal that organised beings are influenced by physical causes to a degree which may essentially modify their character."[5]

But whatever the superficial or ultimate causes invoked to explain the existence of representative forms in widely separated countries, it was usual to ascribe the structural differences between such organisms (and hence their taxonomic status of species, genus, or family) to the topographical distance by which they were separated. This was a generalisation based on the simplest empirical test: observation proved that species from the New World differed from those of the Old by specific characters where species from Australia and, say, western Europe, differed by generic and even familial characters whilst still agreeing in most respects. This was a phenomenon established by Cuvier in his magnificent Mémoire sur les espèces d'elephans vivantes et fossiles (1799) where he pointed out that the African and Indian elephants belonged to different genera, yet any layman could see for himself that these were closely related beings which took the place of each other in different countries. In the nineteenth century it was a commonplace to assert that the further apart two countries were the more distant the 'representation' was in taxonomic terms. Thus Henri Milne-Edwards described the distribution of representative forms of the crayfish:

> "So far as the Crustaceae are concerned...many zoological regions exist, having each a peculiar population which is partly composed of organic types, whose analogues are not found elsewhere, and another part consists of the representatives of species which also exist in other regions. Thus our river crawfish does not exist in America, but is there replaced by a neighbouring species of the same genus; Southern Africa possesses a third species of the same animal, and this organic type is also found in New Holland, but with distinct specific characters [i.e. belonging to another genus]."[6]

He connected an accumulation of organic diversity or morphological distinctness with increasing topographical distance. Such a view was also put forward by Edward Forbes, for he was a fervid believer in the universality of this apparent rule, and he was to use it to great effect in his explanation of the spatial arrangements of animals and plants. Lacordaire, the entomologist mentioned above, thought that it was quite right and proper that there should be different degrees of 'representation' in different regions and that these forms should be marked by increasing identity as distances decreased. In 1842 he wrote that this was an idea which could be applied to whole floras and faunas and suggested that there was a gradation in morphological organisation according to geographical proximity. Hence adjacent regions ought to possess identical organisms and distant ones distinct species and genera, with several shades of dissimilarity in between.

> "When two regions which resemble each other are at the same time contiguous, their species are almost wholly alike; this is witnessed, for example, in France and Germany. If these regions are separated by a considerable interval, their species are for the most part different, but the genera remain the same; it is thus that Spain and the coasts of Syria...possess a multitude of common genera with species almost precisely similar. Finally, if these regions are separated by an immense interval and by natural barriers, nothing continues common to them but the families...It is this diversity produced by distance, which gives to each region its proper entomology."[7]

It was within such a framework of ideas that representative species were used to provide evidence for the delineation of biological provinces and for assessments of their relationships. The closer these forms were in taxonomic terms, the nearer their native habitats must be in a topographical sense.

Naturally, with hindsight, we can see that this view is inadequate to describe organic distribution patterns over the globe. Representative species are not always to be found in two regions which are geographically adjacent, as for instance there are pairs of such species in countries

widely separated, like the Antarctic beech in Chile and Tierra del Fuego and its representative in the Arctic circle. The details of distribution, more often than not, did not conform to the plan. Yet naturalists of the earlier part of the nineteenth century found several ways to circumvent or get round distributional data which did not fit this a priori assertion.

Firstly, since the designation of true species and 'representative' forms depended almost exclusively on the taxonomic skill and virtuosity of the systematist who was describing any flora or fauna, it was easy for a subsequent naturalist to disparage former classifications and to present his own which provided or omitted these forms as required. Men such as the botanist Charles Babington who were known as "species-mongers" because they were liable to make many species where others might see only one or two distinct forms, were thus more likely to find 'representative' species than botanists like Hooker. Hooker was, in the terminology of the time, a "lumper", and personally preferred to group a diverse selection of forms under the rubric of one, variable, species. The latter was therefore less likely to make false representatives in his catalogues of the plant life of India or Australia. But even Hooker acknowledged the existence of some forms which replaced others and were also very near relatives. Thus he listed many such pairs of species which demonstrated a biogeographical affinity between the flora of western Australia, New Zealand and Chile. His colleague Asa Gray, also a taxonomic "lumper", made out II5 "very closely representative" forms which linked the flora of the northern states of North America with that of western Europe.

Secondly - and more notably for my argument in the present chapter - there was a tendency on the part of geologists or the more geologically minded naturalists such as Edward Forbes to turn apparently negative, or at least perplexing and contrary, evidence to their own advantage. Thus when faced with a clear statement of the distribution of 'representative' species which ran counter to the assumption that geographical separation was accompanied by taxonomic differentiation, they claimed that this statement was only concerned with the present day distribution of organisms and that, at some earlier time, things may well have been different and of a nature to provide the 'right' pattern. Forbes noticed that there were species of marine bivalves in the deeper and colder parts of the Mediterranean sea which were close relatives to those in arctic waters off Norway, and proposed that these were faunas of the greatest possible intimacy short of absolute identity. How then could

he account for their evident dislocation, for the close taxonomic relationship of the species indicated that they ought to be geographically adjacent or at least nearer to each other than they were? Forbes, as a geologist, suggested that these two regions - the Mediterranean sea and offshore Norway - had at an earlier period been united and that each of today's biological provinces had then been positioned at the furthest extremes of one great sea. Thus the regions were once truly adjacent and therefore populated with closely representative forms, and were only separated by subsequent geological activity. By invoking geological causes and by being able to think of floras and faunas as having a past existence he was able to counter all apparent inconsistencies in the evidence which contributed to current notions about representation.

We might well ask why was it so important for natural historians and geologists alike to maintain this association between 'representative' forms (ranging from species to genera) and increasing geographical distance? It was, in my opinion, because the science of distribution had reached a stage of development where more and more refined assessments were required and being supplied. The days had, by now, gone when a simple enumeration of plants and animals would suffice; mere curiosity had been replaced by a desire to piece together all the details of distribution to make up a finely textured tapestry from which overall pictures and hidden meanings could be isolated. Correlations such as these were the first fruits of centuries of empirical research, and had been hard won by the labours of generations of collectors, cataloguers and systematists. Furthermore there were then, as there are now, very few rules or "Laws" pertaining to the distribution of plants and animals, and since this was expressly what naturalists were seeking it was unlikely that they should relinquish any generalisation once it had been brought to their attention. "One great thought prevails in natural historical studies" declared Agassiz, "the study of the laws regulating the geographical distribution of natural families of animals and plants upon the whole surface of the globe". This sentiment was echoed by William Swainson who asked "What are the causes that have produced this dissimilarity of creatures? and secondly is there method in all this amazing diversity?" They sought generalisations, and it appeared that the existence of 'representative' species would provide one. They were used as organic indicators of the dissimilarities and similarities between biological regions. By being linked to the areas and countries

in which they occurred, 'representative' forms were therefore organisms which conveyed something of the qualitative differences between floras and faunas, and so they were a useful tool for biogeographers who wished to improve and refine their subject and to describe the living beings of separate countries with increased subtlety and clarity. Such was the manner in which these forms were used by Edward Forbes and Joseph Hooker in the second quarter of the century.

## Edward Forbes

Forbes espoused a system of nature - obscurely designated the "principle of Polarity" - in which representative species *per se* played an important explanatory role and the more general attribute of morphological representation and replacement formed the hub. This system was first unveiled as the *pièce de résistance* of Forbes' presidential address to the Geological Society of 1854, a philosophical gesture which caught his audience unawares[8]. After its publication in the Quarterly Journal of the Society, Forbes went further into details in a paper submitted to the Royal Institution[9], but in the event of his untimely death both presentations were tactfully dismissed as the agitated syntheses of an unwell mind, and the "principle of Polarity" was relegated to a discrete no-man's-land of unacceptable theories. In fact, the whole of Forbes' scientific life had been devoted to the gradual working out and publication of this theory and although only revealed at the end of his life (not that Forbes knew that), it had probably guided and directed his research from his earliest studies at Edinburgh during the 1830's.

He introduced the principle with some stirring words indicating the metaphysical relations between organisms which had already been discerned in nature. Among these he cited "Representation".

> "Of the four relations among organised beings, viz: Affinity (or relation through homology), Analogy, Representation, and Polarity, the three first have been recognised in the distribution of beings in Geological Time; the fourth has neither been observed nor sought for."[40]

Though no-one, I believe, had drawn these three or four elements together in a catechism in quite the way Forbes did here, he was nevertheless quite right in saying that Affinity, Analogy and Representation had all been noticed and promoted to the level of a "principle" of nature before his time. Such had been the life-work of several noted naturalists, including among their number Richard Owen and William Sharp MacLeay. The latter had produced in 1820 or so an entire classification scheme which linked the whole of nature together under

varying degrees of "representation", or, as we would call it today, under a scale of morphological affinities and resemblances. This had nothing to do with 'representative' species that replaced each other in topographical space, however, and was entirely concerned with structural resemblances and the systematic arrangement of these. MacLeay's foremost disciple and populariser, William Swainson,[12] the colonial official who settled in New Zealand and Australia in turn and botanised through these regions with singular unsuccess, had extended and improved on his notions to suggest that there was an element in nature that could be called a "Law of Representation". This, according to Swainson, governed the manner in which each set of animals was related to the next, and that every taxon in some way or another "represented" in its structure or behaviour all other animals.[13] Swainson was, in actuality, trying to explain evolutionary relationships by ascribing morphological similarities between groups to some intangible essence or propensity of nature.

Though Forbes was just as strongly influenced by that curious blend of naturphilosophie and natural theology which was evident in the work of Swainson (and in other British naturalists' writings, such as Owen's and William Carpenter's), he did not confine his researches to the uncovering of a purely abstract law of "representation". He attempted to explain the physical existence of species which replaced each other in topographical space, as well as the general and more mystical (to him, at least) affinities between organisms over time and throughout nature in one all-embracing scheme. This last depended upon his unique and novel principle of polarity.

Forbes' theoretical scheme was based on the idea that the organic kingdom resembled the inorganic in that there was a "manifestation of [a] force of development at opposite poles of an ideal sphere".[14] He gave the example of the way the animal and vegetable kingdoms together made up the entire living world, and yet within each great cohort there were two diverging and mutually "opposite" lines of development. He told his readers that the highest animal was farthest removed in a classifactory sense from the highest vegetable, and they were therefore at the opposite "poles of the sphere of organized beings."

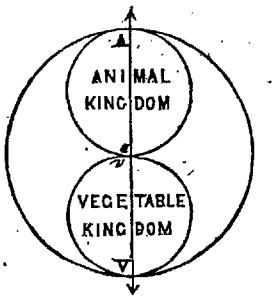
What he planned to do was to demonstrate that polarity could be found as an organising principle or 'force' in the topographical distribution of animals and plants and in the history of life over time.

This was by no means an easy thing to do and it appears to me, at least, that Forbes failed in the attempt. It turned out that instead

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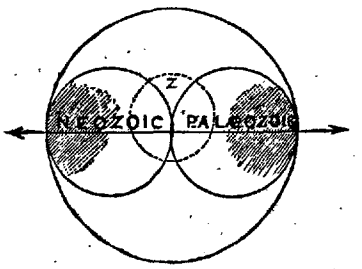
Figure 1

The ordinary illustration of the relation of *Polarity*, in a natural history sense, is that representing the relation of opposition or progression in opposite directions of the Animal and Vegetable series; the meeting point of both being at the points of lowest development of each (*a*, *v*, in the accompanying diagram), where the animal and vegetable natures are almost confounded, whilst the strongest manifestations of each are at A and V, the highest animals being farthest removed from the highest vegetables,—in other words, at opposite poles of the sphere of organized beings.




Forbes 'On the manifestation of Polarity' in the living kingdom.

Figure 2




By a diagram such as the above we may fairly express this view, the shaded portions of the circles included within the great circle of the system of nature representing the maxima of development of generic ideas, and the dotted area, *z*, the region of their minimum productions.

Forbes 'On the manifestation of Polarity' in the fossil record.

of demonstrating an ineffable force of polarity, he made a very striking case for the existence of analagous sets of beings in both space and time linked together by his ideas on representative forms of life. I assume that this was all part of the 'proof' of a principle of polarity but I find that Forbes' precise meaning is often elusive and obscure to the point of abstrusity. Hence I prefer to speak of those theories of his which are more accessible to the modern mind, and to relate these wherever possible to his often-expressed overall aim.

In his first really important geological paper Forbes made a stand for historical biogeography, and determined to explain the distribution of animals and plants in the British Isles through an examination of their history. In 1846 he wrote a famous memoir, 'On the connexion between the distribution of the existing Fauna and Flora of the British Isles, and the geological changes which have affected their area...'[15] Here he identified four or five different sections of British biological populations which had, at one time, belonged to floras and faunas of separate parts of continental Europe, and attributed their appearance in these islands to the effect of geological changes which had, over time, allowed the extension of the several biological associations over contiguous land.

This memoir was an important statement of his philosophy and deserves close attention from historians. Here he described the succession or replacement of floras by floras through topographical space, and set the scene for further discussions relating to their arrangement in geological time. The latter discussions are confined to the two brief articles he wrote supposedly explaining the principle of polarity, which was, in the first instance, designed to account for the way in which different forms of life came into and went out of the fossil record.

These complementary usages are best analysed seriatim, if only for the reason that Forbes himself separated them in different papers. I turn now to his first statement of the distribution of organisms through the single dimension of topographical space, as expressed in the 1846 paper mentioned above. Here he took great pains to show that since the British flora had virtually no species peculiar to itself, it must be derived from other sources through a succession of immigrations as and when land movements permitted. Forbes characterised these sources as, in turn, Germanic, French, Lusitanian, continental Chalk and Scandinavian floras, on the identity between the plants of these areas

and the various parts of the British Isles, and each one was held to be a separate "specific centre".

As the doctrine of "specific centres" was crucial to both Forbes' understanding of British distribution and to his account of life in general, this point begs a little attention. The term itself creates few problems: it was roughly speaking synonymous with that previously coined epithet "centres of creation", and neatly combined an explanation of the obviously still continuing extension of topographical ranges from earlier locations, with a suitable reason for the existence of differences between regions apropos of animal and vegetable forms. Forbes surmised some initial creation of the individuals of species and genera in the places which were most suitable for them, from which they spread until meeting with a barrier, physical or otherwise. Hence he defined specific centres as "the existence...of certain geographical points from which the individuals of each species have been diffused".[16]

Forbes, however, despite his own definition which implied that he meant foci of creation, actually used the expression "specific centre" as a term to convey the whole region over which a 'batch' of species had spread. Thus the arctic flora was one "specific centre" because all its forms were similar and distinctively 'arctic'; Madagascar would have constituted another "specific centre" for its organisms were very different.

What is, however, important for us is the way in which Forbes used this idea. Specific centres formed the crux of his philosophy of nature, and it was towards the justification of their existence that he put forward an account of the British flora and fauna. He drew a metaphysical parallel between the gradual spread and dispersal of one species (broadly speaking a factor of its geological age)[17] and the extent of any of these centres, to postulate that the oldest specific centres were in fact the associations of plants or animals which had spread the furthest, and, in reverse, that the widest flung flora was the earliest created.

Such a proposal was clearly worked out in all its minor detail in the paper under discussion; Forbes demonstrated that this view allowed him to order the five specific centres which had contributed plants to Great Britain, one after the other through time. He produced a variety of evidence, mostly geological, but some botanical and conchological, to show that the land connecting Britain with continental Europe had gone up and down in the correct places and at the right times; and he attempted to date the creation and period of existence of the several floras in relation to geological epochs.

Thus he took it upon himself to describe not only the creation and dispersal of plants which were ultimately to become British species, but also the fate of each set of plants - his specific centres - which contributed members to the population of these islands. He described how although each specific centre of French, German or Scandinavian plants had been created in succession, there were also other floras originating in different parts of Europe (further south for example) at the same time. Forbes himself used the example of the simultaneous creation of floras suitable for cold and icy conditions in the far reaches of Norway, and around the shores of an equally cold glacial sea in central Europe: these were his Scandinavian and Alpine specific centres, and he knew that they had been created at the same time because they contained representative species, and so were analogous.

Forbes was here quite clear as to how he thought that two specific centres might show a mutual relationship. It was through the existence of a pair of representative forms which took the place of each other in particular areas. The degree of 'representation' varied with the distance by which each area was separated from each other, a common enough notion as I indicated in the introduction to this chapter.

He wrote that "It is well known, that this correspondence is recognised in the general facies of the flora and fauna, dependent on generic correspondences, specific representations, and, in some cases, specific identities"[18], and went on to point out exactly what he found in the flora of central Europe:

> "In the case of the Alps and Carpathians, and some other mountain ranges, we find the law maintained partly by a representative flora, special in its region, i.e. by specific centres of their own, and partly by an assemblage more or less limited in the several ranges of identical species, these latter in several cases so numerous that ordinary modes of transportation now in action can no more account for their presence than they can for the presence of a Norwegian flora on the British mountains."[19]

Now ignoring the final phrase which turned out to be a simple puff for Forbes' own explanation of the transport of identical species over considerable stretches of low-lying land, it can be seen that he supposed the alpine flora to form its own specific centre because it possessed species which represented genera from elsewhere. In this case the Alps bore representatives of arctic species. It was to him a striking example of the often-cited parallel between the vegetation of the zones of a mountain and the earth's latitudinal belts: as the elevation of

mountains increased, so the vegetation changed its nature according to the alteration in pressure and temperature, to repeat in miniature the predominent types of vegetal belts found in various latitudes. And for Forbes this analogy between elevation and latitude provided exactly what he was trying to say. He pointed out that the alpine flora represented the arctic through its analogous species and stressed that this was because they had been created under similar conditions in two widely separated regions. In the case of a recent creation of organisms designed for the conditions experienced by present-day mountain tops and the circum-polar regions, or in the case of an earlier one for the climate of northern and central Europe under the glacial period, it was for Forbes a creation that demonstrated a relationship through representative forms.

Thus he asserted that the existence of representative species was the key to understanding synchronous creation:

> "But when announcing and illustrating the law that climatal zones of animal and vegetable life are mutually repeated or represented by elevation and latitude, naturalists have not hitherto sufficiently (if at all) distinguished between the evidence of that law, as exhibited by representative species and by identical. In reality, the former essentially depend on the law, the latter being an accident not necessarily dependent upon it, and which has hitherto not been accounted for." (Forbes' italics)[20]

Here we may paraphrase Forbes' meaning thus: when we find identical species in a climatic band on the earth and in a particular band on the slopes of a mountain, we might suppose them to have been historically isolated by some process not yet fully understood. When we find 'representative' species in the two bands, any sort of historical or 'mechanical' explanation fails, precisely because the species are not identical. Some creative process must have intervened. Thus we discern that there is a creative law - not a mere historical process - related to the existence of representative forms.

Forbes next produced what was in his opinion the most telling evidence for a synchronous existence of specific centres. He claimed that the further separated two or more centres were in purely geographical terms, then the less precise the representation of form by form in each association. Hence if the Chilean antarctic flora, were examined it would be found that this polar vegetation represented the northern one through analogous genera not species. Correspondingly, if the Alps and the arctic were compared the representation was somewhat closer and evidently one of specific forms, in that all the alpine

species belonged to the same genera as those of the arctic. Furthermore, to complete the series, Forbes had in the preceding pages of his memoir clearly demonstrated how mountainous regions close to the northern zone, such as Scotland was to Scandinavia, exhibited total identity with that zone in its flora, and therefore showed no representation at all.

He here proposed a real association between all the specific centres or biogeographical regions which may have existed at any one time: they were all linked by various degrees of representation which, in taxonomic terms, grew fainter and fainter as the literal distance between the areas increased. "Though similar conditions reappear" he claimed, "the relationship of alpine and Arctic vegetation in the southern hemisphere with that in the northern is entirely maintained by representative and not by identical species; (the representation, too, being in great part generic, and not specific)".[21]

Forbes was not unique in this proposal, for, as I have pointed out in the introductory pages to this chapter, such an explicit connection between geographical space and morphological resemblances or dissimilarities had been popular for the greater part of that century. But he certainly was unique in the way that he arrived at these conclusions and in the way in which he was subsequently to put them to use.

Since he had worked so hard to demonstrate the existence of specific centres on the 'flat' so to speak, through the various degrees of representation which one area exhibited with another, he felt sure that equivalent phenomena could be discovered in the fossil record and hence existing over geological time. In subsequent papers he described this view under the label of "Polarity".

Hence in 1854 he drew an analogy between representative forms in topographical space and their counterparts in the fossil record through time. He supposed that consecutive creations (or batches of species) were as discrete in the chronological sense as they were believed to be in the spatial, and that their separation in time was therefore to be demonstrated by representation as it was in space. He called these "unique time-areas" in preference to "specific centres". But instead of looking for representative species he found the idea of genera to be a more useful tool and consequently searched for a succession of analogous genera through a sequence of formations.

In so rejecting species for his basic unit I think Forbes was tacitly conceding the point that 'representative' species were forms of a strictly geographical nature, and that their appearance in the

fossil record was dependent on the topographical extent of any stratum at a given point in time. The history of life was to him like the patterns on a stack of decorated dinner plates where one could be pulled out of its sequence, examined and then replaced or the whole lot could be surveyed in series. He thought representative species were forms restricted to the flat surface of the plates, whereas genera, being ideas or abstractions, connected the patterns on the pile into a set. Species, then, were of little value for a chronological view.

Through geological time Forbes saw the substitution of group for fossil group, as did many of his colleagues. At the generic level he was careful to stress that he did not claim this to be a replacement of the lower groups by any which were higher in their organisation - he was against the doctrine of progression or development - and claimed merely that there was a replacement of one for another of related beings[22]. He attempted to show how each specific centre not only replaced the previous batch of species which he - as others - assumed to have lived in the same region, but also contained species which represented those of the earlier assemblage. Thus, to take an elementary example, he supposed that the Tertiary population of Great Britain possessed a species of mouse which represented the Jurassic form of this rodent. His own example was of the replacement of four rayed corals found in the Palaeozoic by six rayed corals in the Neozoic (his neologism for the more recent geological epochs). Such was the basis of his principle of "Polarity".

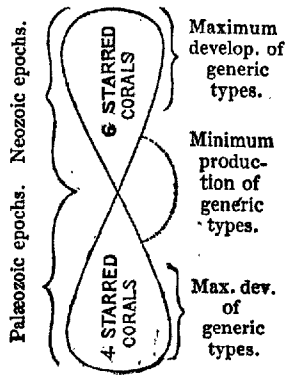
Forbes' own expression epitomised, however loosely, the idea which he tried to convey in explaining his scheme for life. He stated that "genera appear in batches" throughout the ages, and were not regularly brought in and sent out by some divine master of ceremonies. He claimed to find more new genera existing in the early formations of the Palzeozoic period and in the later ones of the Neozoic, than in the epochs between. He stressed that this was a statistic which related only to innovation and the introduction of new genera. Had he thought of it he could well have used the Lyellian parallel of a birthrate of individuals. For, in actuality, Forbes was attempting to describe the "birthrate" of genera, a rate which was noticeably higher in certain epochs than others.

In his attempt to present this suggestion visually Forbes produced a figure which looked like nothing so much as an egg-timer. The wide bits represented the "maximum development of generic types", meaning, in fact, the maximum number of new genera, whilst the constriction in the middle stood for the period of "minimum production", and the top

Figure 3

If we were to shew by means of a detailed diagram the relations in each of these groups of the development of generic types to time, we should symbolise it by a cone or a pyramid, the base or fullest portion of which should be turned respectively towards the commencement of the Palæozoic, or termination of the Neozoic epoch. The last example given will shew this strikingly, though in most instances the groups interlace.

Relations of this kind may be manifested in a low degree, even within the range of a single group.




Forbes on the introduction of new genera over time.

and bottom were the two ends of time spanning the first creation to the appearance of man. Because he thought the relationship of the upper globe of the hour-glass with the lower was one of symmetrical divergence away from the central constriction, he asserted that life was proceeding in two directions.

> "The relation between the Palaeozoic and Neozoic life-assemblages is one of development in opposite directions, in other words, of Polarity."[43]

Polarity was therefore the explanation for the appearance of a progressive increase in the number of genera from a period of minimum development (the 'waist' of the hour-glass) out in opposite directions to a maximum number of new forms at the beginning and end of time. At least if it did nothing else, Forbes' theory demonstrated that not all naturalists believed in the directionality of time, as is sometimes suggested.

But the important point for this thesis is that Forbes held that genera, once introduced, were maintained in the fossil record through a series of replacements where each successive group 'represented' its predecessor. After his period of maximum innovation in the earlier formations of the Palaeozoic, all genera continued to exist (the number of species being immaterial) in one form or another until their place was taken by Neozoic structures; thus the four rayed corals were created for the Silurian and all the Paleozoic types were held to be introduced during this epoch, only to be maintained in a variety of minor forms (each one the result of individual acts of creation) until virtually no new forms were produced at all in the Permian and Triassic; after this poverty of new genera, more were gradually introduced to reach another maximum in the Cretaceous, Tertiary and Modern periods. But these latter were not four rayed, but six rayed corals which therefore 'represented' the former group and played "a corresponding part in the economy of nature".

To summarise these views on representation through time is not easy. Forbes was quite plainly trying to express the birth rate of genera, and took pains to reiterate that he did not deny that there were plenty of genera around in his poor middle period but asserted that there were no new forms then being introduced. When new forms were made manifest they were 'designed' on the same plan as that which had gone before as in, for instance, his less telling case of the Echinoidea taking the place of earlier Crinoidea. These have "replaced others of similar value and served the same purpose or played the same part"

in nature. But this, it might be argued, was a general scheme of things which did not necessarily depend on or implicate 'representation'.

The crucial part of Forbes' theory is thus the emphasis which he laid on the fact that each genus was "maintained" in the fossil record by a series of slightly differing forms, one for every formation or epoch as the case may be, and every one the result of individual acts of creation to suit the body to the conditions it was to experience. These successive acts of creation peopled the earth with a series of genera in which each group took the place of and mimicked earlier forms.

Hence in his anniversary address to the Geological Society of 1854 he singled out aspects of the work of Leopold von Buch and Barrande which encouraged the view that genera were created on the same 'plan' as those which went before: from von Buch he took the unattractive term "chronomorphosis of genera" to describe the "succession of types"; and from Barrande's work on trilobites he chose to stress how his researches into the change of generic characters through time were "of great interest and value" to the Society. In similar vein he praised Davidson's recent description of the Brachipoda for the evidence it provided that each genus occupied a discrete 'area' of time and was therefore 'replaced' by another sooner or later. "With the excellent work done on Brachipods by Mr. Davidson, we can now see how far the ranges of these genera are continuous in time", he declaimed:

> "In other words, whether the theory of unique generic time-areas be borne out among the Brachipoda, now that we may be said to have attained so extensive a knowledge of their generic and specific types...I have no reason to suppose that an a priori hypothesis connected with either time-or space-distribution, influenced Mr. Davidson in coming to his final arrangement, and, therefore, I have been the more curious to see how far that arrangement accorded with geological considerations."[24]

Here, in a cryptic manner, Forbes linked his two notions of the parallel between distribution in space and time: he cited a "time-distribution" and a "space-distribution", both of which he usually subsumed under the label "specific centres". For Forbes the essential property of life was its symmetry, and his work was entirely devoted to the elucidation in one dimension of patterns which he had found in the other. Hence he had described the spatial arrangement of animals and plants into biological provinces, each of which had been given all its organisms at one time (by a Creator) and which was therefore to be considered as a discrete unit. When more than one of these "specific

centres" was in existence - or more properly speaking, created at the same time - then Forbes expected to find true 'representative' species which replaced and were similar in structure to their pair. The intensity of their resemblance was a factor of geographical distance. When he turned to study distribution in time and to muse on more abstract considerations about the history of life on earth, including the general relationships which organic beings exhibited, Forbes attempted to find the same sort of patterns in the fossil record as he had demonstrated in the present day. He wished to be able to state "As in Space, so in Time". It was this dependence on a parallel which gave him his unique theory of a set of successive creations through time which in turn, replaced and represented former creations. He saw the phenomenon of 'representation' as linking the two dimensions into one grand scheme.

Here it would perhaps be helpful if I digressed only slightly to quote at length from a letter which Forbes wrote to Leonard Horner in 1845, (albeit some decade before he proposed the scheme under review) to explain to this eminent geologist exactly what he meant by representation. I take the liberty of transcribing almost all of it for it is not published:

> "Respecting the doctrine of representative species I am very anxious you should understand it, as it is one I lay great stress upon and believe that on its development the fixing of Geology as a science will eventually in part depend.
> Take any genus having a wide geographical (or geological) range, dependent on the distribution of many species, each with its own distinct special range (the sum of the special ranges making up the great range of the genus).
> On comparing the species of that genus inhabiting the several hemispheres (North and South, East and West) we shall find that the prevalent species in the Northern hemisphere for instance is represented by a corresponding species in the Southern - the correspondence or representation depending on such a close resemblance between the two forms, that the critical acumen of the naturalist is usually required to define wherein the distinction lies - though the species is certainly distinct.
> Sometimes a chain of such representatives is kept up.
> Now the same sort of representation of species by species occurs in time - that is to say, species are replaced by similar species in the successive geological formations.
> And in depth - that is, species are replaced by similar species in bathymetrical distribution [i.e.] in the successive zones of depth.
> When I next meet you I will demonstrate this to you by means of specimens. To develop these views will take some time yet. They form part of a system, the first outlines of which I promulgated in a course of lectures when a student in Edinburgh four years ago, delivering them in conjunction with my alchemical friend Samuel Brown, who whether he be right or wrong in his Chemistry is assuredly one of the finest geniuses of our time. I should like you much

> to meet him. I send you with this the prospectus of those lectures - it may amuse you by the impudence of two students putting forth such a document.
> Belive me, dear Mr. Horner, with many thanks for the interest you take in my researches, ever most sincerely..."[25]

Here Forbes, however allusively, stated that space, time and bathymetric depth were all part of the same "system" whereby representative forms were found to appear and reappear in various guises in each topographical province, geological formation or zone in depth.

We can see then that Forbes' hypotheses were designed to include both an idea of geographical representative species, and a more intangible notion of 'representation' through time which was to explain the similarities shown by fossilised organisms in different formations. These two concepts were not really distinguished in his mind or in his work, and indeed, the incidence of the former topographical phenomenon more or less dictated (according to his own predilections) that he should isolate a similar element in geological time, a virtual impossibility without some allowance for a supernatural plan or for a metaphysical 'force' or quality such as a "Law of Representation" as espoused by William Swainson. His theory thus included rather wide notions of what representative species were, because he wanted to understand how genera represented each other through time. The purely geographical phenomenon was inextricably linked and mixed up with his grander ideas about the nature of life and the relationships which we now attribute to a common evolutionary background for all organisms.

## Joseph Hooker

In many ways Joseph Hooker's views about representative species were equally mixed up with notions of a wider and more metaphysical nature. He was well aware of the geographical replacement of one species by another closely allied one, and indeed, was perhaps more sensitive to this phenomenon than either Forbes or any of his geological colleagues. It was systematists such as Hooker who had drawn attention to the prevalence of such forms in nature through their many and varied catalogues, and it was at places like Kew that botanists could carefully sift through specimens and collections to effect some sort of statement about the identity and distribution of certain plants. In the issue over representative species, Hooker saw a purely distributional problem which brought the phenomenon out of the clouds of classificatory theory onto the very real ground. Yet he surmised that these two aspects were in some

way linked and mutually contingent, whilst intuitively rejecting any outright cause and effect relationship. So although he felt no sympathy for Forbes' (or Swainson's) search for the ultimate cause of resemblances and differences in the natural world, Hooker attempted to connect various lesser classificatory objectives and systematic tenets with the solely geographical phenomenon of representation which his own botanical work so plainly demonstrated. And in his confusion, even anguished vacillation, over the relative importance of taxonomically or geographically derived reasons for the existence of representative species, Hooker picked up and discarded most of the ideas about them that were then current. His work and correspondence was thus a rag-bag, the contents of which never, unfortunately, got turned into a patchwork quilt. For Hooker had no all embracing theory like that of Forbes' and he produced no answer.

Hooker had no theory. This I hold to be an important feature in his inability to come to any solid conclusion about representative species and therefore a point to which I will eventually return. Furthermore, I believe it was the very same pragmatic considerations which made him reluctant to espouse either an all-embracing philosophy of nature or a hypothesis to explain these particular forms. And these considerations were almost entirely of a personal nature.

Hooker's peculiarly restricted upbringing - tantamount to a professional training - among the herbarium sheets of his father's ever increasing botanical collection, and his natural sense of precision and order turned him into an uncompromisingly exact naturalist.[26] It was this exacting exactitude which seemed to prevent him from ever reaching a definite conclusion without overloading it with qualifications, and from giving his unmitigated approval to any theory. Of course he did speculate, both in his letters and in print,[27] but he was always careful to add that such remarks were indeed only provisional, saying:

> "I wish it to be distinctly understood that I do not put this forward intending it to be interpreted into an avowal of the adoption of a fixed or unalterable opinion on my part".[28]

Words like these are scattered like confetti through Hooker's large and varied scientific output, far in excess of the neutrality and objectivity that was required of public science during the middle years of the nineteenth century.

Without going too far into that new branch of history 'psycho-history', I think that Hooker may have been so genuinely at a loss to know what to think about many questions that he took refuge in and good heart from the scientific norms of the day, and enthusiastically adopted the stance of a disinterested man of science. In time, the stance, ideals and inclination fused together and Hooker believed himself to be the very man that people saw him as. Eventually (demonstrating how well he had assumed this mantle) he represented British science as its figurehead, the President of the Royal Society. But in his youth, and particularly in his early correspondence with Charles Darwin, he allowed some hesitancy and bewilderment to show through the aggressively self-confident empiricism of his botany. No doubt he was impressed by suddenly becoming one of Darwin's confidants, perhaps a little perplexed at the odd questions he was expected to answer, and certainly was enough of a gentleman to clothe his remarks with a decent modesty, yet the following confession rings true. "Your queries and remarks have opened a wide field for research and investigation, for which I am truly obliged" he admitted, in 1844:

> "These are all subjects which I ought to have attended to, without requiring to be reminded of them by a more industrious Naturalist [a third party]: truly I ought to have been able to answer you on the spot, if I had been half a Botanist, but I seem to know less every month than I did the month before as I find how much there is yet to learn."[29]

So much of an individual character sketch is, in the case of Hooker, explained by the manner in which his personality dictated the sort of science he preferred to do. He was in the eyes of nineteenth century botanists a very great systematist indeed; here there is no danger of Whiggish history, for modern scholars regret the day that he was ever allowed to meddle in taxonomic affairs. He was absolutely at home with the minutiae of classification tables and comparative morphology, and had an extensive knowledge of the floras of far-flung regions principally through cataloguing and arranging his father's justifiably famous herbarium, the foundation of what was to become the Kew Gardens collection.

It was a clear principle with Hooker that classification was essentially a practical matter and that it should enable botanists to determine the plants they had before them. He felt that this objective was best achieved by placing, as far as possible, plants with a maximum number of common characters in closely related groups. In other words, he subscribed to the 'natural' view of French and British naturalists

who had erected on the Jussieus' proposals an elaborate system of relationships, affinities and similarities, in an attempt to describe the web or net of relations which interconnected the plant kingdom. By necessity these were rather more recondite points than those which drew the animal kingdom together, since the latter exhibited its relations through largely external features like legs, feet and skin, or striking anatomical bits and pieces like bones, guts and nerves, where botanical systematists depended on the number, size and position of stamens and stigmas, petals, ovaries and seed-coats, etc., and often had recourse to developmental or embryological factors for their identifications, all of which required a very clear idea of what was being searched for. Now although every conscientious naturalist would examine either animal or plant with all the attention to detail that it needed (as for instance the painstaking investigations of Malpighi, or, in our period, Darwin on barnacles), Hooker aquired a veritable bee in his bonnet about the slapdash standards of his own age and constantly asserted that botany was more difficult than usually believed.[30]

The cynic would here pause to remark that Hooker was, in actuality, justifying the time that he spend on botany and constructing a niche for his future occupation as an expert in that 'difficult' subject. Perhaps there is a lot of truth in such an interpretation. But the historian can also see an awareness of the failure of naturalists to achieve or maintain the ideals of Hooker's science. He wrote of the "rashness", "vagaries" and "recklessness" of other botanists and additionally aimed his tirades at "more well-meaning persons," who,

> "by defective definitions and erroneous classification, crowd our books with imperfectly defined genera and with groups or subdivisions of no practical value."[31]

To Hooker bad classification was synonymous with bad botany. And what started it all was bad comparative anatomy. Thus as an earnest youth and as an even more earnest adult he set about alleviating this state of affairs through his own meticulous work and a series of heavily didactic "Introductory Essays" in which he instructed the colonial botanist in the ways of science.[32] Later he made a determined intervention into science's public bodies where he could influence educational policies and, like his close friend Huxley, delighted in the politics and skirmishes of the government of science. This devotion to nineteenth

century ideals of science (truth, honour and accuracy in its pursuit, and knowledge to be freely available for all) though an essential component of the 'image' of science and accordingly recognised and used as such by its public protagonists, was in Hooker's case none the less strongly felt for all that. Whatever his motives were, he really did believe in Victorian ideals of science.

Hooker therefore made a virtue out of his extraordinarily wide knowledge of botanical fact and his ~~belief~~ interest in pedagogy by claiming that he was "untrammelled by any theories to combat or vindicate" and so gave every side of problems and issues in his writings. It is hardly surprising then, to find that he could not make up his mind about representative species or the more pervasive phenomenon of degrees of representation throughout the plant kingdom. He had a clear idea of the undisputable incidence of different species of one genus appearing in geographically disparate regions; indeed having worked out Darwin's Galapagean plants he could not fail to have noticed this particular distributional point.[33] In an informal note to Darwin scribbled on the back of one of Darwin's previous lists of questions, he wrote of representative species in the several islets of that archipelago:

> "The instances of representative species on the several Islets may be divided into two groups, I) of peculiar genera, as Scalesia (see p.2) and Galapagoa, one Albemarle and one Charles and Albemarle, and 2) extra-Galapagean genera having peculiar Galapagean species. Thus the Euphorbiae are very peculiar, only one species, pilulifura (James Isld.) is mundane, but of 7 others not one is common to 2 islets - Acalypha has 6 species, in the same predicament..."[34]

In other words, true representative species were to Hooker forms peculiar to the individual islets of the Galapagos archipelago and yet which belonged to the same genus. He recognised that the genus itself may be either confined to this general region or spread out over further areas, but understood the term 'representative species' to apply exclusively to peculiar species or endemics. He thus linked the structural distinctness of each species of Euphorbia or Acalypha to its geographical position, no mean feat for this botanist who repeatedly criticised the practice of elevating geographical variants into species simply because they came from different regions. Much of Hooker's work was dedicated to the principle that "Species vary in a state of nature more than is usually supposed", and to a determined 'lumping' of doubtful species or varieties into one larger group exhibiting a wider range of characters;[35] if he could have done so, he would have 'lumped' all the Galapagos species together as geographical variants foreshadowing to a remarkable degree the

sort of comprehension that Darwin was to bring to the same problem. However Hooker found these species to be quite distinct from each other and could not avoid the suspicion that such distinctness was related to their geographical isolation in some way.

Moreover, he seems to have connected the phenomenon of representative species with that of endemicity, or rather the existence of species and genera absolutely peculiar to the one region in which they appear. Of course in one sense this is a truism, since all representative species are, strictly speaking, endemic in their own area, otherwise they would not be representative. But Hooker tended to discuss the problem in terms of forms which were usually endemic in some region or another, so that, in effect, he answered queries about representative species with illustrations drawn from endemic genera, thus indicating that he held their specificity to be a crucial factor in the incidence of representatives. Accordingly, in reply to one of Darwin's questions about the comparative ranges of mundane and endemic species, Hooker explained the latter solely by citing the ranges of representative species in the restricted groups of Cacti (endemic to the New World) and of the Capuchin monkeys (limited to central South America). In further letters on the same issue he continued to associate such representative species with the attribute of belonging to a purely endemic genus or family.[36]

It was this emphasis on endemism which, I contend, led Hooker into confusing relatively straightforward topographical representatives such as the several species of the Galapagos islands, with rather more philosophical speculations about types and typical forms. Endemism was a phenomenon which clearly meant that these taxonomic groups were special to their areas, and therefore typical of that region: kangaroos were endemic to Australia and by virtue of that fact were a typical part of its fauna; the Japanese cherry tree typified its country of origin, as did the lion Africa. Hooker coupled this commonplace idea with his notion that representative species belonged to endemic groups, and wondered if representatives were typical forms or if types were the same thing as proper representative species.

He wrote to Darwin on the subject and confessed:

> "I hardly know what is always meant by a typical form. The character of a group should be founded on the most important objects it contains in the oeconomy of nature. The most important genus of a class is surely /generally either inserted/ the largest or the most widely diffused..."[37]

He therefore suggested that empirical evidence of size (i.e. the number of species) and the extent of dispersal should determine which genera should be classified as typical of their larger group - he was tending towards a statistical view of nature - yet in so saying he directly contradicted his own knowledge that 'type' species like the kangaroo or gladioli were strictly limited in their geographical extent. He was caught in a paradox which stated that typical forms were, and were not, dependent on their wide range, and this paradox was immediately reflected in his assumptions about representative species. We have seen how he connected these living beings with endemism. On the other hand his pragmatic nature told him that a lot of representative species in a genus meant that that genus had more than the 'average' number of species, and was consequently larger in size and, by inference, more widely dispersed than would merit the description of endemism.[38] In fact a lot of representative species made a genus so large and widely spread that Hooker thought that it ought to qualify for the epithet 'typical'.

In such a way Hooker could call to mind several shades of meaning for a proper appreciation of representation: it brought with it connotations of geographical isolation; type; endemicity; and statistical generalisations about size and range, according to the context in which it was applied. He was never to express a definite opinion on the phenomenon because these several inferences prevented him from drawing up a clear-cut statement of the 'pros' and 'cons' of any hypothesis which claimed to answer or account for it. Because Hooker preferred to prove or refute already constructed theories, rather than devise his own, he found that in the absence of any suggestions from naturalists whom he respected, he could not make up his mind how to evaluate and order this amorphous problem. And again, since he took exception to "hasty generalization or loose speculation" and claimed to be "fettered by no professed opinion to support, and had no inculcated theory to eradicate", he had no underlying philosophy of nature which could direct his understanding and provide terms of reference for the interpretation of the appearances.[39]

Thus in 1846 when he was called upon to publish the results of his examination of Darwin's collection of Galapagean plants he was at a loss to explain why there were so many representative forms. Certainly, he noted, this was the most striking point about the flora of this archipelago:

> "As in the case with the Fauna, many of the species, and these the most remarkable, are confined to one islet of the group, and often represented in others, by similar, but specifically very distinct congeners."[40]

He listed the species to be found in each island and remarked that the difference between them was very odd:

> "Were this peculiarity effected only by those species which may have come from the continent of South America , it would have admitted of some explanation, so capricious are the elements which regulate the interchange of species, and so uncertain in their effects even when apparently most uniform in their action. But in this case, the difference is most marked in the distribution of the species that are Galapageian only, the individuals of which are not common to every part of the archipelago, but for the greater part confined each to one solitary islet."[41]

This point he illustrated by stating that out of some 128 species peculiar to the archipelago, only 13 were found on two islets, 2 on three islets and a single species could be found on four. All the other forms were representative species. The only suggestion he had for such a fact of nature was that it might conceivably be due to a lack of inter-island communication, something which Darwin had pointed out when discussing the animal life of the region in his Journal of a Naturalist (1838). Hooker thought that if all the islets were put together, in a few years they would have lost much of their individual character:

> "The strife with its neighbours for position, which marks all stages of the life of any two or more continuous plants, would terminate in a few replacing the many . . . It must be admitted, that the first steps towards ensuring the continuance of many species in a given area, are to isolate them, and to cut off the means of migration; exactly as in a garden the plants are protected from encroachment mechanically, and the seeds of the more volatile collected betimes, to prevent a like effect being naturally brought about."[42]

And that was all he had to say on the matter.

What then can be deduced from this absence of any fully formed hypothesis concerned with an explanation for these problematic species? Was Hooker so much of a sceptic that he failed to find a satisfactory answer? Certainly he was reluctant to make a public statement of his views on any provocative issue, as evidenced by his cautious and qualifying remarks appended to both of his Introductory Essays. Nevertheless he did pass a strong opinion on matters which were dear to him such as, for instance, the necessity for careful systematic botany and an awareness on the part of the practising botanist that species were far more variable and widely spread than generally supposed. So I think that here, on the matter of representative species, Hooker really did not know

what to think about their origins or the way that they were to be drawn into the general scheme of nature. In his letters to Darwin where he is at his most speculative (even that achievement being somewhat tempered by qualifications), Hooker demonstrated some perplexity over the way representative species ought to belong to the most widely spread and large genus and yet were clearly strictly local forms which usually belonged to endemic genera. Thus each representative species in the Galapagos archipelago was confined to its own islet and belonged to a genus which was itself confined to that group of islands. His friend Darwin was, of course, eventually to explain this phenomenon by supposing that the 'parent' of pairs or triplets which now represented each other had indeed once been widespread and had, at one time or another, occupied all the lands which were now colonised by its subspecies. But before the Origin of Species was published in 1859 Hooker was at a loss to know how to link these two apparently distinct and opposing elements of wide range and endemicity. He was, in short, unable to think about the phenomenon in a historical way and to suggest that large and dispersed species - such as his special favourite Senecio - could eventually split up into smaller and mutually exclusive geographical variants.

This inability was, I contend, not restricted to Hooker alone. His botanical colleagues of this pre-Darwinian period were equally unable to posit explanations for geographical representatives and replacements such as those found in the Galapagos. The same sort of data about parallel forms was being collected from other island groups like the Sandwich Islands and the West Indies, and from mountain ranges in Europe, the Americas and the Himalayas. In 1837 F.J.F. Meyen, the Berlin botanist and one of the first botanical geographers to consider the Himalayas, wrote that mountain summits were very like ocean islands in that they presented floras virtually isolated amid a 'sea' of lowland plants, and pointed out that these elevated lands bore representative species of northern genera:

> "...at a height of from 11,000 to 12,600 feet, there prevails on the Himalayah a flora which is entirely similar to that of the Scandinavian peninsula; and at a height of from 7,000 to 8,000 feet our forest trees predominate, which, though differing in species, have nevertheless the same physiognomy as in Germany."[43]

Edward Forbes had discovered a similar fact when he ascended the Carpathian range in 1841, and the American botanist Asa Gray had written

in some detail on the existence of representative forms in the White Mountains and Labrador situated four or five hundred miles to the north. Of these naturalists, only Forbes had attempted to provide any sort of theory to account for their existence.

Gray was very like Joseph Hooker in his reluctance to do anything other than describe the facts as he saw them. In his Statistics of the flora of the Northern United States (1856-7)[44] Gray examined the resemblance which was evident to botanical eyes between this region of America and western Europe. He pointed out that although there were many species actually common to the two regions affinity between them was also exhibited by their pairs of representative species:

> "Two floras may be, perhaps, as nearly related through their allied as through their identical species: at any rate, the comparison in this respect is equally important to be made... The special resemblance of our flora to that of Europe, it is clear, is not owing simply either to the large proportion of genera in common, or to anything striking or important in the few genera nearly or quite peculiar to the two...We must look for it in the species partly in the identical ones (already noticed), and partly in those which closely answer to each other in the two floras."[45]

And he went on to describe about 115 truly representative species, defining them as "Strictly representative species, pretty exactly answering to each other in the two floras, but of which there can be little if any question of specific identity."

The Statistics was, as far as I know, the most sophisticated treatment of these forms that had ever been published. Gray recognised the "impossibility of estimating the degrees of resemblance among species" and pointed out that there were all kinds of representation to be found in nature. One pair of representative species did not necessarily show the same order of difference or similarity as another. "The species of every genus", Gray wrote, "resemble each other in very unequal degrees", and this inequality was to be found in representative forms also. Hence he suggested dividing the latter into five degrees of affinity, where the first category likened mere geographical varieties to each other, and the fifth drew together extremely "divergent congeneric species". Somewhere in the middle of this scale Gray put the organisms which we now know to be proper representative species.[46]

Hence Asa Gray was quite aware that the phenomenon of geographical replacement could be linked in a general way to more taxonomic considerations, such as the relations between varieties and true species. He recognised that all genera are made up from analogous species (for what is the definition of a genus if this is not the case?) and that this

analogy varied in degree. It was therefore quite reasonable for him to insert representative forms into such a scale of resemblance. But Gray, unfortunately, never made very much of this suggestion and it was presented as a simple device to aid the classification and examination of American plants: he appeared to have had no intention of working it up into a theory of representation or resemblance as Forbes undoubtedly would have done with the same data. In fact, it appears that Gray derived this scale entirely from empirical investigations and it was as far as he was prepared to go in the arrangement of information; like Hooker he eschewed public theorising.

## Conclusions

I think that there are some valuable conclusions to be drawn from the manner in which, firstly, Edward Forbes and, secondly, Joseph Hooker considered representative species and the phenomenon of representation in general.

Looking at the immediate thrust of this chapter it will be seen that these two nineteenth century naturalists held that representative species were part of a wider, more abstract, natural consistency. As might be supposed, different men took different views about the way in which these geographical forms were to be integrated with the laws which they believed to unite nature, and so Forbes, on the one hand, and Hooker, on the other, presented quite dissimilar attitudes to these species. Forbes saw them as a physical manifestation in topographical space of a resemblance which thus ought to be found also in geological time. He was certain that there was an analogy between distribution in space and in time, and therefore had no qualms about transferring his ideas about geographical representatives to the fossil record and thus posited the existence of chronological ones. Hooker, by contrast, possessed no such certitude and did not know exactly where to place phenomena such as these in the hierarchy of ideas which he held about nature. He felt sure ~~that~~ on a priori grounds that representative species were part of some greater unknown plan, as evidenced by his remarks to Darwin about connecting them to current notions about "typical" genera which were assumed to be statistically large in numbers and widely spread, but he did not espouse any particular theory and thus restricted his writings to a mere enumeration of their distribution.

Glancing at the other individuals who entered briefly into this discussion, it will be seen that Gray too believed that representative

species were part of a greater scheme of things, as shown by his arrangement of different categories of resemblance, where representative species per se were one item in a list of five grades of resemblances between members of the same genus. William Swainson took this belief in an all-pervading theory of resemblance and representation to the extreme where he absolutely ignored the purely geographical phenomenon and saw only metaphysical relationships between all sections of the animal kingdom. And finally, Charles Darwin interpreted the various forms of life which he found in the Galapagos archipelago as being one stage in a sequence of growth and dispersal of genera, to be followed by a splitting up into new species that would themselves one day increase in numbers and rise to a successful position in the scheme of nature. Representative species were thus, to him, a stage in the normal process of speciation and so part of his grander theory of the evolution of life.

I believe, moreover, that some notable points can be isolated from this study which relate to the discipline of biogeography itself. Despite personal factors which made Forbes and Hooker rather different in their attitude to speculation and theorising in general, I argue that in the second quarter of this century it was the geologists, and not the botanists like Gray or Hooker, who produced distinct theories and explanations for distributional phenomena. By this time, and especially after 1830 and the publication of Lyell's Principles of Geology, geologists were quite prepared to indulge in the construction of grand hypotheses and schemes for the history of the earth and the story of life. Forbes' "principle of Polarity" is only one example - and a rather unsuccessful one at that - from what amounted to a major industry in geological circles. Here I need only cite the names of famous paleontologists such as Louis Agassiz and Richard Owen, Alexandre and Adolphe Brongniart, Alcide D'Orbigny and Roderick Murchison who each in his own way propounded a theory of the progressive history of the earth and its organisms. Here too Lyell's vision of a steady-state earth and its associated uniformitarian tenets stands as a prime example of the sort of all-embracing theory of nature which was to become a characteristic of geological writings of the period. It was not so much the content of these theories, as the possession of one at all which therefore singled out geologists and paleontologists from their botanical and zoological brothers. For, as I have shown, the Hookers and the Grays of this world were content - in public at least - to restrict their work to the itemisation of the facts of distribution and thus proffered no

hypotheses to account for the oddities which they were undoubtedly describing.

The situation as I see it can thus be resolved into two fairly clear cut categories. On the one side there were geologists (or more properly speaking, naturalists with a penchant for the study of fossilised organisms) like Forbes and even Darwin, who laboured under their own systems of nature and attempted to draw into these the phenomena which were found in present-day distribution patterns. Hence the explanation of representative species was seen to be part of a larger search for general laws and the phenomenon itself was incorporated into a more comprehensive account of life on earth. On the other side, by contrast, there were botanists like Hooker and Gray who as practising systematists found more complexity in the description of geographical replacements than any of the geologists. This awareness of the differing grades of 'representation', manifested in some areas by representative species and in others by representative genera and existing as a phenomenon which was in an odd way related to the distance between two countries, prevented them from seeing any possible generalisations in the distribution and degree of this quality in nature. Hooker did not know what to think and so concentrated on the facts alone; Gray suggested that representative species were part of the usual differences found in the comparison of one species, one genus or one flora with another. They had no theory within which these forms were to be dovetailed, and the facts alone did not induce them to make hypotheses for their explanation.

These differences, I suggest, were due to the very different ways in which natural historians and geologists were accustomed to consider nature. Because most geologists - and particularly Forbes - wanted to present a description of the laws which regulated the history of living beings, they tried to incorporate spatial data as additional and supportive evidence for their schemes. Botanists, who were just as concerned to find out the laws of distribution and the origin of organisms, were hidebound by the traditions of their subjects to investigate only topographical phenomena without any preconceived theory to vindicate, and thus allowed the very real complexities of this single problem to confuse them to the point where no theories at all could be proposed.

# Part II

## Chapter 3: The Investigation into Biological Provinces

The first fifty years of the nineteenth century were not simply an arena for the concepts of geologists. Within the natural sciences there were, of course, other disciplines as developed as geology and similarly demanding exercises, with their own cross-section of beliefs, typical practices and precepts. The science of physiology, for example, had had a long and distinguished history reaching back to the experiments of Stephen Hales and Richard Lower, and was now, in the nineteenth century, enjoying increased popularity as questions relating to the ultimate nature of life were asked. Bichat classified living tissues into systems, as in the bone or muscle system, which enabled his successors to study the diversification of the parts of the body; Berzelius published one of his earliest works, the Lectures on Animal Chemistry, and Magendie wrote on "les phénomènes physique de la vie", in 1806 and 1836 respectively; Ingenhousz discovered photosynthesis and Dutrochet osmosis; and Schleiden and Schwann described the cellular arrangement of tissue. Thus physiology was a sophisticated science and physiologists had at their service a variety of important theories and explanatory models with which they could continue to study the living body. One might make an equally valid case for the experimental study of heredity which, at this period, encompassed the diverse researches of Etienne Geoffroy St. Hilaire and Moquin-Tandon on embryonic modifications and monsters, and the plant breeding experiments of Kölreuter on tobacco hybrids, of Karl Gärtner on many groups including the former and peas, and of William Herbert, the Dean of Manchester, on the order Amaryllidaceae. This too was a well developed intellectual discipline with its own rules and standards of acceptability.

But here I would like to make a case for the existence of a 'mature' science of descriptive natural history, one that possessed its own ways of working just as markedly as physiology, the study of heredity, or geology had theirs.

Though historians may debate the true definition of the term natural history[1] and discuss the varying content of this subject through the ages, no-one would, I think, deny that in the nineteenth century investigations into the living phenomena of the world were being pursued with relentless energy. One only has to think of the work of

individuals such as Richard Owen or Robert Brown, Joseph Hooker or Alphonse Decandolle, the most famous comparative anatomists and systematists of their day, and of the host of less prominent natural historians such as George Waterhouse, George Edward Gray, John Gould, William Sharp MacLeay, Thomas Bell, Christian Ehrenberg, or James Dana, to acknowledge this point. What I would like to establish here, however, is that the investigations of naturalists such as these were carried out under the aegis of a particular approach to nature which was every bit as distinctive as that which was characteristic of geologists. In the same way as I outlined a 'geological' attitude which governed the interpretations that men such as Lyell, Forbes or Darwin could derive from the distribution of existing animals and plants, I now intend to present the other side of the coin by describing how natural historians looked at exactly the same phenomena. This latter I call a 'topographical' approach to the study of distribution, for it was, as will be pointed out, concerned with the spatial arrangement of organisms. Just as the geologists had an interest in time, so the naturalists had one in space.

First and foremost, and indeed most obviously as well, a 'topographical' vision of the living world was preeminently concerned with topographical regions. A.R. Wallace, the most distinguished student of distribution whom the nineteenth century produced, fully recognised this outstanding feature of natural investigations and roundly declared that "The first essential is a broadly marked and easily remembered set of regions"[2]. Had he looked back at the collection of theories which had been proposed over the previous two centuries, Wallace would have seen that an itemisation of the regions of the earth had indeed been held as a "first essential" and that it had truly engaged the attentions of naturalists from the time of Linnaeus to his own. Because it was such a pressing concern both to Wallace and to his predecessors, it is appropriate and worthwhile to here trace out a brief history of attempts to divide the earth into a set of living regions, or as we now call them, biological provinces. And in particular, such a history is instrumental in explaining some distinctive theories relating to the wider issue of the creation of animals and plants espoused by Joseph Hooker and others in the early parts of the nineteenth century.

Although a comprehension of the differences of form, habit and behaviour of animals and plants found in one region or another was, and still is, fundamental to man's larger understanding of the world around

him, this was not quite the same sort of thing as an idea of biological provinces. The idea of imposing a set of organic beings which was invariably different from other sets on to the more obvious notion of a purely geographical region was not consciously applied or carried out until well into the eighteenth century, although, as I shall show, there had been an assumption of this nature for more than six centuries beforehand. The superimposition of 'biological' associations on to geographical regions is a concept which was notable for the development of natural history even though it never was 'discovered', 'introduced', or 'made known' at a definite point in time, and, on the contrary, simply slipped into the corpus of biological axioms unnoticed by naturalists.

Such a 'slipping' I believe to be a result of the sheer growth of information through the ages about animal and plant life and about the variety of countries which could support them. Geographical Exploration and investigations into organic nature went hand in hand from the most ancient times to modern eras, and thus, for the earlier centuries of this chronological span, the extent of man's knowledge about his surroundings more or less governed the way he was to comprehend the living products of the earth.

So, not unnaturally, we find that the earliest descriptions of animals and plants both native and foreign to the investigator depended to a large degree on how much he knew about the countries of the earth. Ever since an awareness of the differences between topographical regions had first crept into scientific consciousness, the business of their delineation and configuration, and - most notably - the description of their produce, had been items of some importance. So the historian discovers that the authors of the most ancient documents known to exist certainly recognised that different beings came from different countries. Every cultivated nation of antiquity was eager to chart the face of the earth, and the explorations of the Phoenicians, Cretans and Greeks resulted in a fairly substantial body of knowledge by the time of Ptolemy. His Geography written in the second century after Christ was a compendium for travellers and consisted of a lengthy inventory of all places known to the Roman empire. Yet six centuries earlier Alexander had extended the world's frontiers as far as India and his people were a roving restless set who readily sailed the Mediterranean or caravanned across foreign lands in search of business or of learning. Aristotle, for instance, was keenly aware of the diverse animals which could be seen in foreign

lands and listed the most striking examples known to him, passing from a remarkable description of one of the most mysterious of all biological phenomena, the migration of locusts, to the fact that there was an absence of cicadas on one side of a river in Cephalenia, and to the observation that "in the whole of Libya there is neither wild boar, nor stag, nor wild goat"[3].

Theophrastus too seemed quite familiar with the notion that different regions possessed different plants and even devoted one of the nine books of his History of Plants to "trees and plants special to particular districts and situations". Here he described the gum trees of Arabia and the method used to collect resin, and figs in India that possessed the odd property of having branches that reached down to the ground and rooted, although there is no doubt that he received this information at second hand from travellers.

The study of foreign animals and plants prospered even after the Athenian school, which had been encouraged by Alexander and by the Ptolemies in turn, virtually came to an end when Egypt fell under the power of Rome. Though science itself may not have flourished, the love of the strange and rare and the practice of medicine ensured that both zoology and botany went from strength to strength in Roman times. Medical men, most notably Dioscorides, prepared herbals which were soon illustrated to avoid any scholarly confusion between plants of supposedly specific uses, and men of affairs such as Pliny extracted and epitomised these and other volumes of natural wisdom for the benefit of later readers. Along with the development of the Roman empire came greatly improved means of communication which made possible the transportation of foreign beasts within its boundaries for military and sporting purposes. Hannibal's elephants are something of a cliché, but it is nonetheless instructive to know that Pliny wrote of the arrival of the first elephant in Rome at the early time of 275 BC, and that a very large number were captured from the Carthaginians in Sicily in 252 BC. They must have been a common sight by the period 55 BC when Pompey watched seventeen elephants at his circus, along with a rhinoceros which stole the scene. Pliny himself, if not Pompey, certainly realised that these beasts came from specific regions in and beyond the Empire:

> "Elephants are produced by Africa beyond the deserts of Sidra and by the country of the Moors; also by the land of Ethiopia

> and the cave-dwellers as has been said; but the biggest one by India . . ."[4]

And Pliny discussed other, less foreign, animals in very much the same sort of way and firmly linked each kind to the region in which it was found:

> "The soil of Ebusus chaseth serpents away, but that of Colubraria breedeth them . . . Neither does Ebusus produce any rabbits; which are so common in the Baleares, that they eat up the corn."[5]

Now this sort of awareness was something so fundamental to man's understanding of the natural world that it was hardly likely to fluctuate in rhythm with the more general rise and fall of interest in science through subsequent centuries. As geographical exploration proceeded, so descriptions of the living beings of each country accumulated and something approaching a composite picture of each region began to be built up. However, I would not like to claim it to be a rule that this was an entirely autonomous growth, unaffected by what was going on in the intellectual context of each age, for there was at least one curious example, if not more, of the way in which prevailing concepts regulated this continuing process of exploration and description. The latter came about with the so-called renaissance of the twelfth and thirteenth centuries when translations of Aristotle's works and various treatises from the Arabs - in particular from Avicenna and Averroes - were made available to the West. Early encyclopedias deriving from this movement, written by Neckham and Albertus Magnus, gave many descriptions of species native to Greece and the long-gone Roman empire, with some new ones native to the lands of the Middle East and Asia. Hence natural historians of the West were remarkably ill-equipped to cope with the very different plants and animals found, for example, in deepest Britain. Furthermore, travellers such as Marco Polo and Mandeville (whoever he was beneath his semi-fictional account) were making their own journeys and bringing back to the West personal descriptions of the "kingdoms and marvels of the East". Marco Polo saw new creatures such as the wild asses of central Asia, and experienced delicacies such as rice and ginger. In the Anderab valley he noticed "a great many porcupines" and in Tangut was the first westerner to locate the source of wild rhubarb:

> "Over all the mountains of this province rhubarb is found in great abundance, and thither merchants come to buy it and carry it thence all over the world."[6]

So the flow of information was decidedly from the east to the west, and the facts themselves were related to eastern phenomena. What effect did this have on the practice of natural history in the West?

For an age which had no notion either of the numbers or of the distribution of the animal and vegetable kingdoms, the expression of this knowledge took the form of fitting native floras and faunas into the accounts of plants and animals as catalogued and described by the ancients and their expositors. For the practice of medieval natural history the assumption of a single (Biblical) centre of creation for all forms, such as the Garden of Eden, made it quite natural to expect that, in the main, plants and animals were the same throughout Christendom, and that correspondingly the species listed by Aristotle, Dioscorides, Avicenna and others would be found also in the West. So, motivated partly by practical concern with medicaments and simples, and partly by genuine interest and affection for nature, natural historians went out into the fields and woods of Europe to collect and identify local species as if they were those of Greece and Arabia.

Despite presenting an apparently insuperable problem, since it was founded on an untrue assumption, similar attitudes of mind inspired the great succession of field naturalists through the thirteenth and fourteenth centuries who pursued the same activities as their early medieval precursors, and who at last recognised and advertised the fact that many species were not included in ancient lists. This quite naturally inspired considerable 'home grown' interest in the breasts of men such as Frederick II for the birds and beasts of their native lands. Frederick produced one of the most important medieval works on zoology, the Art of Falconry, almost entirely based on his own inquiries into the life and habits of birds. In parenthesis, it could be added that Frederick also established one of the earliest menageries which included as its pièce de résistance the first giraffe to appear in Europe. And at a lower, but no less appreciative level, the stonemasons of Gothic cathedrals and the miniaturists of medieval manuscripts embellished their works with vivid and delightful portrayals of their native birds, beasts and flowers. Bartholomew the Englishman delighted in explaining his quite considerable knowledge of local items of interest, juxtaposed against received wisdom. His description of the domestic cat is perhaps too well known to quote here, but he showed a similar sympathy for England's indigenous birds and wrote of the differences between domesticated and wild species which enjoyed or fled from man's company.

> "Also briddes and foules beeth iknowe by places that they wonne in. For some briddes and foules as it seemeth of company and wonynge neigheth men, as hennes, gees and sparowys, storkes, and swalowis. And some dredith and fleen and ben aferde of conversacioun of men, as foules of woodes, of moutaynes, of ryvers, of mareys."[7]

On a more scholarly level, the subsequent centuries saw naturalists such as Gesner in Switzerland, Matthioli and L'Obel in northern Italy, Fuchs, Dodoens and Brunfels in the Low Countries, and, in Britain, Turner and Caius, supplementing and extending the flora and fauna of bookish learning with lists and descriptions of local forms. This turned out to be an absorbing and satisfying task, and under the guiding influence of ancient literature an increasingly complete picture of regional life was built up in the magnificent Herbals, Kreuterbooks and Florilegia of the fifteenth and sixteenth centuries. And there was much more that did not get into print, as the manuscripts and drawings of many a great modern collection well testify. Lists such as these, whether in book or manuscript form, were at first essentially addenda or supplements to Dioscorides and others and automatically included his species with all their various identities, names and properties (viz. Fuchs' herbal, 1542) where, only a few decades later, they included many 'new' species which were unknown to earlier authorities and accordingly so marked. Indeed, by the end of the sixteenth century Dodoens and William Turner were producing works which were not so much supplements to the ancients as true replacements. Turner added a third part to his Herbal of 1568:

> "wherein are conteined the herbes trees rootes and fruytes whereof is no mention made of Dioscorides Galene Plinye and other olde Authores."[8]

Continuing foreign travel and the colonial expansion of Europe into the East and West Indies, China and Japan, and most notably, into the New World, led quite naturally to the introduction of novelties such as tobacco, the sweet potato and tomato, or the tulip, paeony and Arabian horse to delighted European courts. The reading public were eager to obtain a coup d'oeil of the natural phenomena of these fascinating and strange regions, as evidenced by the numerous editions of descriptive travelogues. The letters of Anghiera to the Spanish court about their colony in the New World excited immediate attention throughout Europe as the only source of authentic information; these letters, known as the Ocean Decades, were written from 1494 and continued, with interruptions, to the year of his death in 1525, although they were only first published

in 1516. Monardes, the best known and most widely read Spanish physician in the sixteenth century, made the American materia medica known through his writings. He published the first book on American drugs in 1565 which ran to countless editions. And this period saw literary revivals of earlier voyages such as the collection of anecdotes and descriptive details about the sea travels of Sir Francis Drake and the regions which he visited, in The World Encompassed published in 1628.

So there were ever more pressing reasons for Renaissance and then seventeenth century naturalists to take a lively interest in the plants and animals of their own lands, and in those of distant countries. Herballists like Camerarius, Colonna and Gerarde[9] who pandered to the continuing desire for medical advice were joined by systematists such as Clusius, Bauhin and Johnson, and by garrulous yet informative writers like John Parkinson. The excitement generated by the produce of foreign parts was such that Thomas Johnson was acclaimed for exhibiting the first bunch of bananas to be seen in England in his shop in Snow Hill, having received them from Bermuda in 1633. Their fame was so great that he eventually had an engraving made of them to be included on the title page of his edition of Gerarde's Herbal.

Thus there was no possibility of avoiding the fact that the earth supported a great diversity of forms and that different geographical regions teemed with quite distinct sorts of life. Nevertheless, the origins or reasons for such a phenomenon were not, as far as I know, commented on in any of these treatises. That plants were arranged to occupy separate countries when, as was now constantly being shown, they could equally well live in England or continental Europe with the attention of gardeners like John Tradescant the elder and his son, was not a fact that was noticed. Even in the very place where it could have been noticed, such a striking phenomenon was ignored: John Parkinson gave an ample account in 1629 of the ornamental and introduced plants in gardens of this time, thereby showing just how commonplace it was to be aware of the riches and variety of the natural world, and moreover, just how intense an interest was generated in the actual cultivation of foreign plants. But nowhere did he ask why these exotics were native to one single region when they could also live in Europe[10].

Insofar as an answer was available to Parkinson and his contemporaries, it would have been one based on Biblical creation. No doubt they would have assumed that plants had either diffused from the Garden of

Eden or from Mount Ararat after the Flood to the places which they now occupied, and that it was Divine will which disposed them the way they were found. Despite the wealth of data which seemed to indicate a reality which could not be explained by these means, little conflict seems to have been generated in naturalists' minds by adhering to a belief in Biblical origins whilst demonstrating scholarly interest in facts that would ultimately invalidate such a view. Even Linnaeus, who was the first naturalist to ask himself in print whether all these different kinds of animals and plants could truly have fitted into the Ark, decided that they evidently had managed to squeeze in because that was the way that God had planned it. In later life, Linnaeus was to allow that a certain amount of hybridisation had taken place after the Flood, especially among plants, which had given rise to the existing diversity in that kingdom.

Linnaeus' views were important in another respect, for they generated the context within which his successors were to work and to attempt to understand questions like these about the distribution of organisms. By stipulating the existence of 'species' as real and constantly reproducing entities and a set of correlated axioms, he made it possible for naturalists to link each different form with the area from which it came, and subsequently to a belief in multiple creation.

As might perhaps be expected with all this awareness of the complexity and richness of the natural world, there had come a gradual formation of the aim to reduce it to order and to discover the true regularities of nature. Attempts were made through the seventeenth century to reduce the (relatively) overpowering mass of different kinds of life to one interlocking relationship which had some important and fundamental meaning. Thus the age of classical taxonomy, and the works of Bauhin, Clusius and John Ray. In contrast to earlier naturalists such as Gesner, these seventeenth century classifiers invested nature with her own meaning instead of that of some external supernatural world which was manifested by signs and symbols[11]. Naturalists before Neckham, we are told, saw the objects of natural investigations as things which possessed only the incomplete shadow of a transcendent message completely external to the thing itself[12]. But by the seventeenth century natural historians investigated living bodies by direct observation and comparison and were agreed that nature consisted of objects which had their own meaning, not that of another world or Divine being. Hence they began to search for

the identity of this second inherent quality which gave the natural world its real significance.

In many ways this search was perhaps the purest expression of Platonism that history has seen. It took the form of an ever more engrossing inquiry into comparative anatomy and taxonomy for the isolation of a single character or property - an 'essence' - which would simultaneously define and encapsulate the form from which it was derived, and which, when arranged in a hierarchical system, would mirror the true order of nature. Essences were different things to different people: Gaspard Bauhin attempted to arrange his plants according to their natural relations (roughly speaking, our modern botanical Orders) and so foreshadowed Linnaeus' conviction that the essential property was one concerned with affinity and descent, and also anticipated the "natural system" of Jussieu which was eventually to replace Linnaeus' scheme; John Ray, on the other hand, at first divided the plant kingdom into cohorts based on the essence of physiognomy, for example on the shapes of leaves, stems and fruits, and then later presented a natural arrangement akin to that of Bauhin but one which concentrated on smaller, more closely knit groups (our genera) clustered around a typical form. In much the same way, the "species concept" was Linnaeus' essence, and, many years further on, the notion of "descent with modification" was Darwin's essence. Indeed I think that it is quite valid to claim that essences still exist for modern naturalists, as in, for example, the concept of the genetic code.

So Linnaeus, as others before him, sought for the essential property of the living world which would define and characterise his forms and allow a true ordering of them in the way that nature, not reason, dictated. He found it in the idea of 'species' as a discrete and indissoluble unit, inextricably binding individuals together by descent, generation after generation with a definite constancy of structure. Not simply a collection of similar beings, Linnaeus' species were metaphysical constructs which by their very existence proved that nature was at root capable of an ordered arrangement which had been, and was to remain, always the same. In the Systema Naturae of 1735 he set out the propositions which had led him to this view:

> "1. . . . Each living being is propagated by an egg and . . . every egg produces an offspring closely resembling the parent. Hence no new species are produced nowadays.

2. Individuals multiply by generation. Hence at present the number of individuals in each species is greater than it was at first.
3. If we count backwards this multiplication of individuals in each species, in the same way as we have multiplied forward (2), the series ends up in one single parent, whether that parent consists of one single hermaphrodite (as commonly in plants) or of a double, viz. a male and a female (as in most animals)"[13]

[Linnaeus' italics, sic]

His fourth proposition summed up the three statements given above with virtually irrefutable logic. In his own words:

> "As there are no new species (1); as like always gives birth to like (2); as one in each species was at the beginning of the progeny (3), it is necessary to attribute this progenitorial unity to some omnipotent and omniscient Being, namely God, whose work is called Creation."[14]

Since species were only species by descent, Linnaeus put the onus on God for the providing of the very first individuals. He thus asserted that there was a real living bond between the moment of the origination of each species (i.e. its creation) and the forms which were now in existence; to paraphrase his meaning, Linnaeus implied that every single reindeer in Lapland was descended from the one pair that had tripped out of the Ark at what was virtually the beginning of time. Or, more validly, he supposed that there was an unbroken line of living beings stretching from the Garden of Eden to the present day, and that, for instance, the snakes of today were direct descendants of the Paradisical serpent which had wrought such havoc.

Of course Linnaeus was not the first to think this. My point is that he emphasised it more and drew the idea of a Creation into the current body of natural science. He thus laid special emphasis on the moment of creation, and on the fact that the Creator must have given each living being the shape and constitution which it was thereafter to possess for all time. Mice were created as mice and not rats, and the lily of the fields was distinct from either tares or wheat. He therefore made the study of the origin of species a proper object of inquiry, and, although the species were held to be a product of divine will, he allowed his followers to consider why it was that each form possessed the shape and characters that it did. The Linnaean approach enhanced the importance of the question of why God had created so many species, and stimulated inquiries into the relation between form and function.

The ultimate cause for this diversity was assumed by Linnaeus and by his successors to rest with God. The reason, evidently enough, was that every species had been constructed by its divine maker to be perfectly suited and adapted for the conditions which it was to find in the place where the Creator positioned it. Mice were mice because God had wanted to give the world a small gnawing animal, and locusts were locusts because He wished to occasionally gather them up into swarms and send them off to ravage ungodly countries. However, these examples are trite in the face of the considerably sophisticated views which arose after Linnaeus' statements, and which portrayed visions of finely adapted species each exquisitely fashioned to carry out its role in nature. The work of the anatomist John Hunter, for instance, embodies to an extreme degree the ensuing delight with describing all the intricate and fascinating structures and processes with which organisms were blessed. This was an activity which permeated eighteenth century natural history even down to the most obscure level: little known authors such as Jacob Klein described recondite features of the hearing apparatus of fish[15], and others such as William Gould discussed the ecology and social structure of British ants[16].

What is important for my argument is not so much the way the species concept helped naturalists to focus their attentions on God's plan for nature and the suitability of every form for its function, but is rather the way in which this latter idea furthered a concept of 'place'. As species had been created, according to Linnaeus, in the shape which they now possessed, and this shape was evidently the one which the creator held to be most suitable for the organisms concerned, then, it was assumed, species had also been created in the places that they now occupied. 'Form', 'suitability' and 'place' were now an indissoluble triad, so that organisms, for instance the polar bear or reindeer, could only be considered as species which were perfectly constructed for the conditions in which they were to live, and not suited for anywhere else.

So I claim here that with Linnaeus' work of the mid-eighteenth century there came together the notion of different types of animals and plants, and the notion of 'places' or 'spaces' which were occupied by these different forms. In other words, as species were real entities connected by descent to a distant moment of creation they must therefore have been created like today's forms and where they are now. For

Linnaeus the where of the matter oscillated between the Garden of Eden and Mount Ararat, depending on how far away from the eventual site of the Ark his species were now situated: if they were very distant from Ararat, then he called in the Garden of Eden and suggested that these species had survived the Flood without being in the Ark.

But for Linnaeus' successors, it seemed more probable to suppose that the where of the matter lay in the geographical sub-divisions of the globe itself. They disregarded a single Biblical centre for all creation and now thought in terms of many creations, each species in the area where it was found: they thought of the kangeroo in Australia, the maple tree in North America, the camel in northern Africa.

Clearly there was here a parallel being drawn between what we may call a constancy of structure (the 'form' of every being given by God at the creation) and a constancy of place (the creator had sited his forms in the general area that he intended them to live through an endless succession of generations). Yet I think that the symmetry which such a parallel gave to the first Linnaean taxonomists for example was essentially supportive and reassuring, and not primary ground for such a belief. William Curtis' Flora Londinensis (1777-87) or indeed his explanation of Linnaeus's system of Botany (1777) were volumes in which such a dual constancy was implicit not explicit, and he described plant species from only one or two specimens confident in the belief that the structure was constant through all individuals (both now and throughout time) and that they had lived in the same place since their creation.

What was crucial, was the explanatory power that the species concept gave to the nascent study of geographical distribution.

Up to this period, the later part of the eighteenth century, all the facts of different species in different places had hardly been organised into any idea that specific areas carried particular floras or faunas. North America was the home of the sweet potato and tobacco yet there was no notion of an American flora as such. Rhododendrons and azaleas were known to live in Japan and parts of continental Asia, but there was no clear idea of the group as a typical and characteristic inhabitant of the Indo-Asiatic land mass. But now, with a species concept that linked each individual to the area in which it was found through an original act of creation, naturalists began to think in terms of regions and so in terms of floras and faunas.

Thus Buffon was able to point out that for practical reasons each

geographical region must possess different forms of life, although it ought to be remarked that his reasons were markedly different from Linnaeus'. Buffon's philosophy dictated that all organic life originated near the north pole in some warmer period and had moved south over the globe as the earth progressively cooled. Because the three major land masses of the world were juxtaposed at their northernmost extremities and separated by vast oceans in their southerly parts, this flow of organisms from the north to the south meant that the original population was rendered disjunct. Then, he supposed that there would be some kind of structural "degeneration" from the primary forms of life into the beings which occupied, for example, the New World or Australasia. Nonetheless in later years (and especially in 1830 when Charles Lyell wrote of his suggestions) he was to be acclaimed as the first naturalist to make this statement in unequivocal terms; with somewhat unimaginative imagery he wrote:

> "We are to see her [Nature] traversing the surface of the Earth, like a sovereign, dividing her empire among the animals, assigning to each his proper element, climate and subsistence."[17]

This new approach was given real substance by the results of continuing exploration and travel: Banks and Solander who travelled with Cook on his first voyage to the southern hemisphere, and the two Forsters who accompanied him on his second visit to these regions, all contributed information to an eager audience about the floras found in Australia and New Zealand, viz. the associations of species that were living in each region, instead of snippets of description about one or another species of gum tree or Proteaceae. They attempted to make complete collections of the flora and fauna of any area visited, and their eventual publications were intended to be surveys of the totality of plants or animals inhabiting those lands. Banks and the two Forsters thus thought of regions each with their own special kinds of life. Other naturalists demonstrated the same faculty. Gronovius wrote of the Flora Virginica (1739-43), Donovan described the Natural History of British Insects (1794-1807), Bulliard, the Herbier de la France (1780-95), Sibthorpe and Bauer, the Flora Graeca (1806-40), whilst more mobile naturalists accompanied the surveying ships of Europe to the south seas and elsewhere, in the great procession of exploratory voyages which characterised the end of the eighteenth and the beginning of the nineteenth centuries. Hence La Billardière wrote of the plants collected during

the expedition of La Perouse (1799), Robert Brown of those relating to Flinder's voyage (1814), John Richardson on those of Franklin's (1823), Alexander von Humboldt on those of his own exploration of central South America (1816-25), and so on, leading through most of the names and ships that are familiar to historians of the early nineteenth century: Gaudichaud-Beaupré and the Uranie; Brongniart and the Coquille; Darwin and the Beagle; Joseph Hooker and the Erebus and Terror; Huxley and the Rattlesnake, etc.

So from the closing years of the eighteenth century it was a commonplace to consider plants and animals in terms of the region from which they came and of the association to which they belonged. Species were held to have been created where they now stood, and thus any description of the different kinds of beings found in the world ought to pay regard to the places in which they were found.

Taxonomists 'invented' the "type-specimen" to convey this information in one restricted sense. "Type-specimens" were the first individuals to be properly and fully described from any species new to science and were elevated to the rank of standard, so that all subsequent specimens had to be compared against this one to establish their identity[18]. It was, in the first years of the nineteenth century, crucial to know from whence the "type-specimen" came, for position was now an essential part of the gamut of diagnostic features that went towards the characterisation of plants and animals. Thus, if by any quirk of nature the first guinea pig to be described was found in central America instead of in its true haunts of further south, later specimens would be classified as being found outside their proper range and so perhaps as new species[19].

Moreover there was in more general terms another important aspect to this connection between kinds of beings and their places in nature. Naturalists could not in future examine either species or the metaphysics of nature without in some way accounting for geographical distribution as something which God or other cosmic forces had set out at the Creation. Thus the men usually credited with the founding of biogeography in the first years of the nineteenth century, that is, Karl Willdenow, Heinrich Link, the younger Forster and Humboldt, saw that to elucidate the reasons for the patterns which they discerned in nature would give them a greater understanding of life itself. If they could find the cause for biogeographical distribution, then they

would be closer to a knowledge of those mysterious laws and forces which regulated nature at a deeper level. Heinrich Link told his readers in 1838 that the "flora of a region is one of its distinguishing features":

> "it determines its character. To ask a reason for a plant being found in one station and in no other, is like inquiring why the domestic fowl is not provided with peacock's feathers".[20]

In other words, each region presented a flora or fauna that was appropriate for the conditions there found. Link went on to describe exactly how he intended to ask why the domestic fowl did not have the tail of a peacock: he sought a cause for the facts of distribution. This cause would explain other, more fundamental aspects of nature.

Such a view was, I contend, popular both among the romantic and Naturphilosophie inspired naturalists of the German school as above, and among British circles where they tended to glorify a God and not a cosmic force. They all took the study of distribution as a tangible and accessible path towards a deeper knowledge of nature and her laws, and to an understanding of the creation of beings.

Now if one recalls to mind the point made previously that at the turn of the eighteenth century the notion of species was bipartite (or even tripartite), consisting of an idea of differences in kind or structure and an idea of the geographical position of that body (mediated by the notion of 'suitability', where each sort of organism was appropriate for its place in nature), then it will be clear that nineteenth century naturalists were faced with two possible courses of action in understanding life.

They could, on the one hand, turn to examine the structural differences between beings of all kinds and attempt to isolate the regularities of form which must have been God's 'building-blocks' or which were quintessential elements of nature herself. This we can see in the work of Naturphilosophie comparative anatomy (Oken and Goethe) and, in an attenuated form, in the investigations of British naturalists like Richard Owen, W.S. MacLeay and William Swainson, or those of Louis Agassiz, into the problems of ideal types and the structure of metaphysical archetypes[21]. They were attempting to reach the ultimate nature of nature by probing deep into the anatomical differences which she presented.

On the other hand, naturalists could approach the same goal by a different route, that of the geographical arrangement of species. This was an equally important part of the post-Linnean definition of species and should therefore be able to provide an account of nature's essential elements just as readily as comparative anatomy. Augustin Decandolle, the first in the long line of famous botanists who bore that name and one of the 'founding fathers' of nineteenth century biogeography, laid strong emphasis on this philosophical aspect of plant distribution in his important memoir on Géographie botanique (1820). He told his readers that the subject could be divided into three parts of which the most significant was the study of "habitations", or the botanical provinces of the world:

> "Tous ou presque tous les végétaux, livrés à eux-mêmes, tendent à occuper sur le globe un espace déterminé; c'est la détermination des lois d'après lesquelles se fait cette circonscription végétale, qui constitue l'étude des habitations."[22]

And these laws would allow philosophical botanists to understand "l'origine même des êtres organisés", which as he rightly said was a subject "le plus obscur de la philosophie naturelle".

Hewett Cottrell Watson was to echo these remarks some forty years later, indicating that the topic was as obscure in 1859 as it had been in 1820 but that there was every reason to continue to believe that "phyto-geography" would unveil the secrets of creation. After defining the scope of the inquiry which he called phyto-geography, Watson pointed out the aims which should be kept in mind:

> ". . . the ultimate objects to be sought by phyto-geographical investigations, are neither the countries of plants nor the plants of countries. These enquiries are only preliminary efforts towards ascertaining the necessary relations or causal conditions by which plants and places are connected together."[23]

That is, he wished to concentrate attention on what it was that made one species live where it did and another elsewhere, so that eventually some "ultimate" and "necessary" cause was made evident. In fact Watson espoused a theory of transmutation to account for the differences between forms that he found inhabiting separate regions, and was aggrieved to find that Darwin, as he thought, had stolen his thunder.

But the most cogent expression of the point which I am describing was that put forward by Joseph Hooker. He firmly believed that the laws

of distribution, once isolated and confirmed, would enable philosophers to understand more thoroughly the "mystery of mysteries", as Herschel called the creation of species. In 1855 Hooker wrote that there was much yet to be done within the science of botanical geography before "great questions" such as these could be settled, but it was clear to him that settled they would be:

> "Yet all these elements must be approximately settled before we can attempt a solution of those great questions involved in Botanical Geography, which place it as a philosophical study in the foremost ranks of science: we allude to the laws which govern the development, progression, and distribution of forms and species . . ."[24]

Thus in the second quarter of the nineteenth century the topic of the arrangement of animals and plants was, apart from any intrinsic interest it might bear for the description of nature, a subject that could lead to the discovery of the prime cause for nature existing in the way that she did. The study of distribution was therefore for some naturalists an inquiry of the highest philosophical order, which led them to reflect on the creation of forms and the reasons why they were sited where they were. The Parisian entomologist Lacordaire described the study as one where the scholar considered "external circumstances" first (that is, the physical factors which determined the 'micro-distribution' of organisms) and then, "if these are insufficient" reasons to explain the locations of living beings, the naturalist had to turn to higher and divine causes:

> "At the origin of things, Providence placed these animals in the places where we now see them, adapting each to the climate under which it was destined to live, and conferring on it at the same time a sufficiently flexible organisation to admit of its departing more or less from the centre of creation."[25]

These last few paragraphs relating to the reason why biogeography was held to be an important field of research for nineteenth century naturalists, lead me back into my main argument as to the significance of <u>regions</u> to this study. In the passages cited above, it will be seen that all four scholars were concerned for one reason or another with the idea of botanical or zoological provinces. Decandolle took pains to define a botanical region as one which contained aboriginal species (i.e. forms which had been <u>created</u> there) before he went on to discuss how botanical geography could reveal the laws of creation

itself. Watson pointed out that his botanical geography was not so much concerned with the delineation of provinces and the plants which characterised each region, as it was concerned with the search for an ultimate cause for these facts. Hooker too emphasised that the itemisation of floral data should take second place to the philosophical considerations of the subject, but was anxious to stress that they should not therefore be ignored and that, on the contrary, nothing could be done until proper facts were ascertained. And Lacordaire spoke of a Providence positioning all species in their places, but also providing them with sufficient flexibility to disperse into different conditions away from the point of their creation.

Since the data of distribution were believed to hold a clue to the origin of beings (by virtue of the fact that each species was thought to have been created in the area where it now lived), naturalists were able to begin to describe the regions in which each species, or set of species, lived in terms of a "centre of creation". That is, they believed that all forms had been called into being at one place or another by a God (or other mystic force) who had specially designed each plant and animal for the spot it was to occupy. If then naturalists could trace out the limits to the range of every species they might be able to deduce what it was that determined the kind of being which God supplied. If there were no snakes in Ireland then evidently the Deity did not find conditions suitable for the creation of snakes, whereas, on the contrary, they were patently suitable for the common lizard and smooth newt which did live there and in Britain also. By adding more and more pieces of this sort of information together, naturalists such as Watson and Hooker hoped to achieve an inkling of the 'higher' plan for nature. The commonest procedure was to map out the extent which any one species covered - not an easy task as Hooker often complained, and made difficult by the variability found in nature - and to add them all up to derive a composite range for a whole flora. This area was designated a "centre of creation" or a "specific centre" according to personal proclivities, and was assumed to enclose all the species which had been put there at the creation. It is important to note that these terms did not usually mean the point at which species or floras were called into existence, or the point at which (to use one modern scholar's delightful imagery) an aboriginal pair of rhinoceroses sprang up out of the ground. The latter meaning was described by the word focus. Instead they commonly meant the area which these forms covered, and their

boundaries were the dividing line between one group of products and another. Within this area naturalists could believe that species had arisen in pairs, all in the same spot, or some here and some there throughout the total country available, or, like Agassiz, who was the only person to hold this view, they could believe that God had created every single species and every single individual all at once. By far the majority of naturalists held to the former belief of creation in pairs as, of course, the Bible and Linnaeus dictated, but there was considerable argument as to whether they had all arisen in the same spot (espoused by Decandolle, father and son, and H.C. Watson) or in different places within the limits of their specific area (Hooker, Forbes and Wallace).

Now though the history of these different ideas is undoubtedly fascinating and well deserving of attention, it is here my intention only to point out how natural historians were brought to an examination of and search for the boundaries between each biological province or "centre of creation". The dividing line between the ranges of sets of species was an important issue for it demarcated conditions at once suitable for some of God's beings and unsuitable for others. By assigning regions in which characteristic sections of nature could be found, naturalists were making a statement about where creation had taken place. Augustin Decandolle divided the world into 20 botanical provinces and thus implied that he believed a special creation to have taken place the same number of times (all at once or over time is here immaterial to my point). His son preferred to talk of 27 great topographical divisions. H.C. Watson divided the flora of the British Isles into 18 provinces, consisting of 38 sub-provinces and 112 counties and vice-counties. William Swainson proposed five geographical provinces for the worldwide distribution of mammals, and Agassiz modified these into six for all vertebrates. In 1858 P.L. Sclater wrote on the General geographical distribution of the members of the class Aves and gave six regions for the worldwide distribution of birds, and several workers after him attempted to fit other groups of animals into his regions. One such worker was Albert Gunther who in 1858 provided a geographical study of reptiles, and another was T.H. Huxley who in 1868 revised Sclater's divisions to accommodate his own ideas about the origins of birds. Later, Edward Blyth made seven regions on the basis of mammals and birds and introduced the land of Lemuria to the six named provinces of Sclater's. And of course in 1876 A.R. Wallace published his monumental two-volume

The Geographical Distribution of Animals in which he established evolutionary zoogeography on its modern foundation, and in which he progressively sub-divided the world into smaller and smaller regions to account for the peculiarities of life which each one exhibited. Sclater's words summed up what all these naturalists were trying to do:

> "But I suppose few philosophical zoologists, who have paid attention to the general laws of the distribution of organic life, would now-a-days deny that, as a general rule, every species of animal must have been created within and over the geographic area which it now occupies . . .
>
> Assuming then that there are, or may be, more areas of creation than one, the question naturally arises, how many of them are there, and what are their respective extents and boundaries, or in other words, what are the most natural primary ontological (sic) divisions of the earth's surface."[26]

To chart the different sorts of life on the earth was to chart the variety of creation and to ascend to the reason which lay behind it.

This strong desire to establish fixed regions of organic difference led to several interesting corollaries. The most evident one was that, as soon as a certain interest in the delineation and description of biological provinces was manifested, naturalists began to compare and contrast one with another and to note what kind of differences and similarities there were. The study of phytogeography here came into its own, and I would hazard a guess that its rapid rise to the level of a scientific study by the turn of the eighteenth century was undoubtedly related to precisely this point. Plants were recognised to characterise their countries more markedly than animals which moved around and which themselves depended on the vegetation of each country to exist at all.

Botanical geographers such as Joseph Banks and Alexander von Humboldt were to notice that though the physical accoutrements of several lands may be the same, the plant life was usually different. Humboldt pointed out that floras existing under the same climatic and geographical conditions were themselves analogous and not identical. How could this be, however, if God had created each set of beings specially for the conditions presented by chosen areas? Furthermore, they noted that several countries were geographically at odds with each other yet supported remarkably similar beings as in the case of heathers and heaths being found at the Cape of Good Hope and in northern Europe, two very dissimilar spots on the globe. And again, botanists were puzzled to find that although each species of plant seemed to be native to one or more country

many of them could be successfully reared as garden plants or hothouse exotics, and that introduced plants and animals often ran wild in a land which God had never intended them to occupy. All these questions and more like them were the natural result of increased interest and information about biological provinces and their characteristic features.

Moreover some more historically minded naturalists began to look at the past existence of botanical or faunal provinces to see if they had remained the same through time. William Clift of the Royal College of Surgeons was pleased to be able to report in 1832 that

> "All the genera to which these fossils [giant kangeroo and wombat] are referrable, are now found inhabiting the Australasian Continent, a remarkable coincidence . . ."[27]

And Richard Owen was to confirm this apparent rule that fossils were of the same general kind as the present day inhabitants of each region, by examining Charles Darwin's specimens of giant armadillos and sloths from South America, a country which today supports somewhat smaller members of the same families. Yet there was also evidence seeming to contradict this apparent constancy through time: a fossil horse had been discovered in North America where living ones had all been introduced in recent times; a fossil elephant was found in Australia in deposits contemporaneous with the 'diluvium' of Europe; and Adolphe Brongniart was issuing descriptions of fossil plants - most particularly those of the carboniferous deposits - which indicated that botanical provinces had once possessed very different boundaries and climatic characters from those of the present day. There was sufficient evidence for this latter view to enable geologists such as D'Orbigny, the younger Brongniart, John Lindley and even Alphonse Decandolle himself, to assert that there had not been any botanical provinces before relatively recent geological times, and that the history of plant life on the earth had been one of gradual diversification (through successive creations) from one widespread and uniform flora. Louis Agassiz, on the other hand, defended the view (which turned out to be the right one) that every period in geological time had had zoological and botanical regions just like, though not necessarily identical to, those of today:

> "It would be, however, sometimes amusing, were it not actually distressing, to see the manner in which some geologists deal with fossils, considering them simply as the characteristics of certain rocks, and hardly yet dreaming that there may be such a thing as a special zoology of the different geological periods, and that during each, local faunae may have existed with peculiar animals etc."[28]

Yet another feature of this inquiry into what characterised a topographical region was an increased interest in the way some strictly limited floras or faunas mirrored each other by possessing 'representative species' such as the Galapagos finches or ecological pairs such as a marsupial and a placental mole, wolf or rabbit. This interest naturally went hand in hand with an awareness of botanical or zoological provinces, for how could one form of region A 'represent' another of region B unless each was confined to its own topographical area?[29] It even came to the point with Edward Forbes' work that certain zoographical areas could be designated entirely on the basis of whether they had, or did not have, representative species of certain shells. Once again, however, Louis Agassiz fiercely contested this assumption.

But there is one point which as yet remains unmentioned and on which I would like now to dwell. I have briefly spoken of a few of the issues which were brought to the attention of naturalists through a search for organic regions and the delineation of their boundaries, and of the facts of distribution which were made apparent when they began to compare and contrast these regions. Some of these have been alluded to in other chapters. What I now turn to is the way in which naturalists of this second quarter of the century tried to characterise their regions so that they could be considered as separate entitites. What were the features which they thought to be most telling in any discussion of the differences and similarities between biological zones?

In Watson's words, the main point was to isolate the predominant species of each region:

> "The Botanical character of a Flora is determined by the predominance of species exhibiting similar peculiarities of form or structure . . . Hence the numerical predominance of species, referred to the same order or genus, gives a botanical stamp or character to the flora of a country, thus furnishing a ground for comparison of it with the flora of any other."[30]

Other naturalists would go further and claim that it was not so much one predominant species which characterised a flora, as it was the ratio which the main classes or families held to each other. Thus an equatorial island was known to present many more ferns - and even tree ferns if the climate was moist and warm enough - than similar islands in the north Atlantic: the ratio of cryptogams to phanerogams was therefore characteristic for each land. On a more detailed level the relative incidence of the six or seven most ubiquitous families changed according to the conditions and climate of each region, so that in one land like

the Pampas of South America grasses and compositae would preponderate over leguminosae or cruciferae, when in any other land the order might be reversed or certainly different. It was these proportions or ratios which characterised the separate floral provinces in the minds of Alphonse Decandolle and his colleague Joseph Hooker. Decandolle devoted the greater part of his compendium Géographie botanique raisonnée (1855) to a discussion of the various methods for depicting the areas of plants, and favoured a multiple estimate of different proportions between species, genera and families, as well as a count of the absolutely endemic or cosmopolitan species which each flora contained[31]. Hooker itemised five arithmetical points in his Introductory Essay to the Flora Novae Zelandiae (1853-55) which connected the plants of New Zealand to those of Tasmania, Australia, Chile and Tristan d'Acunha, as well as the small Antarctic islands dotted around in the southern seas. Each land, he wrote, "hence forms a botanical region, more or less definable by its plants"[32].

This itemisation of the arithmetical peculiarities of each region was quite frankly based on population censuses, which were, at least in England, now decennial events and the focus of extensive intellectual concern. Introduced in 1801 to determine if the population of these islands was decreasing (as was feared) or increasing, nothing of course could be decided until a second count was made in 1811. After it was found to be increasing even the flamboyancy of the Regency could not assuage a revival of Malthusian fears of a population explosion, and so the ten yearly figures were examined with more than an abstract interest in the state of the nation[33]. H.C. Watson likened his work on the areas covered by British plants to a census, with the important qualification that "in the former we count up only species or habitats" whilst in the latter it was individuals who were counted.

> "We cannot count the individual plants of a species as we would count the people of a kingdom; and in an island so large as Britain, we cannot ascertain the number of special localities, unless it be for some few extremely local species. Their census must therefore be vaguely estimated by the experience of the individual observers, who will never agree in their estimates, or it must be tried by some test which is adapted to show the number of spaces (not the number of precise places) in which each one occurs."[34]

This particular use of population statistics was an important feature of natural history in the nineteenth century and it constituted a notable element in the attitude which I earlier referred to as a

'topographical' approach to the facts of distribution. Natural historians used botanical arithmetic and the relative incidence of certain species or families to characterise their botanical or zoological regions in exactly the same way that government officials analysed the data that came in from population censuses. In some cases, as in Watson's remarks and in others to be described below, naturalists made this an explicit analogy for their distributional work and wrote of the "census" of living beings. More usually the link was only implicit. Thus, for instance, the terminology which naturalists employed to describe their populations was taken from human society: the words "nation", "metropolis" and "kingdom" were popular expressions in biological works where distribution was discussed, and, in Darwin's writings even the word "clan" came up. Furthermore the very use of the term "statistics" implied cognizance of a transfer of this science from the realms of man to those of nature, as John Hutton Balfour demonstrated by defining the "statistics of vegetation" as the counting up of the plants of each kingdom[35].

This was, I contend, an analogy which permeated the work of distributionists in the first half of the nineteenth century. It characterised the purely 'topographical' approach to their phenomena which many naturalists presented and regulated the extent to which they could interpret the data of nature. As such it demands some further attention from me here.

There was much in the context of the first half of the nineteenth century to encourage such an enthusiasm for statistics. There was great interest shown in the subject from all intellectual quarters which was, some ten or twenty years later (in the third quarter of the century), to build up to a crescendo of intense admiration and exaltation of the arithmetical method. Thus during the middle years of Victoria's reign (about 1860-80) the populace of Britain was bombarded with batteries of statistics which outlined, in turn, the trading power of the Empire, the need for social, medical and philanthropic action, the migration of country folk to the newly developing towns, and which notified the middle classes of their relatively sudden existence[36]. In the period with which I am dealing, before 1859, much of this later absorption with numbers is already evident as in, for example, the publication of Government Blue Books, the institution of censuses themselves, the introduction of more and more mathematics into the physical sciences and statistics into the earth and life sciences, and in the publication of analyses of death and

sickness rates in medical journals such as the Lancet from the 1830's onwards[37]. Typical of such a mounting interest was the demand for volumes with dry titles like MaCulloch's Statistical account of the British Empire (1837), Bisset Hawkins' Elements of Medical Statistics (1829), and C.T. Thackrah's The effects of the Arts, Trades and Professions and of Civic status . . . (1832).

Yet until the start of census taking, statistics in Britain was only a science of intelligent guesses. Both population and vital statistics before this time were highly defective and based on records collected for entirely different purposes as, for example, taxes or parish registers. However, vital statistics and their congeners the Bills of Mortality and assurance tables had excited concern ever since John Graunt and William Petty pioneered the numerical method as applied to human society in 1662 and 1690 respectively. Additionally, the population controversy, fed by an inadequacy of contemporary data, began in 1750, and flourished to the point where it was still raging in 1801 when the bill for the taking of a census was under discussion. It continued to agitate the British people until about 1840 or so, when the General Register Office was created and the census was amended to include categories which we now recognise as standard characteristics.

So historians could hardly look back at these facts and then claim that statistical procedures were special to the nineteenth century alone. Like all topics, this one had a long and eventful history.

What I would like to do here is to draw out one particular thread in this eventful history which played an important part in the establishment of an arithmetical method in botany and zoology. It was this thread which gave botanical geographers the means to see an analogy between population statistics and the study of distribution. It was, furthermore, a thread concerned with purely descriptive statistics, a subject which gave the discipline its name and earliest content before the advent of what we may call 'political economy' in the eighteenth century.

The statistics of botany and zoology were clearly founded on the descriptive methods brought into use by the very earliest commentators who wrote of the organisation, people, customs and produce of the countries of the world. The name of statistics was formerly applied to any collection of facts which might be of interest to a statesman or learned individual and it denoted - quite evidently - the comparative description of states. It may be curious to the modern statistician that his title

derives not from political arithmetic but from the analysis of different countries, but to the historian of biology this derivation seems quite right and proper for here too the term 'statistics' was used to signify a comparison between botanical or zoological regions.

The intellectual exercise of so describing states (which the Germans called Staatenkunde, a term which I also shall use) can be traced back as far as Aristotle, whose Politeiai contained monographs describing no fewer than 158 diminutive Greek states. And quite naturally, the awakening of political life in renaissance Italy gave rise to similar compilations relating the pertinent facts of every city-state. But the subject only reached its fullest development with the activities of German authors of the eighteenth century, and particularly with the work of scholars at Göttingen University who established the form which later investigators were to follow[38].

Here, at Göttingen, the polyhistor Gottfried Achenwall (1719-72) established the content of the Staatenkunde tradition, and defined statistics as the description of the constitution of states, a description which was to include the whole complex of data which might be made available. He thus laid out the foundations for the enormous breadth and scope of subsequent treatises which, I may add, are unfairly slighted by modern readers as being mere compendiums. Compendiums they may indeed be, but at least that was what they were meant to be and there was a tradition which demanded that they should include everything. Achenwall's own work on Spain in 1748 encompassed the history, geography, climate, natural produce and 'industry' of the country, the population and its distribution, the national character, political constitution, the state of science, currency and finance, and a short sketch of military and naval forces.

Such a broad format is readily familiar to anyone who has read travelogues of the seventeenth century such as Acosta's Historia natural y moral de las Indias (Seville 1590 and London 1604), John Ogilby's "Accurate Descriptions" of America, China, Africa and Britain (around 1670), or indeed, Peter Knox's account of the island of Ceylon (1681), the first in the English language, and Guy Miege's Relation of three Embassies from his sacred Majesty Charles II to the Great Duke of Muscovie (1669). During the eighteenth century this tradition continued and similarly inclusive works were produced. Sir Hans Sloane's account of Jamaica (1707-25) in which he described over 800 new plants, also included a

description of the "Inhabitants, Air, Waters, Diseases, Trade &c of that place, with some relations concerning the neighbouring Continent and Islands of America". The Jesuit missionaries to Japan sent detailed reports back to France as, for instance, Xavier de Charlevoix did with his Histoire du Japon (1754), which included fine illustrations of town plans, costumes, buildings and ceremonies, in addition to a series of 35 Japanese plants. Indeed, towards the close of the century many of these works were almost entirely devoted to natural history as, for example, in Griffith Hughes' The Natural History of Barbados (1750) and Mark Catesby's The Natural History of Carolina (1771), although others maintained all the eclecticism and generality of the Staatenkunde genre as in Molina's The Geographical, Natural and Civil History of Chile (1809).

All these works were 'omnium gatherums' of facts relating to the countries involved. They dealt with topics which were of interest to the educated man and covered the politics, produce and resources, and the people of foreign lands. Information for the statesman was thus metamorphosed into information for the intelligentsia and works were titled accordingly, often including the telling phrases "Observations natural, moral and political", or "A History Natural and Civil", to indicate their scope. The description and comparison of states lived on in the books which we are now pleased to call travel literature, but which in reality are part of the continuing Staatenkunde tradition.

This is a notable point for historians of natural history because these volumes formed the first channel for communications relating to the natural produce - that is, the plants and animals - of each country explored and described. The Staatenkunde genre (if I may so mix languages) was a vehicle for a full exposition of the living beings of foreign lands, as, for example, in the works of Sloane and de Charlevoix mentioned above where they described the plants of Jamaica and Japan in among all the other details. Thus the proper place for notices pertaining to the plants and animals of different regions was one in close association with discussions on the political and civil phenomena of the same area and an enumeration of its population and other salient features. Hence for the duration of the Staatenkunde tradition in travel literature it was the case that natural and civil history were linked together in the most intimate way.

The kind of biology which was put forward in these works of the seventeenth and eighteenth centuries was of a simple enumerative sort (as

were the other statements) more or less exclusively given over to lists and brief descriptions of items which came to the author's attention. Such brevity may have been the effect of the fact that not many travellers were also naturalists, but it ought to be said there is little difference in the quality of description between Molina's natural history of Chile and John Ray's Observations Moral and Physiological made in a journey through part of the Low Countries . . . with a catalogue of plants not native to England (1673). The latter author was a naturalist, and the former was not, yet their accounts of plants are very much the same. Neither attempted to draw the botanical or zoological data into a coherent whole or to provide informed comment on the general relations of the flora and fauna of one country to those of others. For, as I have already mentioned in an earlier part of this chapter, such a discussion of floras in distinction to isolated species and kinds of plants was a feature of the late eighteenth century and after, due to the significance with which the "species concept" of Linnaeus invested the study of regions.

But this enumerative and descriptive idiom became less and less usual as travellers devoted increasing time and trouble to making full collections of the living beings of any country, and were keen to have their work vindicated by a properly accurate description (by noted naturalists if they themselves were not capable of so doing) and by appropriate publishing space. Sir Hans Sloane represented a whole breed of gentlemen-scholars who delighted in writing of their grand tour or foreign experiences, and Sloane was the most knowledgeable, assiduous and munificent of all eighteenth century travellers. He left his collections to establish the core of the natural history section of the British Museum, and an elegantly illustrated two volume treatise on the West Indies. Mark Catesby, from a different sort of background, nevertheless outdid even Sloane with the accuracy and beauty of his descriptions of the birds, beasts and flowers of Carolina, Florida and the Bahamas. Both men were determined to make their works scientific and were as precise as their data would allow, and the inclusion of a wealth of fine engravings (Sloane 284; Catesby 220) was for primarily taxonomic reasons, although no doubt aesthetic and pecuniary interests were also furthered.

With the development of a science of natural history in its own right due to intellectual concerns which have been outlined previously, books describing the full range of Staatenkunde subjects were more or

less replaced by works such as these of Sloane's or Catesby's almost entirely given over to natural phenomena. But natural historians did not forget their heritage. It was, in fact, their heritage which set the new science of biogeography on its feet. The very heart of these developments in natural history was to be found at the University of Göttingen, for so long the site of a humanist education which specialised in the topics embraced by Staatenkunde literature. The 'founding fathers' of biogeography, who first introduced the analysis of regional floras and methods appropriate for the depiction and delineation of botanical provinces, were all Göttingen based or trained. These were K.L. Willdenow, H.F. Link, J.R. Forster (father and son), and Alexander von Humboldt, a distinguished line of naturalists that spanned the closing years of the eighteenth century and the opening of the next, and which, in succession, produced a series of justly acclaimed treatises on botany and the distribution of plants.

K.L. Willdenow, the Berlin systematist and teacher of Humboldt, outlined the principles of botanical geography in his Grundriss der Krauterkunde of 1792. He recognised that plants fell into distinct geographical groups and advocated the investigation into regularities of distribution. These were seen to be at once physical (such as temperature, soil composition and structure, and the amount of light received), geological (i.e. historical), geographical (height above sea level, nearness to ocean borders and lakes), and lastly social, which included phenomena such as a tendency to be gregarious like the bamboo, and the diversity of life which each region might present. He thus interlaced all the points of geography and geology which characterised each area with the organisms which they supported, two aspects of the one Staatenkunde tradition which must have been completely familiar to him and to his readers. The only thing that was missing was any detail about the human population of chosen regions.

Not so, however, for the Forster family and for Johann Friedrich Blumenbach, all three pupils of Willdenow at one stage or another during his travels through Germany. The Forsters, an indefatigable team of father and son, wrote on the geographical and ethnographical features of Australia and the South Seas after accompanying Cook on his second voyage of 1772-5 . The elder Forster's most notable publication was Observations made during a voyage round the World (1778) in which he displayed a sensitive awareness of the scientific and philosophical

currents of the day, and wrote on the distribution of plants and the varieties of the human race which he had encountered during the search for the southern continent. His son, after a literary travelogue distinguished only by its independent publication which preempted the Admiralty report, turned to a series of botanical, philosophical and ethnographical essays in which he linked social history, politics, plants and anthropology. Both father and son took a deep interest in the study of primitive races and included analyses of the physical differences of mankind in their biological works. Blumenbach, a close friend, was equally interested in problems of the distribution of organisms though he was especially fascinated by anthropology. The Staatenkunde tradition took the form in his work of a notable statement that the races of mankind were comparable to those of animals, and that man should be viewed as an object of natural history, the "most perfect of all domesticated animals". His Handbuch der Naturgeschichte (1779) contained an abundance of morphological and ecological findings on which he constructed theories of the relations between the creation and existence of man, animals and plants.

Humboldt too conformed to this broadly inclusive Staatenkunde genre. The 34 volumes with which he saw fit to describe his experiences and findings in South America were a tribute to the humanistic school in which he had been trained. Seven volumes were devoted to the Rélation Historique, the histories of the countries which he visited, two volumes to the zoology, one to the political economy of Mexico, three to the astronomical and geographical observations, three to plant geography, and the final eighteen to the systematic botany of the South Americas under the authorship of his travelling companion Ami Bonpland, and, after his retirement from scientific life, C.S. Kunth. Furthermore, he expressed considerable interest in the relations between men and plants, mostly, it is true, of a practical nature such as the introduction of species of economic importance and the following of man's progress through the world by weeds. Yet elsewhere he drew an elegant parallel between the history of man and the spread and range of plants, indicating his affection for the Göttingen school of thought. In his short Essai sur la géographie des Plantes (1805) he wrote that now, after his insights into nature, the history of navigations and wars and the nutritional value of plants would all have to be included in assessments of their distribution. These were the facts which "lient la géographie

des plantes à l'histoire politique et morale de la homme"[39].

Humboldt's words were both a fitting climax for the tradition in which he was so honourably reared, and an indication of what was to come with the botanical geography of the nineteenth century. For when naturalists of the new century demanded and attempted to supply informed assessments of the floras and faunas of lands and seas, and struggled to separate these into biogeographical regions, they turned to their nearest and oldest acquaintance for suitable models and examples. That is, it was to the human race and to demography that they turned. They remembered that social and biological information were part of the same Staatenkunde tradition.

Thus, in 1830 Charles Lyell included a chapter on the geographical distribution of mankind in his general discussion of the phenomena of organic distribution for the Principles of Geology[40], and he pursued the analogy further to explain how he thought new species came into and old species left the history of life, that is, the pattern of creation and extinction which he discerned in nature. He gave, in volume three, a detailed example of his belief that a change in species took place over time through a piece-meal process of extinction and creation, so that there was never any clear dividing line between the organisms of one period and another but instead a gradual blending which was often obscured by intermittent and irregular fossilisation or subsequent geological activity. This was to lead him to an explanation of his statistical method for estimating the relative ages of Tertiary deposits by the proportions of ~~mineralised~~ fossil species which were extinct in comparison to those still living in the present day. This proportional technique is examined at greater length in the following chapter where the content of statistical biogeography is given in some detail. Here however I would like to note that Lyell explicitly used an analogy with human populations and, in particular, with the taking of a census, to describe exactly what he thought happened in the animal kingdom. His reasoning was based on the idea that if a periodic census was taken on a population in which some families were dying out and others were growing up, then, assuming that the birth and death rates were to remain constant, each census would describe rather different sets of individuals and portray quite diverse pictures of life at any one time. In short, the census would make it look as if there had been major changes in the constitution of the "nation" or overall group when, according to Lyell,

there had been nothing but the regular and gradual procession of events, births and deaths, which provided the content of any large assembly. It was the taking of a census which forced these artificial 'breaks' in the chain of continuity and which gave a false impression of 'periodisation' in human affairs or in the history of nature.

> "In order more distinctly to elucidate our idea of the working of this machinery, let us compare it to a somewhat analogous case that might easily be imagined to occur in the history of human affairs. Let the mortality of the population of a large country represent the successive extinction of species, and the births of new individuals the introduction of new species. While these [previously cited geographical and geological fluctuations] are gradually taking place everywhere, suppose commissioners to be appointed to visit each province of the country in succession, taking an exact account of the number, names and individual peculiarities of all the inhabitants, and leaving in each district a register containing a record of this information. If after the completion of one census, another is immediately made after the same plan, and then another, there will, at last, be a series of statistical documents in each province. When these are arranged in chronological order, the contents of those which stand next to each other will differ according to the length of time between the taking of each census. If, for example, all the registers are made in a single year, the proportion of deaths and births will be so small during the interval between the compiling of two consecutive documents, that the individuals described in each will be nearly identical; whereas, if there are sixty provinces, and the survey of each requires a year, there will be an almost entire discordance between the persons enumerated in two consecutive regions."[41]

Lyell's example was devoid of any acknowledgement of the possiblity of changing rates of births and deaths be they of human beings or of lesser species[42], but his analogy between the taking of a census and the description of nature was quite clear. He was employing the same analogy as that which H.C. Watson was to use in his Cybele Britannica (1847-1859) and which I cited some few pages previously, that the organisms of particular regions could and should be counted and assessed in the manner demonstrated by demography. Watson referred to the fact that botanists were most concerned with the enumeration of species and their greater or lesser frequency in certain areas, and likened these interests to the taking of a census:

> "But between the human and the floral census of a country, there is this important difference, that in the former we count individuals, while in the latter we can count up only species or habitats."[43]

Evidently this fine distinction did not worry Lyell, although he was ready to admit that his analogy had its limitations as, for example, the mere passage of time was not the sole criterion for a proper estimate of the differences any two populations might exhibit, when such possibilities as disease and migration could also alter human ratios[44].

One further example of such an explicit analogy between human and animal or plant associations comes in a tangled metaphor which Darwin originally intended to be included in the Origin of 1859. Here, he attempted to take into account - as Lyell had not - the effects of changing birth and death rates on the gradual alteration of the constitution of groups. In 1858, in the long manuscript of Natural Selection, he explained how he thought that there were more varieties occurring in the genera which had more species than not. In his own words "where many large trees grow, we expect to find saplings", Darwin thus described his prediction that varieties were more numerous in genera which had at one time or another experienced a great deal of speciation. "To explain my meaning further by a loose simile", he wrote:

> " - if a nation consisted of clans of very unequal sizes, and if we . . . divided the population into two nearly equal halves, all the large clans on one side, and the many small clans on the other side; we should expect to find, on taking a census at a moderately long interval that the rate of births over deaths was greater in the larger clans than in the smaller; and we should expect to find it so, notwithstanding that we knew some of the small clans were now rapidly increasing in size and some of the larger clans declining . . . What the rate of births over deaths is to our clans, I suppose the production of varieties to be to the number of species in a genus . . ."[45]

And like Lyell and Watson, Darwin went on to admit limits to the analogy and then to extend it a trifle further by likening the passage of varieties into species as a process similar to the growth of a child into maturity: "Each child does not grow up to man's estate, nor by any means do I suppose that each variety becomes converted into a species".

So there was here, in at least three philosophical tracts of the ~~second quarter~~ middle of the nineteenth century, a plainly evident use of a demographic model to describe and explain biological populations. Other naturalists, as I have hinted, conformed to a more implicit use of the idea that they were taking a census of animate beings, and many of them therefore contributed enthusiastically to the new science that was then being built up of a statistical biogeography. It is with this last topic that my next chapter is involved and there I shall examine the use

to which botanical and zoological arithmetic was put in the analysis of floras and faunas of different biological provinces. Here, however, I would like to reiterate my point that biogeographical statistics of the early nineteenth century were conducted under the guiding light of an analogy drawn from the similarities between the distribution of the human and non-human populations of the earth. Such an analogy was made possible by the long-continued tradition of the joint consideration of these two topics: biological and human data had been held to be part of the same Staatenkunde investigation for two centuries before the nineteenth opened, and despite the fact that most biological texts of a descriptive and regional nature had eliminated socio-political details by the end of the eighteenth century, the two concerns were still close enough for cross-analogies and transfers of thought such as this one.

## Conclusions

The science of natural history in the earlier half of the nineteenth century can thus be characterised as one which was properly speaking 'topographical' in kind. Though this might at first appear to be a statement so obvious as to be a truism, it does in fact bear considerable importance for the historian. Naturalists of this period were concerned with identifying, comparing and contrasting biological provinces for several very well defined reasons, and most of their more detailed investigations were into problems which arose from this activity. In passing, I alluded to the study of the physical and climatic features which governed the extent of specific ranges, and the inquiry into 'representative' forms. Moreover the way in which biological regions were compared was also 'topographical' in the sense that naturalists chose to describe them in demographical terms, and itemised the statistics of each population as if they were conducting a census.

This 'topographical' approach to nature was more a legacy from the past than one of the nineteenth century's own making, although the general popularity of the statistical method in this second period should not be ignored as an agent in the modelling of nineteenth century natural history. The latter enthusiasm for arithmetical methods and the development of demography encouraged and directed the path that a newly established study of distribution took. But I think that the history of natural history had a greater influence in this respect. It was the sequence

of past events which provided the frame within which our naturalists worked.

Naturally most of the concepts and attitudes of any age arise out of what has gone before, and natural historians of the nineteenth century were no exception to this rule, for they based their science on themes which had been constantly before the eyes of their precursors. Their problems were as old as man's awareness of nature itself. In ancient times a continuing exploration of the globe and an expansion of man's geographical boundaries went hand in hand with the transport of useful plants and animals and the introduction of novelties to civilized nations. This ever widening knowledge was accompanied by increased cognizance of the fact that species lived in different regions, a cognizance which was made concrete with a late medieval examination of the living beings of Europe under the guiding light of ancient and Arabic texts. In the wake of all this apparent diversity came attempts to order it, though it was not until Linnaeus introduced a 'species concept' that naturalists enjoyed much success in this direction. Linnaeus allowed the coming together of ideas about 'kind' and the more obvious notion of the geographical region (mediated by the idea of 'suitability') so that natural historians could now speak of biological regions, determined at the start of life by a providential God. Hereafter they sought the laws of creation and the ultimate causes of nature by delineating the differences in the anatomical structure and in the topographical arrangements of the animate world. Thus any statement about the 'plan' exhibited in geographical distribution was also a statement about God's first intentions and the principles on which he placed beings on different spots on the earth.

But most of these early statements were presented to eighteenth century readers in volumes that were not expressly natural history books and which were instead general and broadly inclusive tracts on the economic, social, political and biological features of particular geographical areas. This was a long standing tradition reaching back to the first origins of 'statistics' in the comparative description of states, and which continued virtually unchanged through to the end of the eighteenth century as evidenced by the genre which we now call travel literature, but which by rights ought to be termed part of the Staatenkunde tradition. The inclusion of biological details in these 'statistical' works encouraged naturalists to think in terms of regions and in

terms of the close association which biology bore to human and geographical data. Thus when they eventually came to frame their own theories of the arrangements of animals and plants in treatises without the latter details, they still retained some of the earlier intimacy by drawing an analogy between the distribution of organisms and human beings. So the first truly distributional works emanated from the source of the Staatenkunde tradition itself - the University of Göttingen - and were books in which the authors were pleased to link the natural and the civil together. This again enforced a purely 'topographical' approach to the phenomena of distribution.

## Chapter 4: Statistics in Distribution Studies

The outstanding characteristic of nineteenth century Britain must surely be the deliberate pursuit by its inhabitants of facts. In area after area spokesmen called for an accumulation of solid information and the community laboured to respond in an appropriate fashion. And even though the richness and complexity of this vigorous century almost defy generalisations, it is nevertheless apparent that this period was one concerned with numbers as the most desirable sort of fact attainable. Its approach to the sciences in particular was one of quantification. Victoria's long reign saw the mathematically equipped men taking over physical investigations with a relentlessness hitherto confined to astronomy alone, and familiarity with numbers became something of a byword for 'proper' scientific procedure. Mathematical predictions led to exciting physical discoveries like the existence of the planet Neptune. The science of heat had been put into mathematical form by Fourier, the newer one of electromagnetism being similarly treated by Ampère. Young's empirical concept of the wave motion of light was given arithmetical form and content by Fresnel. Faraday's ideas were given mathematical shape by James Clerk Maxwell whilst figures of the past like Kepler and Newton were saluted for their calculative genius and for the mass of empirical data on which their formulae were based[1].

Nor were the physical sciences alone in this trend. Geologists turned to the researches of physicists such as Fourier and Thomson to aid them in their investigations into the internal temperature and age of the earth. At a less geophysical level, men like Lyell introduced statistical methods into paleontology for the relative dating of strata by a comparison of their fossil content. And naturalists ushered in the nineteenth century with a rapidly developing penchant for statistical surveys of animal and plant distribution patterns which gave natural history a broadly arithmetical base, and allowed its practitioners ultimately to stand on the threshold of the next century in possession of several new, extensively mathematical, sciences of biometry, ecology and genetics. Darwin himself presented evolution as a theory of probabilities, and the Origin of Species (1859) was a masterpiece of statistical reasoning presented in lucid prose.

Much of this awareness of mathematics must be assumed to have been the result of a gradual osmotic effect operating throughout the sciences under the successful example of astronomy. The queen of the sciences had demonstrated how effective the combination of large masses of data and mathematical ability could be, and so astronomy was particularly acclaimed through the nineteenth century as a model for lesser studies. In his influential treatise on the method appropriate for science, John Herschel dictated that the best kind of statement was a quantitative one and glorified Newton's inverse square law as the very acme of modern science. Public bodies such as the British Association for the Advancement of Science and the Royal Society fêted astronomy and her technique, in the former through their Committees on Standards and "Reports on the Progress of . . .", and in the latter through the sponsorship, amongst other things, of scientific voyages like the Ross expedition in the teeth of Government opposition. Individuals too reflected on astronomy and its message for science: Lyell hoped that his style of geology would be to the earth what Newtonian astronomy was to the heavens, and likened his Principles (of geology) to the Principia; similarly Darwin did not object when he was called the Newton of biology by T.H. Huxley, and he himself drew attention to the parallel in the Origin.

In short the nineteenth century seems to have been a period when a good round figure was worth a thousand words, and the application of a numerical reasoning was the essence of a scientific approach to nature. This appreciation of mathematics was particularly evident in the 'newer' disciplines such as biogeography. In 1845 Joseph Hooker exclaimed, "We must know the absolute numerical amount of peculiar species", and complained that:

> "no-one has attempted this, all seem to dread the making [of] Botanical Geography too exact a science, they find it far easier to speculate than to employ the inductive process. The first step to tracing the progress of the creation of vegetation is to know the proportions in which the groups appear in different localities, and more particularly the relation which exists between the floras of the localities, a relation which must be expressed in numbers to be at all tangible."[2]

He thus felt the introduction of numbers to botanical science to be the first essential step in making it an exact study, as did his correspondent Darwin, who was to echo Hooker's view by regretting that zoologists "seldom go into strict and disagreeable arithmetic like you

botanists so wisely do".[3]

But the real spokesman for botanical geography was surely Alphonse Decandolle, son of the great Genevan botanist and humanist Augustin Decandolle who had himself written on the significance of statistics for the study of distribution. Alphonse continued the investigation that his father's work had opened up (particularly in Decandolle père, Statistique botanique et agricole de la France, 1808-1813) and wrote of the benefits of mathematical analysis and comparison for biogeography. He visualised the use of statistics as the mark of a proper science, and was anxious that botany should not, so to speak, miss the boat:

> "Il ya dans chaque science, art ou objet d'étude, une partie statistique, soit numérique. On la retrouve en agriculture, en médecine, dans toute les branches de l'administration, dans les sciences physiques, naturelles, et jusque dans les sciences morales. Elle occupe une très grande place dans la géographie botanique. Pour moi, j'en conviens, j'aime les chiffres autant que d'autres les détestent . . ."[4]

And elaborating on these remarks in the preface to his important work Géographie botanique raisonnée (1855), Decandolle fils confessed that he was dedicated to the principle of arithmetical exactitude in distribution studies. He intended to illustrate the arrangement of the vegetable kingdom through the use of proportions and the decimal system. Furthermore he took a leaf out of Lyell's book and claimed that such a usage established a precedent and a principle of reasoning that could not thereafter be ignored, which hence entitled him to call his treatise "géographie botanique raisonnée"[5]. By bringing statistics to the investigation of distribution, Decandolle asserted that he had transformed this study from a state of mere description and fact-collection into a science which was now able to advance and progress. He wrote of statistical techniques:

> "Cette appréciation des méthodes, ainsi que la discussion des faits et la tendence à rechercher les causes des phénomènes, m'ont paru établir une assez grande différence entre mon travail et la plupart des traités de géographie botanique, dans lesquels on se contente de décrire des pays ou de citer des faits."[6]

Here perhaps Decandolle was succumbing to the temptation to make a general condemnation of his precursors and contemporaries, in much the same way as Lyell some twenty years earlier had distorted the aims and achievements of geological theorisers before his time. Decandolle

may indeed have possessed polemical motives of the same order as Lyell's which have been brought out in all their complexity by M.J.S. Rudwick and Roy Porter in recent papers[7]. Yet in many ways the botanist had accurately assessed his own position, for of those naturalists who had used statistical methods or attempted to generalise about floral relationships and historical causes, few had done so with his precision, consistency and scope. The Géographie botanique raisonnée was undoubtedly one of the great contributions to this science and stood with Humboldt's Voyage aux régions équinoxiales du Nouveau Continent (1805-1834) as a classic of biogeographical literature.

But the point which here demands attention is not so much Decandolle's unsubtle self-advertisement, but rather the fact that he saw himself as giving an apparently amorphous body of information shape and method. He outlined the techniques of analysis, the modes of reasoning and their limitations, and the extent to which conclusions could be drawn, all of which were extensively substantiated by his own detailed example. And this example was one propelled by what we can only call statistical monomania: "Elle occupe une très grande place dans la géographie botanique," he had truthfully written in his preface, but a naturalist may be forgiven for wondering - after reading the two substantial volumes that these words introduced - how Decandolle allowed plants into the book at all. Such a frivolous remark is not without justification either. Decandolle deliberately treated the facts of distribution as data which was to be processed and tabulated in the search for higher laws, and each plant or specimen was therefore only useful as a single unit in the mass of raw material which had to be reduced to the form in which it was to be deployed.

But what of the years immediately preceding the publication of this influential treatise in 1855? Decandolle stated that previous works had been confined to mere description and the cataloguing of facts ("on se contente de décrire des pays ou de citer des faits"). This was not absolutely the case. The years spanning the period 1805 (when the first volume of Humboldt's great travelogue and scientific commentary was issued) to 1855 (when Joseph Hooker published the Flora Novae Zelandiae) included a series of notable works marked by informed comment and judicious assessments and in which considerable effort was expended on unsophisticated statistics. These years saw both a growing interest in distribution, as evidenced by the increase in the number of publications expressly concerned with this aspect of animal and

plant life, and interest in the presentation of information so discovered in a generalised and readily usable manner. Thomas Bell was writing on the distribution of mammals as was George Waterhouse; John Gould and C.J. Temminck wrote on that of birds; Edward Forbes on marine life, Thomas Wollaston on insects; and Hewett Cottrell Watson and William H. Harvey on the distribution of plants; and in eclectic publications such as the Edinburgh Philosophical Journal ("New" after 1835) interest had risen from a virtual blank before 1835 to an annual presentation of some three or four geographical accounts by the years 1854-5. And in the majority of these cases (some of which will crop up again in later pages) naturalists tried to set out their results in a comprehensible way, often using figures, proportions or ratios to emphasise a point and collecting these into tables where appropriate.

As this effort quite markedly differentiates the biogeographical investigations of the period 1810 to 1855 from those which antedated them, the use of statistical methods takes on considerable historical importance. Following Decandolle's thesis we might even say that the introduction of such techniques acts as a visible indicator of the state of the science, an introduction which was to flourish under the Genevan's watchful eye. Though this suggestion ignores the splendid contribution from geologists to the biogeographical theories of this era, I nevertheless believe that such was indeed the case for the rather atheoretical study of plant distribution. Hence I put forward the view that botanists like Robert Brown and Joseph Hooker saw the establishment and success of arithmetical methods in related (and not-so-related) disciplines, and, themselves wishing to make distribution a "scientific" study, they consequently used figures and tables wherever possible. These were not so much a shorthand device for conveying the wealth and diversity of information that was being gathered in foreign lands, as rather a visible sign of the 'maturity' or imminent 'maturity' of their subject.

Some naturalists, of course, were more conscious of what they were doing than others, and I have already quoted from two such self-aware men words which expressed the desire to make botany an "exact science" (Hooker) by giving the "partie statistique" (Decandolle) her dues. Nevertheless their careful and often sententious statements of intention do not mean that they did not appreciate the practical value of statistics. Decandolle and Hooker used such techniques to excellent effect, as will shortly be made apparent. Yet there were many

naturalists who can hardly have thought deeply about why they used botanical statistics, but just went ahead and did so. H.C. Watson, the philosophical botanist who divided the British flora into 'provinces' in a series of important books through the 1830's and forties, and Lacordaire, the Parisian entomologist who wrote of the geographical distribution of insects, both used numerical methods because they were, in the first instance, useful for the arrangement and evaluation of their data. Furthermore, statistics had been so readily absorbed by the botanical community of the early years of this century that by Watson's time they were an integral part of the intellectual equipment of certain scholars.

Thus I think we can see a spectrum of usage, ranging from a deliberately effective marshalling of statistical methods to a more or less unthinking acceptance of their value and utility. It is now appropriate to ask exactly how such orderly processes were used, and what naturalists meant when they talked of "strict and disagreeable arithmetic" as Darwin so wryly called it. How were the details of distribution assessed in an arithmetical way? The answers to these questions illuminate in a particularly striking fashion the sort of biogeography which was then current and the manner in which investigations were pursued and presented. Few historians of science have realised that the study of distribution before Darwin was sufficiently developed to require the battery of techniques which usually accompany 'maturity'. However, distributional investigations before the advent of evolution theory evidently possessed tried and tested methods of procedure and a well established framework within which to work and publish results; these signs of sophistication I now contend actually hinged on the employment of statistical methods of the simplest kind, and, in particular, the techniques which went under the name "botanical arithmetic".

## Botanical arithmetic

Within a generalised attempt to make biogeography more "scientific" through the use of mathematical or numerical data, I believe the most notable - and certainly the most prevalent - feature was the employment of proportional ratios to express a variety of phenomena. And here, as in so many aspects of plant geography, Alexander von Humboldt was the first to establish the rules of the game. In every one of his three

great botanical tracts which described the floras encountered during his methodical exploration of equatorial America over the turn of the eighteenth century, he demonstrated the peculiar aptness of ratios for a detailed understanding of the finer points of plant distribution. His books published over the first two decades of the new century were devoted to a "scientific" rendering of botanical geography, and I think it fair to say that of the mere handful of comparable treatises on biogeography, it was Humboldt's contribution which most clearly set the standard for future work and which consequently generated the tenor of subsequent investigation.

Turning for the moment from arithmetic per se to more general questions of the development of biogeography, it was certainly the case that Humboldt had had intellectual predecessors in this field. This point is amply illustrated by the publications of the group of philosophical naturalists and humanists based on Göttingen during the last quarter of the eighteenth and first years of the nineteenth centuries. H.F. Link and Frederic Stromeyer, both attached in their time to the University of Göttingen and the botanical gardens of Berlin, wrote extensively of the principles of plant geography and local floras. Humboldt's former teacher, the then widely famed botanist K.L. Willdenow, explained 'Pflanzengeographie' to his pupils and reading public, and in so doing encouraged not only Humboldt but also his friends the two Forsters—the father and son team who had sailed with Cook on his second voyage to the southern continent, and had published their botanical and distributional results before Humboldt even set sail for the New World.

Yet none of these writings enjoyed quite the same impact on natural inquiry as did Humboldt's books. His three major botanical tracts examined the geography of plants from an exceedingly comprehensive viewpoint that was hitherto without precedent in its careful discussion of physical, climatic and geographical factors, and which included the assessment of phenomena like sociability and the differentiation of 'types' of vegetation such as forest, heath or grassland, in addition to inquiries into the separation and origins of distinctive floras, the powers of dispersal and transmission of seeds, acclimatisation and the cultivation of plants by early man.

Humboldt's watchword for these studies was simply Precision, and so detailed charts, tables and graphs were presented throughout all thirty-four volumes of his Voyages aux régions équinoxiales du Nouveau

Continent (1805-1834) and the various extensions and revisions of that colossal work. Though tables and graphs were not new in botanical literature, such a profusion of them was exceptional. He intended to give an overall view of the wealth of data thus made available. Tables were distributed freely to reduce a plethora of information into a manageable form. Especially characteristic and indicative of this preoccupation was Humboldt's invention of the 'isotherm', a line drawn on maps to link spots with the same temperatures.

Part of this activity was manifested in his study of plant geography. Here too, tables and charts featured as essential items in the portrayal of his subject, and here also the calculation of simple numerical ratios appeared as a new technique.

In 1805 Humboldt prefixed a short Essai sur la géographie des plantes to a 118 page consideration of the physical and botanical facts relating to the distribution of plants over mountains[8]. The latter information was also crammed onto a large chart of an ideal mountain which must surely rank as the most detailed (yet most interesting) diagram of botanical distribution ever published. Perhaps the best guide to the breadth of Humboldt's interest in vegetation is in this attempt to chart an amazing diversity of knowledge. "Le tableau indique . . ." he wrote,

> "la végétation; les animaux; les rapports géologiques; la culture; la température de l'air; les limites des neiges perpétuelles; la constitution chimique de l'atmosphère; sa tension électrique; sa pression barométrique; le décroissement de la gravitation; l'intensité de la couleur azurée du ciel; l'affoiblissement de la lumière pendant son passage par les couches de l'air; les réfractions horizontales, et le degré de l'eau bouillante à différentes hauteurs."[9]

The Essai itself with its illustrative tableau aspired to a grand correlation and inter-relation of all physical and organic phenomena. He described the "physiognomie" of vegetation which depended on an understanding of the relative proportions of major botanical families such as grasses, mosses or compositae and the preponderance or dominance of one or more forms over the others, or not, as the case may be. Thus pine forests in which the one species occupied the land to the exclusion of any other plants except possibly some shrubby undergrowth and brambles, was one example of the way species could form an "assemblage"; tropical rain forest on the other hand exhibited an abundant and complicated diversity in which no one species predominated.

Furthermore Humboldt saw that dominance could be either by sheer mass of individuals or by the number of different species of any one group of plants. Writing of the relative proportions of ferns (Cryptogams) and composite plants (Phanerogams) in the northern zones, he pointed out how ferns dominated en masse yet the composites did so by their larger number of species:

> "Dans une région boréale ou les Composées et les Fougères sont aux Phanérogames dans les rapports de 1:13 et 1:25, une seule espèce de fougères peut occuper dix fois autant de terain que toutes les espèces de Composées ensemble."[10]

He was, in fact, making it quite clear that botanical geography was a study of "assemblages" and that these could be analysed and compared most satisfactorily through the use of proportional ratios. As above, the ferns of one region presented the ratio of one species to every 25 Phanerogams, whereas the Composite plants (themselves members of that great kingdom) presented the proportion of one to thirteen species of the whole flora. From this we clearly deduce that compositae species are twice as numerous as fern species. Yet the ferns were individually so plentiful that any one species of fern might be found to cover areas ten times as great as the compositae, although the latter had more species to have a go with. The simplest numerical reckoning had given Humboldt something of value to pass on to his readers, something which gave a more complete picture of the constitution of boreal zones than any descriptive passage.

Naturally a man of Humboldt's exactitude did not dispense with absolute numbers but in his later, less literary works on plants and distribution he tended to subjugate these to the presentation of data as parts of one thousand, fractions of unity or ratios. Such detailed analyses were not strictly speaking necessary for all his geographical interpretations, as his own Essai plainly demonstrated in the long discussion on the migration of cultivated plants in the wake of mankind[11]. Proportions here were quite inappropriate. Yet his contemporaries seemed to ignore statistics when they could have been useful, as, for example, his old teacher Willdenow did in his popular introductory textbook, Grundriss der Krauterkunde (1792) where botanical geography was certainly included under the rubric "History of Plants"[12]. Willdenow found no need to introduce numerical methods into his sub-divisions of the plant life of Europe into five types of flora corresponding to the Northern, Helvetic, Austrian, Pyrenean and Apenninian kinds of

vegetation[13]. Humboldt on the other hand unleashed the full force of his mathematical powers whenever he felt the data could be so treated and subdivided the plant life of the northern hemisphere into fifteen types of association, and indeed the plants of equatorial mountains into six altitudinal associations, primarily on the basis of the ratios of major families.

The Prolegomena to Humboldt's long list of new species and genera discovered in tropical America (1815-1825) was his hymn to the statistical method[14] and revolved around his effortless mastery of the new technique which he dubbed "botanical arithmetic". Not actually published until 1816, this last botanical work formed the penultimate section of the Voyages aux régions équinoxiales, and contained a thorough investigation into the floras of the "aequinoctal" zone of not only the New World but of the Old also. He drew in results from work published by other botanists on the plants of extra-tropical latitudes to provide a balanced and comprehensive view. Thus he compared, for example, the distribution of annual species (both monocotyledonous and dicotyledonous plants) in the tropics with those of temperate and northern zones, and calculated the proportion of annuals to the whole of the flowering plant kingdom in each region. Concluding that the ratios signified that annual forms made up a greater fraction of temperate vegetation than that of the areas to the north or south, he wrote that these plants were evidently more suited to the conditions presented in intermediate latitudes. And in the following passage he incidently coined the term "botanical arithmetic" to describe the use of ratios such as these:

> "Thus we may pursue the foundations of the arithmetic of Botany further, [and] it will appear that the annual monocotyledones and dicotyledones are especially suited to the temperate zone in which they make up one sixth of all the Phanerogama, for, according to the observations of Decandolle, in the equatorial region they are barely one twentieth part of the whole and in Lapland, one thirtieth."[15]

It is easy for the historian to see how statistics like these could be multiplied and arranged in a table. Humboldt gave, for instance, details of some eleven natural families in France, Germany and Lapland and worked out the proportions which every group exhibited to the whole for these three areas. In this way he showed how the family of grasses, the Gramineae, had respectively 284, 143, and 49 species

in each region, whereas the family was demonstrably a consistently important and regular feature of the botany of these countries for their proportions to the whole ran as 1/13, 1/13, and 1/10[16].

Again in the table illustrated here he worked out the ratio of families to the whole flora according to latitude[17]. The grasses in this table bear the relationship of 1:15, 1:12 and 1:10 in the tropical, temperate and arctic zones respectively, and remained a not negligible part of the flora of each region. By contrast such typically equatorial plants as the Euphorbias decreased from a ratio of 1:35 to only one species in five hundred at the arctic circle.

It is tables such as these that I believe to mark the establishment of statistical biogeography. However, though Humboldt may have been the first so to calculate and tabulate ratios relating to distribution, he was not alone in the appreciation of statistical methods and the botanical table. In later years, and especially during the 1850's when young Joseph Hooker and Alphonse Decandolle were beating the drum for arithmetical exactitude, Humboldt's name was frequently linked with that of Robert Brown as the two founders of 'proper' distribution studies. Humboldt himself apotheosised Brown as botanicorum facile princeps, a designation which united him with the great botanists William Sherard and Linnaeus, on the strength of his investigations into the plants of Australia. It was an opinion echoed by contemporary botanists of the early nineteenth century but one which did not, unfortunately, induce many of them to dig into their pockets and subscribe to Brown's first and major work the Prodromus Florae Novae Hollandiae (1810) of which only 24 copies were sold[18]. This disappointing failure led Brown to publish only one other book (and that as an appendage to someone else's work) and to confine further contributions to brief memoirs or notices in the learned journals of the day. One of the more striking examples of this reticence was that his important announcement of the discovery of naked gymnosperm ovules (which allowed substantial revision of the classificatory position and level of organisation of the Conifer group) was published as an appendix to Captain King's Narrative of the Surveying Voyages of H.M.S. Adventure and Beagle etc.[19]

But Brown's General remarks geographical and systematical on the Botany of Terra Australis, appended to Flinders' voyage of 1814 (which was quite reasonable as it was with Flinders that Brown sailed to Australia) was also reissued in a separate form in the same year[20].

| CLASSES ET ORDINES NATURALES. | RATIO CUJUSCUNQUE CLASSIS VEL ORDINIS ad totam copiam Phanerogamarum locis planis provenientium: In Zona æquinoxiali (Cal. med. 27°.) | In Zona temperata (Cal. 10°—14°.) | In Zona glaciali (Cal. 0°—1°.) | ADNOTATIONES. |
|---|---|---|---|---|
| Agamæ cellulosæ. . . . . | 1 : 5 | 1 : 2 | 1 : 1 | |
| Filices . . . . . | | 1 : 60 | 1 : 25 | Germ. $\frac{1}{48}$ Gallia $\frac{1}{73}$. |
| Monocotyledones. . . . . | 1 : 6 | 1 : 4 | 1 : 3 | |
| Cyperoideæ. . . . . | 1 : 60 | 1 : 30 | 1 : 9 | |
| Gramineæ. . . . . | 1 : 15 | 1 : 12 | 1 : 10 | |
| Junceæ. . . . . | 1 : 400 | 1 : 90 | 1 : 25 | Amer. bor. $\frac{1}{150}$ Gallia $\frac{1}{82}$. |
| Glumaceæ vel tres ord. præced. | 1 : 11 | 1 : 8 | 1 : 4 | |
| Labiatæ. . . . . | 1 : 40 | 1 : 25 | 1 : 70 | Amer. bor. $\frac{1}{40}$ Gallia $\frac{1}{24}$. |
| Ericinæ et Rhododendra. . . . | 1 : 130 | 1 : 100 | 1 : 25 | Amer. bor. $\frac{1}{36}$ Gallia $\frac{1}{133}$. |
| Compositæ . . . . . | 1 : 6 | 1 : 8 | 1 : 13 | |
| Rubiaceæ. . . . . | 1 : 29 | 1 : 60 | 1 : 80 | Gallia $\frac{1}{73}$ Germ. $\frac{1}{70}$. |
| Umbelliferæ. . . . . | 1 : 2000 | 1 : 30 | 1 : 60 | Amer. bor. $\frac{1}{57}$ Gallia $\frac{1}{53}$. |
| Cruciferæ. . . . . | 1 : 3000 | 1 : 18 | 1 : 24 | Amer. bor. $\frac{1}{65}$ Gallia $\frac{1}{19}$. |
| Malvaceæ. . . . . | 1 : 50 | 1 : 200 | 0 | Am. bor. $\frac{1}{183}$ Gallia $\frac{1}{143}$ Germ. $\frac{1}{227}$. |
| Leguminosæ. . . . . | 1 : 12 | 1 : 18 | 1 : 35 | |
| Euphorbiaceæ. . . . . | 1 : 35 | 1 : 80 | 1 : 500 | |
| Amentaceæ exclusis Casuarin.. | | 1 : 45 | 1 : 20 | |

Adjecimus differentias notabiliores quas offerunt Zonæ temperatæ boreales utriusque Continentis. In universum minus fides habenda numeris absolutis quam rationi qua crescunt vel decrescunt numeri a polo versus æquatorem aut ab æquatore versus polum.

From Humboldt's Prolegomena of 1815, p xviii.

Figure 4

following page 135

This work, issued as it was two years before Humboldt's final botanical work the Nova Genera et species plantarum, and furthermore written in English not Latin, undoubtedly received considerable attention from naturalists whether they were stirred by nationalistic pride or not.

Brown's account of the botany of Australia was statistical without the tables. As he was himself terse almost to the point of absurdity, his prose is unequivocal and precise where Humboldt's would have been purple. His writings were, however, never unintelligible even when dealing with the complexities of discrimination between floras and the various relations of the species and genera of which they were made up. Hence his descriptions were valued for their clarity, and his botanical geography for a style which conveyed statistical or numerical results and patterns in a manner with scant room for ambiguity. To explain the distribution of that odd and peculiarly Australian family of Proteaceae, which also has three genera in South Africa, Brown gave the following lucid passage:

> "Proteaceae are chiefly natives of the Southern hemisphere, in which they are most abundant in a parallel included between 32° and 35° lat. but they extend as far as 55°S. lat. The few species found in the Northern hemisphere occur within the tropic.
>
> Upwards of 400 species of the order are at present known, more than half of these are natives of Terra Australis, where they form one of the most striking peculiarities of the vegetation. Nearly four-fifths of the Australian Proteaceae belong to the principal parallel, in which, however, they are very unequally distributed; the number of species at its western extremity being to those of the eastern as about 2 to 1, and what is much more remarkable, the number even at the eastern extremity being to that of the middle of the parallel as at least 4 to 1. From the principal parallel the diminution of the order in number of species is nearly equal in both directions: but while no genus has been met with within the tropic which does not also exist in the principal parallel . . . several genera occur at the south end of Van Dieman's Island which appear to be peculiar to it."[21]

In a couple of hundred words Brown encapsulated the distribution of a family which was to occupy as many pages in the next flora of Australia that was to appear, viz. the Flora Tasmaniae of Joseph Hooker published in 1860.

Brown thus saw the scope of arithmetical botany and, like Humboldt, applied proportional reasoning to a wide range of phenomena. As above,

ratios were used to portray the dispersal of one family which varied in species from the west to the east of its range as 2:1, and from the "eastern extremity" to the middle as 4:1. Yet other ratios supported descriptions of the overall composition of the Australian floras and their relations to other botanical provinces like those of the Cape of Good Hope and the southern part of South America. Reflecting on the odd and apparently illogical relationship between these three austral continents, Brown epitomised the case thus:

> "The four remaining orders [of the 11 which constitute one half of the species] are Myrtaceae, Proteaceae, Restiaceae and Epacrideae. Of these Myrtaceae, though it is . . . very general, has evidently its maximum in Terra Australis, more species having been already observed in that country than in all other parts of the world; Proteaceae and Restiaceae, which are nearly confined to the southern hemisphere, and appear to be most abundant in the principal parallel of New Holland, are also very numerous at the Cape of Good Hope; and Epacrideae, at least, equally limited to the southern hemisphere, are, with very few exceptions, confined to Terra Australis."[22]

He concluded - rightly as it turns out - that Australia enjoyed a relationship with South America which did not include any families found in the Cape, and conversely, that there were families common to the Australian and African continents which did not have any representatives in South America.

The detail which Brown and Humboldt advocated and illustrated in their writings was further advanced and reiterated by their botanical colleague Augustin Decandolle, the 'founding father' of the distinguished line of Swiss naturalists to bear that name. Decandolle too was absorbed by the problem of plant distribution and gave his opinions to the French reading public in a justly appreciated little essay, the Essai élémentaire de Géographie Botanique of 1820. First published in the Dictionnaire des Sciences Naturelles edited by F.C. Levrault, it was issued separately in the same year from Paris and Strasbourg. From this source the young Charles Darwin learnt his botanical geography, as did his friend and botanical mentor Joseph Hooker, and, no doubt, the younger Decandolle (Alphonse) also who was to write on the same subject himself. It was quoted with approbation in the second quarter of the century by those very pupils who had evidently been brought up in the tradition of numerical fluency.

The Essai élémentaire divided 'géographie botanique' into three

sorts of investigation which should, as Decandolle stressed, be pursued as an integral whole. The first section, concerned with the physical factors of "La température, la lumière, l'eau, le sol, l'atmosphère", was thus intimately connected with the second investigation of "stations" or as modern biologists would call them, 'habitats', like those of moorland, marsh or coastline. The final section was devoted to the inquiry into what Decandolle designated "des habitations" or the grand divisions of the vegetable kingdom into botanical provinces, in which he included all the points of distribution which depended on the origins (i.e. the history, not initiation of forms) of plant life[23]. He was particularly interested in the correlated movements of organisms and the geological structure of the earth, and therefore set aside a fair portion of this third section for an explanation of the way he believed floras to have been formed successively through geological time, each one existing during a period which had a completely different geological formation from those periods which preceded or succeeded it. He was to use botanical arithmetic to demonstrate these beliefs in other publications, as, for example, in his contributions to the debate on whether the fossil record exhibited a "progression" from the earliest to the latest forms of life. More will be said about this particular subject in a later part of this chapter.

But in the Essai élémentaire Decandolle recommended the use of statistics through his own example. In a manner equivalent to that of Brown or Humboldt he estimated the relative proportions of various botanical cohorts, as in for instance the ratio which monocotyledonous, dicotyledonous and acotyledonous plants bore to each other over the northern hemisphere. Over and above these two eminent colleagues however, Decandolle clearly explained one particular advantage of botanical arithmetic for the study of "habitations". Moving onwards from Brown and Humboldt's usage he demonstrated that a knowledge of the proportions between species and genera or families gave valuable biogeographical information. Such a computation was, of course, a mere extension of the then established practice of taking the ratio of families to larger subsections of the vegetable world like the Phanerogams or even the whole flora of one region. I might add here that this latter calculation was carried out by simply numbering the species which each group contained. The number of species was of value for quantifying the differences between floras in an immediately vivid manner: that is, one flora with 100 species could be quite plainly distinguished

from another with 10,000. Decandolle however showed that the relation between species and genera would prove to be a more sophisticated tool than the latter, and could provide an indication whether a country sported a diverse or monotonous flora.

Thus he wrote that the more species there were for every genus (say, 16 species to one genus on average) so the more constant and monotonous the plant covering. Correspondingly, the fewer species there were per genus then the more diverse the flora. Illustrating his meaning he cited the example of France which possessed an average of 7⅓ species per genus, the British Isles with 2⅓, and the Canaries archipelago with 1½. He wrote of these figures:

> "Pour achever ce qui relatif a cette espèces d'arithmetique botanique, comme l'appelle M. de Humboldt, et pour montrer jusqu'a quel point elle peut peindre l'aspect général de la végétation des pays divers, je dirai encore qu'on a tiré quelque parti de la comparison du nombre proportional des espèces et des genres d'un pays. Plus le nombre moyen des espèces de chaque genre ou de chaque famille est borné, plus l'aspect de la végétation présente de variété; plus, au contraire, ce nombre est grande, plus les coup d'oeil du pays présente de monotonie dans les formes."[24]

His "coup d'oeil du pays" showed that France had more species per genus than the Atlantic island group and consequently presented a "monotonie dans les formes", whereas the Canaries with only one and a half species for every genus (a one-to-one ratio is most rare and extraordinary) evidently possessed a wealth of different sorts of plants, even though the total number may be quite small.

This might appear to be a paradox in that Decandolle's monotonous areas seem to have more species (each of which, by definition, is a different form) than his diverse areas. But the crux of the matter is that genera possess a greater distinctness of form than species and so it is their numbers which are the important element in estimates of the type of vegetation. The frequency of higher orders of distinction makes for richness, not the total number of closely-related species.

But one must assume on this argument, I think, that absolute figures ought to accompany the ratios as a guide. For suppose an area has 1½ species per genus, but only 10 genera in all, then the number of species is only 15; but another equal area could have 6 species per genus, and 100 genera, and so with 600 species be far richer. Here we must remember that Decandolle's word "variété" does not necessarily

mean 'plenty' but implies instead a notion of 'complexity', for it was not the relative abundance or crowding of regions which he wished to illustrate but rather the existence (or absence) of extremes within each association. However, he might perhaps have done better if he had calculated the average number of genera to 100 or 1000 species (viz. the same ratio but the other way around) as his son was to do, and as a modern biogeographer P. Jaccard has recently (re)discovered.

This index of diversity, if we may call it such, was independent of the absolute numbers of either species or genus. Thus Decandolle could compare the vegetation of islands and continents without complicating factors of a priori assumptions that areas of large topographical extent must possess a greater number of species than oceanic islands. The ratio therefore revealed fundamental 'laws' about the proportions which could be expected on certain lands: continents usually possessed many species to each genus and islands only few.

This last method for botanical arithmetic in phytogeography turned out to be very popular. It caught the imagination of the young Charles Darwin and in his naturalist's notebooks relating to the Beagle voyage of 1831-36, he tried to work out just such relative numbers of species to genus. Later in his "Species" notebooks he reflected that though the "Flora of islands are poor" still the number of genera was relatively high, "For instance, the temperate part of Teneriffe: the prop. of genera 1:1"[25]. Equally, the method was so familiar to Joseph Hooker that when he wrote to Darwin about botanical distribution over the decade 1844-54, he insouciantly assumed that Darwin would know all about the differences between "continental" and "insular" proportions, where the first exhibited Decandolle's "monotonie" and the second, "variété".

* * *

In retrospect then, it can be seen that at least three well-known naturalists attempted to incorporate statistics into plant distribution studies: Decandolle père, Humboldt and Robert Brown were throughout their writings elaborately involved with utilising "botanical arithmetic" for the reduction and interpretation of their facts and for the intended advancement of their science. And though it does not really matter - historically speaking, that is - if this triumvirate was or

was not the first to comprehend and organise distribution in this manner (although the question certainly excites antiquarian interest), it does seem that they themselves claimed to be the 'founders' of botanical arithmetic and indeed of the science of plant geography itself. The notable point is, I believe, that these men thought that they were the first to bring order into chaos, and congratulated each other publicly for so doing. The three formed a mutual admiration society: Decandolle praised Humboldt for furthering "la marche du raisonnement" and, with Brown, designated him the leading luminary in developing the philosophical side of this science; Humboldt referred to Brown as Botanicorum facile princeps, and to Decandolle as "un savant"; Brown, perhaps a little less generous or flowery in his prose, merely referred his readers to these other "excellent" philosophers in the field.

Furthermore after one or two decades, by the years 1840 to 1859, a second generation of naturalists such as Hooker, the younger Decandolle and Hewett Cottrell Watson acclaimed them as the "most able contributers to geographical botany" (Decandolle) although these younger men, as I have already indicated, believed themselves to have "taken up a chaos of facts, and reduced them to science" (Watson) all over again.

However Humboldt, Decandolle père and Brown do seem to have stood alone in their sophisticated use of statistics during the early years of the century. In those comparable works which might have used such techniques, they are quite plainly absent.

Willdenow, for example, the eminent professor of Botany at Berlin and Humboldt's teacher, was clearly concerned with geographical distribution in his works and yet neither the Phytographia of 1794, nor the series of volumes and supplements to the Enumeratio plantarum horti regnii Berolinensis (1809 onwards) which was ideal for such statistico-geographical remarks, contained any such numerical statements. His History of Plants (1805) as already mentioned, which enjoyed considerable fame in British botanical circles, especially in Edinburgh, the 'seat' of botany in these islands, included purely descriptive remarks of a limited value. "The warmer the climate, the greater must be the number of wild growing plants" was one of Willdenow's more exact statements, and one which was substantiated with a list of the number of species in selected countries proceeding from north to south, from a total of two species in South Georgia to nearly five thousand in tropical Madagascar[26].

Willdenow's successor at Berlin, the equally renowned botanist H.F. Link, continued this solely descriptive convention in his own Enumeratio plantarum horti botanici Berolinensis (1821-2) and, more tellingly, in Some materials for the illustration of the Botanical Geography of the south western parts of Europe[27] in which despite praise of phytogeography ("Botanical geography forms a distinguished but hitherto neglected branch of geology") he simply listed the plant species of southern Europe with terse remarks on their range. Of the distinctive topographical arrangements of the blue and white forms of periwinkle, he said only "Vinca minor in the north of Europe, V. major in the south".[28] True as this may be it does not equal the sort of detail which Humboldt was espousing.

As in Germany, so in France: little seems to have changed in French distribution studies from the year 1783 when the littérateur Giraud-Soulavie wrote of the physical factors limiting plant dispersal, and (perhaps the first so to do) gave a map depicting the limits of floras[29], to the year 1830, when Jean Lavy devoted a substantial volume to the "État général des végétaux originaires" - his only claim to fame in an otherwise obscure biography - which was almost entirely devoted to species lists for each region thus examined[30].

Elsewhere in Europe the situation was much the same. There were increasing numbers of publications or parts of publications relating to distribution as a separate topic of inquiry, but, as yet, little cognizance of the arithmetic of botany. A notable exception was, however, present in the work of Joakim Schouw of Copenhagen. His Grundtraek til almindelig Plantegeographie of 1822, with its German translation of 1823[31] was a valuable contribution to the understanding of the arrangement of German plants. During his wanderjahre through that country and northern Italy he had not only attempted to order the botanical results of his travels but also to absorb the latest in phytogeographical teaching from Decandolle and Humboldt, and returned to Copenhagen to take up the chair of botany with particular responsibility for introducing this 'new' subject to eager pupils. The book contained charts and tables of factors such as temperature, pressure, insolation etc., and numerical analyses of the kind favoured by Humboldt were used to a small extent, as in, for example, his estimation of the fraction of the whole flora which certain plant orders held[32]. Nevertheless, Schouw's close links with both Humboldt and Decandolle place him rather more in the position of enthusiastic

disciple, than in a position of equal and independent appreciatior of botanical arithmetic. Important as this work was, I believe Schouw's publication to have been only one of the first in a line of conscientious attempts to apply - not invent - a new analytic technique.

And in England, where very few serious or scholarly efforts were being made to identify the arithmetical regularities in plant geography, only Robert Brown deliberately used such methods. The first two decades of the nineteenth century were here almost bereft of any biogeographical literature, which is why, no doubt, Brown's distributional remarks stood out in isolated spendour and were heralded (not only by the British) as an important contribution to the science.

However, provincial naturalists were stirring themselves primarily through the conviviality and good exercise of the field club excursion which led to a charming series of local floras, hand-lists, and guides for the botanist[33]. One Nathaniel Winch from Newcastle on Tyne was then rather more well known for his guides to the vegetation of Northumberland, Cumberland and Durham than he is today, and for his labours ascended to some national recognition. In particular, Winch took strongly philosophical views on the whys and wherefores of distribution, and his Essay on the geographical distribution of plants through . . . Northumberland, Cumberland and Durham (1819 and second edition 1825) was something of a manifesto for the searching out of causes instead of purely descriptive botany. Yet Winch too disregarded the advantages which a numerical or computational approach to his data might have yielded.

So much then for the first quarter of the century. Statistics were not in any sense a widely known or used tool for biogeographers, even though the subject itself (biogeography, that is) was generating considerable interest throughout botanical centres of Europe, and though a succession of scholarly works had been published purportedly delineating different floras and the factors which contributed to their topographical limitations.

How did botanical arithmetic fare in later years? After the Browns and Humboldts of this world had set the example, did other naturalists follow suit? It would appear that they did, and, from the 1830's the numerical method, coupled with the construction of sometimes elaborate tables, became a regular and even essential part of distributional surveys. The "numerical relations" between plants,

and then between animals and also fossil floras and faunas became one of the most popular enquiries which practising naturalists could undertake. Perhaps it was with something approaching relief that naturalists seized on an exercise which actually gave a point to their collections and classifications, and which allowed them to busily calculate ratios and set these out in columns of figures as a statement of the peculiarities of that particular group of living beings. For it appears that the construction of a table was the aim, rather than the discovery of any statistical regularity. Although this is simply a historical guess, I suspect that faced with all the mountains of facts which had been - and were still being - supplied, naturalists were rather at a loss to know exactly what to do with them. Until, that is, Humboldt and his colleagues unveiled "botanical arithmetic".

Schouw's work in Copenhagen was the only use of Humboldtian methods that can, in truth, be directly traced to a personal or intellectual contact with the 'source'. Other scientists adopted the technique so rapidly that it soon became public property so to speak, and few publications of the 1830's and 1840's made express reference to their methodology as one following any particular paradigm. Nevertheless those few who did, firmly placed the bouquet at Brown, Humboldt and Decandolle's feet.

Turning now to a coup d'oeil of these two decades from 1830-1850 it will be seen that most serious biogeographical work contained statistical analyses of some sort or another. In the following pages I shall give examples which not only constitute the more notable efforts of this period, but which also mirror the wide range of use to which numbers - and especially proportions - were put. The technique proved to be so popular that even comparative strangers to the study of distribution valiantly attempted to use figures in an effective manner.

So, for example, Rudolph Wagner, the anthropologist, physiologist and comparative anatomist of Erlangen, made an essay into the comparison of numerical relationships which seems oddly beyond his immediate interests. In 1833 he compared the totals of specified groups of animals such as mammals, birds and insects in different successive authorities, ranging from Linnaeus to Fabricius[34]. His primary aim was to demonstrate how rapidly the morphological sciences were advancing and, secondly at the end, to illustrate the relative abundance of microscopic forms such as Infusoria in the several parts of Europe. And although his columns of figures were arranged to facilitate comparison

he did not, of course, use ratios or proportions to illuminate his conclusions, since the expressed purpose was to discuss these in terms of absolute numbers.

But truly phytogeographical estimates were also being published. In the same year of 1833 the young Edinburgh student H.C. Watson made one of his earliest public statements in what was to become a long and distinguished career. As a student of Robert Graham's he had early developed a taste for the field-trips which the latter had recently introduced and encouraged at the University (parallelling similar developments at Glasgow through the agency of W.J. Hooker, and at Cambridge through J.S. Henslow[35]) and in particular for their lengthier excursions into the remoter and botanically unexplored parts of the Highlands. One such trip yielded the data on which his 1833 paper was based, Observations made during the summer of 1832 on the temperature and vegetation of the Scottish Highland mountains in connection with their height above the sea[36].

Watson already had decided ideas about the proper study of distribution, and had gone to the trouble and expense of having a small guide to these ideas privately printed in 1832 for distribution among his friends. The Outlines of Geographical Distribution[37] paid especial attention to the vegetation of differing heights, something that had rarely been investigated in Britain, and to, as Watson termed it, "a few illustrations of the arithmetical distribution of British species and families". These were considerably extended and formalised for his 1833 paper of which I here illustrate a page giving a table of the "Altitudinal Elevation" of Highland plants[38].

In this paper Watson listed and described the 306 species which he found growing on Scottish mountain-sides above an elevation of one thousand feet. He then separated these into assemblies according to height, and subsequently into tables as shown, tabulated against the altitude at which each family occurred. Thus he displayed both the number of species from named natural orders (i.e. families[39]) at one height, and the spread of these orders over a range of elevation from 1,000 to 4,320 feet. More notably, he also gave the proportions of the same relative to the total flora. Hence in the table illustrated, Watson calculated that the natural order of Rosaceae with 20, 12 and 5 species at 1-2,000 ft, 2-3,000 ft, and 3-4,320 ft respectively, formed a larger proportion of the whole flora at each altitudinal zone than, say, the heathers (Ericeae) which were usually considered to be at their maximum

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Figure 5

*TABLE of the Altitudinal Elevation of Highland Plants.*

| Natural Orders. | Numbers. 1000–2000 Ft. | Numbers. 2000–3000 Ft. | Numbers. 3000–4320 Ft. | Proportions. 1000–2000 Ft. | Proportions. 2000–3000 Ft. | Proportions. 3000–4320 Ft. |
|---|---|---|---|---|---|---|
| Ranunculaceæ | 3 | 6 | 3 | 1/34 | 1/50 | 1/27 |
| Cruciferæ | 9 | 7 | 5 | 1/30 | 1/28 | 1/16 |
| Cistineæ | 1 | ... | ... | 1/273 | ... | ... |
| Violariæ | 4 | 3 | 1 | 1/68 | 1/91 | 1/80 |
| Droseraceæ | 3 | 1 | ... | 1/90 | 1/273 | ... |
| Polygaleæ | 1 | 1 | ... | 1/273 | 1/273 | ... |
| Caryophylleæ | 9 | 12 | 9 | 1/30 | 1/15 | 1/9 |
| Lineæ | 1 | ... | ... | 1/273 | ... | ... |
| Hyperacineæ | 1 | ... | ... | 1/273 | ... | ... |
| Geraniaceæ | 2 | 1 | ... | 1/136 | 1/273 | ... |
| Oxalideæ | 1 | 1 | 1 | 1/273 | 1/273 | 1/80 |
| Leguminosæ | 13 | 7 | 1 | 1/21 | 1/26 | 1/80 |
| Rosaceæ | 20 | 12 | 5 | 1/14 | 1/15 | 1/16 |
| Onagrarieæ | 4 | 3 | 1 | 1/68 | 1/91 | 1/80 |
| Haloragieæ | 1 | ... | ... | 1/273 | ... | ... |
| Portulaceæ | 1 | 1 | ... | 1/273 | 1/273 | ... |
| Crassulaceæ | 1 | 1 | 1 | 1/273 | 1/273 | 1/80 |
| Saxifrageæ | 7 | 9 | 8 | 1/39 | 1/26 | 1/10 |
| Umbelliferæ | 5 | ... | ... | 1/54 | ... | ... |
| Caprifoliaceæ | 3 | 2 | ... | 1/91 | 1/91 | ... |
| Rubiaceæ | 4 | 2 | 1 | 1/68 | 1/91 | 1/80 |
| Valerianeæ | 1 | ... | ... | 1/273 | ... | ... |
| Dipsaceæ | 1 | 1 | ... | 1/273 | 1/273 | ... |
| Compositæ | 32 | 18 | 6 | 1/8 | 1/15 | 1/13 |
| Lobeliaceæ | 1 | ... | ... | 1/273 | ... | ... |
| Campanulaceæ | 1 | 1 | 1 | 1/273 | 1/273 | 1/80 |

| Natural Orders. | Numbers. 1000–2000 Ft. | Numbers. 2000–3000 Ft. | Numbers. 3000–4320 Ft. | Proportions. 1000–2000 Ft. | Proportions. 2000–3000 Ft. | Proportions. 3000–4320 Ft. |
|---|---|---|---|---|---|---|
| Vaccinieæ | 4 | 4 | 3 | 1/68 | 1/46 | 1/27 |
| Ericeæ | 10 | 9 | 2 | 1/27 | 1/26 | 1/16 |
| Gentianeæ | 2 | ... | ... | 1/136 | ... | ... |
| Boragineæ | 4 | 1 | 1 | 1/68 | 1/273 | 1/80 |
| Scrophularineæ | 14 | 8 | 3 | 1/19 | 1/35 | 1/27 |
| Labiatæ | 7 | 2 | 1 | 1/39 | 1/91 | 1/80 |
| Lentibularieæ | 1 | 1 | ... | 1/273 | 1/273 | ... |
| Primulaceæ | 3 | 1 | ... | 1/91 | 1/273 | ... |
| Plumbagineæ | 1 | 1 | 1 | 1/273 | 1/273 | 1/80 |
| Plantagineæ | 3 | ... | ... | 1/91 | ... | ... |
| Polygoneæ | 7 | 3 | 3 | 1/39 | 1/91 | 1/27 |
| Euphorbiaceæ | 2 | ... | ... | 1/136 | ... | ... |
| Urticeæ | 3 | 1 | ... | 1/91 | 1/273 | ... |
| Amentaceæ | 14 | 10 | 2 | 1/19 | 1/26 | 1/16 |
| Coniferæ | 2 | 2 | ... | 1/136 | 1/91 | ... |
| Empetreæ | 1 | 1 | 1 | 1/273 | 1/273 | 1/80 |
| Juncagineæ | 1 | 1 | ... | 1/273 | 1/273 | ... |
| Orchideæ | 5 | 5 | ... | 1/54 | 1/54 | ... |
| Melanthaceæ | 1 | 1 | ... | 1/273 | 1/273 | ... |
| Junceæ | 10 | 10 | 6 | 1/27 | 1/26 | 1/13 |
| Cyperaceæ | 18 | 20 | 7 | 1/15 | 1/13 | 1/46 |
| Gramineæ | 25 | 13 | 7 | 1/11 | 1/21 | 1/11 |
| Total of Sp. | 273 | 183 | 80 | | | |
| Total of Ord. | 48 | 38 | 25 | | | |

From H.C.Watson's 'Observations made during the summer of 1832 on the temperature and vegetation of the Scottish highland mountains in connection with their height above the sea' p 323.

in the Highlands[40].

Watson was to make the study of the spatial arrangements of plants very much his own through his dictatorial yet unofficial dominance of (first) the ill-fated Botanical Exchange Club, and (later) the newly formed Botanical Society of London. He bullied the Society into bringing out a standard checklist known as the London Catalogue of Plants (1844 and many subsequent editions) which he alone collated. His magnum opus, the Cybele britannica; or British plants and their geographical relations (1847-59, and further volumes 1860 onwards) was undoubtedly one of the cornerstones of topographical investigation from the time of its publication to 1859, when Darwin gave botanists evolutionary theory to buttress their distributional studies. In it he devoted much space to "those arithmetical comparisons to which phytogeographers commonly seem to attach much importance". Thus on a numerical estimate of the incidence or absence of species in precisely demarcated "Provinces" and "Vice-counties" over the British Isles[41], he managed to take the first step in a nationwide census. Accessory to this was his clear differentiation between mapping the individual points where each species had been sighted (in modern terminology 'point' maps) and fixing on an area within which given plants might be expected to appear. Watson himself devised a "test which is adapted to show the number of spaces (not the number of precise places) in which each one occurs"[42].

The Cybele[43] contained many well reasoned statistics of "geographical relations" including his special love, that of altitudinal variation in plant associations, but also many other interesting and probably some innovative ratios such as the proportion of species per unit area in separate parts of Britain (e.g. 0.30 species to 10 miles, or, more properly, one species to every 30 square miles, in east Britain) and, conversely, the acreage over which any one species ranged (e.g. 32.16 square miles per species in the same region as before)[44].

In Germany too the "simplest reckoning" had reached a stage in which numbers were duly appreciated. The Prussian botanist and plant physiologist Franz Meyen, who had enjoyed the patronage of Humboldt in arranging his travels through western South America, wrote in 1836 a Pflanzengeographie in which a full thirty page section was given over to the "Statistics of Plants"[45]. This was later translated by the Ray Society and published in 1846 for the edification of British naturalists; both Darwin and Hooker owned well-thumbed copies and congratulated

each other on the merits of possessing such a Society as this one which issued translations[46].

Meyen described, for the benefit of those who did not know, how to use numerical data:

> "The method . . . is founded on the simplest reckoning, by which we find out the number of species of the smaller, as well of the larger groups of plants, and compare the numbers obtained with each other, or with the whole number of all the species of a country."[47]

And lest the advantage of so doing still evaded the reader, he stressed that:

> "Statistical inquiries into the absolute and relative numbers of species have led to a fixed law, according to which the different groups of plants, viz. families, genera and species have been distributed in each zone."[48]

It was, I think, indicative of the state of the science that Meyen felt not so much that there was a gap in investigations which statistics should fill, but rather that now was the appropriate time to spell out what this technique represented.

This second quarter of the century experienced, as could be expected, a comparable statistical activity in zoological and geological studies. The latter discipline seems to have taken arithmetical analysis in a slightly different manner from that which characterised natural historians' writings, and for this reason I prefer to discuss geological statistics separately on subsequent pages. Here, though, it is quite in order to draw in comparable examples from the geographical investigations of zoologists, and particularly from inquiries into entomology and marine invertebrates, such as corals, which have immediate parallels with the distribution of plants. For since insects eat and often live on plants, and corals are fixed like plants to the sea bed, the methods of phytogeography would here be most suitable.

The Parisian entomologist Lacordaire, a man of affairs, one of four brothers in public circles and the compiler of the insect section of the Suites de Buffon, had part of this Introduction à l'Entomologie translated into English and published at length in the Edinburgh New Philosophical Journal through 1839[49]. In every department of geographical distribution he used the tabular format for presentation of data and the computation of ratios.

Citing the botanical method, Lacordaire calculated, for example,

the number of insect species per genus, as had Decandolle some twenty years earlier. In the table given here he quoted figures which enabled him to conclude that though species may increase from northerly regions like Siberia to those of the southern hemisphere, genera, on the other hand, are relatively more numerous in the north. "From this it follows", he wrote:

> "That the absolute number of genera augments from the north to the south, since Europe has more than Siberia, and South America more than Europe; but it will be seen, at the same time, that this number does not increase in the same proportion as the species, but that it follows, on the contrary, an inverse progression."[50]

Lacordaire was therefore using the "simplest reckoning" to make quite elaborate statements about the structure of insect populations of these areas.

His Geographical Distribution presents an interesting exhibition of the variety of usages to which naturalists were now prepared to employ arithmetic. He gave, for instance, proportions to indicate the sparsity of "phytosaprophagous" insects (which exist on decayed plant matter alone) compared with ordinary plant or leaf-eaters, and furthermore to compare saprophages with dung-eating beetles in different areas (see Figure 7).

Similarly, he listed the 22 families of beetles and bugs and itemised the number of genera of each which were confined to one of eight predetermined regions (Figure 8). An immediate parallel with H.C. Watson's tables of altitudinal distribution springs to mind, and indeed except for the different taxa employed they are exactly the same. Lacordaire then gave the "proportion to 100 genera" existing between these numbers just as Watson had given "Proportions" on his table.

And again, Lacordaire presented a grande finale with the close-packed columns of figures which conveyed the relative numericity (by species) of all insect families over the known regions of the globe (Figure 9). Each vertical column enclosed a hierarchical arrangement of families according to the number of species they presented in any one area. Consequently, reading across the page gave the conscientious naturalist an idea of which families were most in evidence in the different parts of the world. For instance he might discern that the three northernmost landmasses of North America, Lapland with Siberia, and Asia all had the same family as their most plentiful insect - the Carabidae - whereas Africa and Australia possessed the Lamellicornes in

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Figure 6

| Country. | Species. | Genera. | No. of Species, per Genus. |
|---|---|---|---|
| Siberia, | 465 | 169 | 2.7 |
| Europe, | 5,677 | 715 | 7.9 |
| North America, | 2,403 | 541 | 4.4 |
| South America, | 8,112 | 1209 | 6.7 |
| Africa, | 2,942 | 674 | 4.3 |
| New Holland, | 320 | 162 | 2. |

From Lacordaire 'On the geographical distribution of Insects' Edin.New Phil.J. 27 p 346.

Figure 7

| | Number of Phytophagous Species. | Phyto-saprophagous Species are to the entire amount of Phytophage,— |
|---|---|---|
| Lapland, | 529 | : : 1 : 261 |
| Sweden, | 1438 | : : 1 : 219 |
| England, | 2622 | : : 1 : 180 |
| France, | 3276 | : : 1 : 188 |

From Lacordaire 'On the geographical distribution of Insects' Edin.New Phil.J. 28 p 171.

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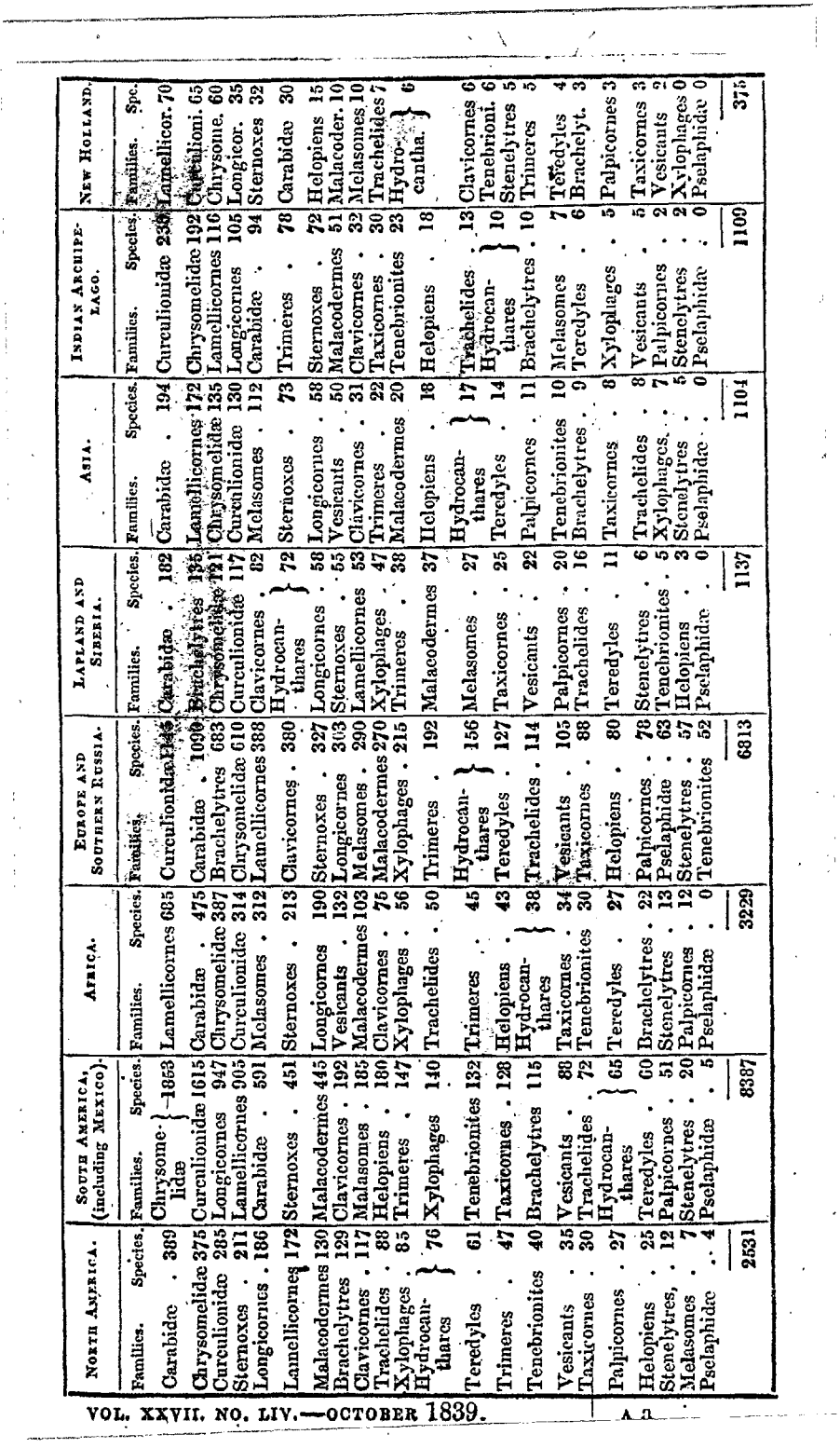
Figure 8

| Families. | Total of Genera. | No. of Genera proper to | | | | | | | | Proportion to 100 Genera. | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Regions 8. | Regions 7. | Regions 6. | Regions 5. | Regions 4. | Regions 3. | Regions 2. | Region 1. | Endemical. | Sporadical. |
| Carabidæ, . . | 183 | 6 | 2 | 8 | 7 | 11 | 20 | 24 | 105 | 57 | 43 |
| Hydrocanthares, | 26 | ... | 1 | 4 | 5 | 1 | 7 | 3 | 5 | 19 | 81 |
| Brachelytres, . | 72 | ... | 1 | 3 | 3 | 2 | 17 | 14 | 32 | 44 | 56 |
| Sternoxes, . . | 114 | 1 | 2 | 2 | 3 | 15 | 15 | 22 | 54 | 47 | 53 |
| Malacodermes, | 54 | 1 | ... | 1 | 5 | 2 | 9 | 9 | 27 | 50 | 50 |
| Teredyles, . . | 31 | 1 | ... | ... | 2 | 4 | 10 | 3 | 11 | 35 | 65 |
| Clavicornes, . | 63 | 1 | ... | 4 | 5 | 7 | 7 | 11 | 28 | 44 | 56 |
| Palpicornes, . | 11 | 1 | ... | 2 | 1 | ... | 2 | 4 | 1 | 9 | 91 |
| Lamellicornes, | 197 | 3 | 3 | 5 | 7 | 9 | 11 | 33 | 126 | 63 | 37 |
| Malasomes, . . | 124 | ... | 1 | 1 | ... | 2 | 14 | 22 | 84 | 67 | 33 |
| Taxicornes, . | 54 | ... | ... | ... | 2 | 6 | 6 | 8 | 32 | 59 | 41 |
| Tenebrionites, . | 56 | ... | 1 | 2 | ... | ... | 3 | 12 | 38 | 67 | 33 |
| Helopidæ, . . | 35 | ... | ... | 2 | 2 | 2 | 1 | 4 | 24 | 68 | 32 |
| Trachelides, . | 26 | ... | .. | 2 | 2 | 1 | 3 | 6 | 12 | 46 | 54 |
| Vesicants, . . | 19 | ... | ... | 1 | 3 | 2 | 2 | 3 | 8 | 42 | 58 |
| Stenelytres, . | 14 | ... | ... | 1 | ... | 2 | 1 | 3 | 7 | 50 | 50 |
| Curculionidæ, . | 350 | 1 | 3 | 1 | 12 | 17 | 17 | 59 | 240 | 68 | 32 |
| Xylophages, . | 56 | ... | 1 | 1 | 4 | 7 | 9 | 8 | 26 | 46 | 54 |
| Longicornes, . | 348 | 1 | 1 | 1 | 3 | 12 | 17 | 47 | 266 | 76 | 24 |
| Chrysomelidæ, | 328 | 1 | 3 | 3 | 10 | 11 | 29 | 49 | 222 | 67 | 33 |
| Trimeres, . . | 38 | ... | 1 | 2 | 1 | 4 | 2 | 6 | 22 | 57 | 43 |
| Dimeres, . . | 12 | ... | .. | ... | ... | ... | 2 | ... | 10 | 83 | 17 |
| | 2211 | 17 | 20 | 46 | 77 | 117 | 204 | 350 | 1380 | 62 | 38 |

It appears from this table that the sporadicity of genera is less than might be supposed; the result would no doubt have been different, if the number of regions were more considerable, but the fact would remain not less true upon the whole. It will be observed also that the Carabidæ, which constitute of themselves at least nine-tenths of the creo-thalerophagous genera, are those whose geographical extension is most considerable; but this holds true only among the coleoptera. When the whole class is taken into account, the phytothalerophaga have an indisputable superiority.

From Lacordaire 'On the geographical distribution of Insects' Edin.New Phil.J. 28 p 177.

Figure 9



| North America. | | South America, (including Mexico). | | Africa. | | Europe and Southern Russia. | | Lapland and Siberia. | | Asia. | | Indian Archipelago. | | New Holland. | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Families. | Species. | Families. | Species. | Families. | Species. | Families. | Species. | Families. | Species. | Families. | Species. | Families. | Species. | Families. | Spe. |
| Carabidæ | 389 | Chrysomelidæ | 1853 | Lamellicornes | 685 | Curculionidæ | 1145 | Carabidæ | 182 | Carabidæ | 194 | Curculionidæ | 238 | Lamellicor. | 70 |
| Chrysomelidæ | 375 | Curculionidæ | 1615 | Carabidæ | 475 | Carabidæ | 1090 | Brachelytres | 135 | Lamellicornes | 172 | Chrysomelidæ | 192 | Curculioni. | 65 |
| Curculionidæ | 285 | Longicornes | 947 | Chrysomelidæ | 387 | Brachelytres | 683 | Chrysomelidæ | 121 | Chrysomelidæ | 135 | Lamellicornes | 116 | Chrysome. | 60 |
| Sternoxes | 211 | Lamellicornes | 905 | Curculionidæ | 314 | Chrysomelidæ | 610 | Curculionidæ | 117 | Curculionidæ | 130 | Longicornes | 105 | Longicor. | 35 |
| Longicornes | 186 | Carabidæ | 591 | Melasomes | 312 | Lamellicornes | 388 | Clavicornes | 82 | Melasomes | 112 | Carabidæ | 94 | Sternoxes | 32 |
| Lamellicornes | 172 | Sternoxes | 451 | Sternoxes | 213 | Clavicornes | 380 | Hydrocanthares | 72 | Sternoxes | 73 | Trimeres | 78 | Carabidæ | 30 |
| Malacodermes | 130 | Malacodermes | 445 | Longicornes | 190 | Sternoxes | 327 | Longicornes | 58 | Longicornes | 58 | Sternoxes | 72 | Helopiens | 15 |
| Brachelytres | 129 | Clavicornes | 192 | Vesicants | 132 | Longicornes | 303 | Sternoxes | 55 | Vesicants | 50 | Malacodermes | 51 | Malacoder. | 10 |
| Clavicornes | 117 | Malasomes | 185 | Malacodermes | 103 | Melasomes | 290 | Lamellicornes | 53 | Clavicornes | 31 | Clavicornes | 32 | Melasomes | 10 |
| Trachelides | 88 | Helopiens | 180 | Clavicornes | 75 | Malacodermes | 270 | Xylophages | 47 | Trimeres | 22 | Taxicornes | 30 | Trachelides | 7 |
| Xylophages | 85 | Trimeres | 147 | Xylophages | 56 | Xylophages | 215 | Trimeres | 38 | Malacodermes | 20 | Tenebrionites | 23 | Hydrocantha | 6 |
| Hydrocanthares | 76 | Xylophages | 140 | Trachelides | 50 | Trimeres | 192 | Malacodermes | 37 | Helopiens | 18 | Helopiens | 18 | | |
| Teredyles | 61 | Tenebrionites | 132 | Trimeres | 45 | Hydrocanthares | 156 | Melasomes | 27 | Hydrocanthares | 17 | Trachelides | 13 | Clavicornes | 6 |
| Trimeres | 47 | Taxicornes | 128 | Helopiens | 43 | Teredyles | 127 | Taxicornes | 25 | Teredyles | 14 | Hydrocanthares | 10 | Tenebrioni. | 6 |
| Tenebrionites | 40 | Brachelytres | 115 | Hydrocanthares | 38 | Trachelides | 114 | Vesicants | 22 | Palpicornes | 11 | Brachelytres | 10 | Stenelytres | 5 |
| Vesicants | 35 | Vesicants | 88 | Taxicornes | 34 | Vesicants | 105 | Palpicornes | 20 | Tenebrionites | 10 | Melasomes | 7 | Trimeres | 5 |
| Taxicornes | 30 | Trachelides | 72 | Tenebrionites | 30 | Taxicornes | 88 | Trachelides | 16 | Brachelytres | 9 | Teredyles | 6 | Teredyles | 4 |
| Palpicornes | 27 | Hydrocanthares | 65 | Teredyles | 27 | Helopiens | 80 | Teredyles | 11 | Taxicornes | 8 | Xylophages | 5 | Brachelyt. | 3 |
| Helopiens | 25 | Teredyles | 60 | Brachelytres | 22 | Palpicornes | 78 | Stenelytres | 6 | Trachelides | 8 | Vesicants | 5 | Palpicornes | 3 |
| Stenelytres, | 12 | Palpicornes | 51 | Stenelytres | 13 | Pselaphidæ | 63 | Tenebrionites | 5 | Xylophages | 7 | Palpicornes | 2 | Taxicornes | 3 |
| Melasomes | 7 | Stenelytres | 20 | Palpicornes | 12 | Stenelytres | 57 | Helopiens | 3 | Stenelytres | 5 | Stenelytres | 2 | Vesicants | 2 |
| Pselaphidæ | 4 | Pselaphidæ | 5 | Pselaphidæ | 0 | Tenebrionites | 52 | Pselaphidæ | 0 | Pselaphidæ | 0 | Pselaphidæ | 0 | Xylophages | 0 |
| | 2531 | | 8387 | | 3229 | | 6813 | | 1137 | | 1104 | | 1100 | Pselaphidæ | 0 |
| | | | | | | | | | | | | | | | 375 |



From Lacordaire 'On the geographical distribution of Insects' Edin.New Phil.J. 27 p 349.

common, and Europe and India, Curculionidae. In this way numerical methods illuminated problems of distribution which perhaps would never have been otherwise noticed.

Turning from entomology to marine invertebrates, both Edward Forbes and the American naturalist James Dana presented their results in equally telling tables. In 1843 Forbes produced a series of "conchological tables" to illustrate his Report to the British Association for the Advancement of Science on the mollusca and radiata of the Aegean seas[51]. In these he attempted to show the distribution of marine shells according to depth in one or more of eight zones into which he had divided the sea bed, and the percentage of, say, the "Celtic forms" in each assemblage. James Dana did much the same thing with his succinct tables of polyp distribution: in 1847 he composed the one illustrated here to signify how limited in their extension coral polyps were[52]. Each column represented the number of species peculiar to the region named at the head, so that looking at, for instance, columns 2 and 4 it will be seen that of fifty species found in the Pacific ocean only four are also found in the East Indies or Indian ocean.

To cite more examples would, I think, be superfluous. Enough has been said to convey the marked predilection for numerical distribution studies during the period 1835 to 1845. This trend was to continue unabated through to the work of Joseph Hooker and to culminate in Alphonse Decandolle's remarkable Géographie Botanique Raisonnée of 1855, and with which I opened this chapter. Statistics were freely and readily used to point out the most striking features of animal and plant associations, and often posed more questions than they could possibly answer. By 1852 "the statistics of vegetation" were such an essential part of botanical education that textbooks like John Hutton Balfour's Class Book of Botany defined them for tyros, and declaimed that it was a subject which "involves the consideration of the number of known vegetable species in the world"[53].

* * *

With this pattern of assimilation in mind it is a suitable moment to focus attention on corresponding movements in geological affairs. Up until now I have avoided any correlation of botanical arithmetic with statistical practices of a similar nature in the earth sciences because there seemed to be a case for the thorough examination of the range and

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Figure 10

blish as a fact, that a large part of zoophytes are confined to a small longitudinal range. This will be seen from the following table, exhibiting, in a general manner, as far as known, their geographical distribution. Each column gives the number *peculiar* to the region specified at top:—

| | East Indies, Indian Ocean, or Red Sea. | Pacific Ocean. | West Indies. | Pacific, and the East Indies or Indian Ocean. | Extra-tropical. | Doubtful. | Total. |
|---|---|---|---|---|---|---|---|
| TRIBE ASTRÆACEA. | | | | | | | |
| *Fam.* Astræidæ, . . | 37 | 50 | 29 | 4 | 3 | 16 | 139 |
| Fungidæ, . . | 14 | 29 | 6 | 6 | 0 | 10 | 65 |
| TRIBE CARYOPHILLACEA. | | | | | | | |
| *Fam.* Caryophyllidæ, | 13 | 7 | 9 | 2 | 13 | 5 | 49 |
| Gemmiporidæ, . | 4 | 5 | 1 | 2 | 0 | 2 | 14 |
| TRIBE MADREPORACEA. | | | | | | | |
| *Fam.* Madreporidæ, . | 30 | 42 | 4 | 8 | 1 | 7 | 92 |
| Favositidæ,* . | 14 | 15. | 5 | 3 | 0 | 4 | 41 |
| Poritidæ† . . | 5 | 14 | 6 | 2 | 0 | 1 | 28 |
| | 117 | 162 | 60 | 27 | 17 | 45 | 428 |

James Dana 'On the geographical distribution of Zoophytes' p 44.

versatility of this technique within one closely circumscribed area such as botany.

For, as I have previously hinted, few scholars attribute any high degree of sophistication to biogeographical investigations of the pre-Darwinian era and so, if nothing else, I believe these preceding pages to be necessary to sketch out a history which repairs such a view.

Furthermore, the introduction of arithmetical procedures evidently helped naturalists to organise not only their facts, but also their thoughts as well. Thus in the development of distributional science the increasing use of numbers and tables acts as a sort of indicator to the state of organisation of this new study. It is the appreciation of botanical arithmetic which encapsulates the difference between surveys like those by Willdenow and Link, and those by Decandolle the younger and Joseph Hooker.

Yet were there any sentiments more specific than mere appreciation? Did naturalists apart from Hooker and Decandolle find any purpose in so ordering their data, and was there a conceptual side to "Tabellenstatistik"? I must here assert that for botanists and zoologists the answer is No. No-one was asking why statistical methods were used, and it appears to be the case that the results of calculations such as Watson's on the relative proportions of plant families at different heights did not lead him - or anyone else - on to the construction of explanations for that phenomena. In other words, these statistical tables did not give botanists any new ideas, despite the fact that they presented them with stimulating and unexpected problems which demanded explanation. Watson, for instance, over some thirty years or so did not add any new concepts to his first outline of the distribution of montane species although he refined and supplemented this work to an extensive degree in the Cybele Britannica. He was concerned only with providing the details of distribution with a hitherto unprecedented (in his opinion) precision, and expressed his aims thus:

> "A first call on the phyto-geographer is to ascertain where the plants are now distributed, and in what manner and degree such present distribution accords with present geographical conditions . . . The ingenious minds that take their delight in inventing causal hypotheses to account for these present seeming relations, through reference to supposed conditions of the past, will work more easily, and perhaps with more truthful results, if supplied with properly arranged data truly illustrating the present. They may then possibly find out, instead of feign, phyto-geographical and phyto-geological histories."[54]

Here, with a passing swipe at Edward Forbes' "phyto-geological" theories, Watson epitomised the aims of his colleagues. The figures and the data themselves were the object of distributional researches, for the time being at least.

This attitude might account for the fact that historians have noticed that several biological 'statisticians' of this period appear to have produced more figures than they could satisfactorily handle. For instance, Martin Rudwick has described the failure of the Tertiary paleontologist Heinrich Bronn to synthesise his data in the light of any clear theory to test[55]. I suggest that we should look at this, and parallel cases, the other way around and postulate instead that Bronn was here working within the confines of a discipline where "Tabellenstatistik" was a proper end in itself. It could well be added that we can see a similar preoccupation with numbers for numbers' sake in the modern subject of ecology - itself the intellectual descendent of distributional studies of the nineteenth century - where recent critics have asserted that the science has little theoretical content and only an arithmetical technique which has 'run wild'. Perhaps this is a characteristic especially typical of biogeography?

But more than this, I think that the aims of biogeographical arithmetic were limited because the method was derived not from 'real' Laplacian statistics, nor even from mathematical science, but from social surveys and the Staatenkunde tradition of descriptive censuses. As I outlined in a former chapter, the botanical arithmetic of the nineteenth century was very closely connected with its origins in the earlier sort of statistics - the comparative description of states - and its structure and purpose were governed by this heritage. Just like human population surveys, biogeographical information had to be processed in some elementary way and then published before it could be genuinely useful. But once the populace had been numbered there was not much else that could be done: the final figures were the whole point of the exercise. Similarly, I contend that the whole point of botanical statistics was to count up the species and to work out a set of conventional ratios. The results of both activities in the human and non-human spheres may indeed reveal something unknown or unexpected (as the total population of Britain was revealed in 1801) or vindicate a particular hypothesis (whether the population was increasing or decreasing) but, at root, these were studies where the figures were the object of the task.

I think therefore I have described what it meant to be a student of distribution in the earlier half of the nineteenth century, that is, I have given some idea of the sort of inquiry he would pursue and the ways in which he used his facts. And, in particular, in the foregoing pages I have stressed that numerical analysis for botanists and zoologists alike was a system whereby the relative proportions of one group with another could be established. This appeared to be an end in itself, and thus, for these years, the ultimate statement about the arrangement of animals and plants that could be made.

It is not entirely unexpected to find that geologists were also well aware of statistical procedures, and that they discovered that fossils were amenable to the same sort of interpretative machinery. Fossilised organisms were, after all, only animals and plants of former times, and what applied to them in the present day must surely be valid for those of the past. And so, though botanical arithmetic may have been primarily concerned with spatial distribution and with presently existing bodies, and geological arithmetic, by contrast, with the arrangement and relations of a succession of historical beings, the two studies were very much the same. As the one interested itself in proportions through topographical space, so the other concerned itself with these over time. Hence Decandolle father and son compared the present floras of England and France in the same manner as Lyell, Murchison or Forbes compared the fossil assemblages of the geological table in Europe.

However, despite these evident similarities, 'geological statistics' differed in one particular way from those employed in purely topographical exercises. It is this one attribute which facilitates a separation or distinction between the employment of statistics in either discipline. Geologists - and this is my point - used the comparative evaluation of fossil populations to promote and vindicate theories relating to the history of the earth since its formation, and the history of the life supported by that earth through time. In other words, geologists had theories to prove and they found statistics to provide useful biological ammunition. Indeed theirs was such an active and often polemical espousal of figures that the statistical method became almost exclusively associated with the single issue of the history of the earth. So in the final pages of this chapter I want to examine this question in a little more detail, and discuss in turn the computations which are found in geological literature and the (two) theories of the earth they were designed to support.

Geological statistics

Following Buffon's example in the first instance, many geologists of the early years of the nineteenth century adhered very firmly to the idea that the earth was undergoing some sort of unilinear and non-reversible change. Men such as Cuvier, Buckland, Alexandre and Adolphe Brongniart, Adam Sedgwick and R.I. Murchison believed that the earth had experienced since its formation a progressive and directional change through a succession of geological epochs, and that its living beings too had progressed from simple to more complex bodies in accordance with world conditions. Indeed, as Peter Bowler has recently pointed out, geologists such as these accepted the notion that the apparent 'advancement' of life through the ages was directly caused by the changes in environment, not through any sort of Lamarckian ideas of biological change matching altered external conditions, but through an assumption that each set of beings was created already suited for its surroundings. As the earth developed from an original primal state (usually postulated as one that was very hot, and in later years as one with a high concentration of either atmospheric water, or carbon dioxide) to the conditions of the geologically recent period, so life itself changed to accommodate a series of different factors[56]. In other words, they believed that the state of development of living beings, as represented by the fossil record, was a mere effect or biological offshoot of the geological structure and events of any one age which could be independently induced from the nature of its deposits.

Hence with Bowler we may call this particular understanding of life "directionalist", since the progress of complexity as evidenced by the fossil record depended, at root, on the successive changes of the crust of the earth and not on any internal or integral property of 'improvement'[57].

Thus in the work of Cuvier historians can see a clear interdependence between every geological epoch and the beings it supported[58]. For Cuvier all forms of life had to be extinguished every so often to permit a new creation of forms suitable for the next epoch. Each being was so perfectly adapted to its own peculiar conditions that it simply could not live at any other time. William Buckland took these last ideas further to develop a sympathetic understanding of the totality of any one environment with all its diverse elements of hyenas, cave bears and antelopes in his justly famous reconstructions of Pliocene faunas[59]. And

Adolphe Brongniart and Alphonse Decandolle mapped out the changes in the vegetation of Europe from the earliest geological times to the present day to demonstrate how fossil floras also depended on geologically determined conditions through a succession of eras.

Adolphe Brongniart was the son of Cuvier's co-worker Alexandre Brongniart who, with Cuvier, had identified and described the strata and fossils of the Paris basin. This masterpiece of stratigraphical analysis did much to confirm a 'directionalist' point of view for it presented striking evidence for the differentiation of formations on the basis of their fossil content which varied according to the conditions under which the deposits were laid down[60]. Adolphe Brongniart followed in his father's footsteps, but turned to the study of fossil vegetables and became the virtual founder of paleobotany through the publication of his Histoire des végétaux fossiles (1828).

Since plants were more dependent on their surroundings than animals, Adolphe Brongniart felt that his work should be of great value for determining the course of the earth's development, and so, by surveying the plant fossils of the various geological periods (and in the process identifying and naming more specimens than had ever been done before), he tried to reconstruct the physical history of the globe. His work was an "Exposition chronologique des périodes de végétation et des flores diverses qui se sont succédé a la surface de la terre"[61]. Each one of these successive floras was different from the next, and was characterised by readily identifiable features. These features were not, for Brongniart, exclusively qualitative and dependent on the extinction of particular species at each 'change-over', but included also differences of a quantitative nature. Hence he noted the relative proportions of the major plant groups such as mosses, ferns, cycads or flowering plants for each epoch, and saw that these shifted gradually towards the proportions held by these groups in the present day.

Therefore he reasoned, "sous le point de vue de la proportion numérique des espèces des différentes classes"[62], that, for example, in the Carboniferous period ferns and their allies constituted five-sixths of the then known flora, whereas today they made up barely one-thirtieth. And, "au contraire", he continued:

> "les plantes dicotylédones, qui composent plus des trois cinquiemes des végétaux vivans, n'existoient probablement pas à cette époque."[63]

The preponderance of ferns and the lack of any dicotyledonous (i.e. advanced) plants in the Carboniferous signalled two things to Brongniart. Firstly the conditions must have been eminently suitable for ferns (d'une température plus élévee et d'un climat plus humide), and secondly they were patently not suitable for advanced forms of plant life like the dicotyledons.

After successive calculations of this sort - obviously the same as the botanical arithmetic which has hitherto been discussed - Brongniart concluded that the history of plants could be divided into four great "règnes", each one of which was characterised by different proportions of the main classes. Each one was more 'perfect' than the last in that it more nearly approached the ratios of today and was marked by the introduction of more and more advanced forms of life. Brongniart concluded his Prodrome to the Histoire des végétaux fossiles with a small table illustrating these results and where he listed the numbers of species in different classes through his four periods and today. He proudly remarked that these facts seemed to confirm that life was indeed created in a series of units according to the "révolutions de notre globe"[64].

Alphonse Decandolle followed Brongniart's interpretation of the fossil record almost to the letter. He added to and revised the lists of species and, at one time, divided the fossil flora into fourteen epochs instead of four, but he recognised "with M. Brongniart . . . that the vegetable kingdom appears to have been gradually becoming more perfect"[65]. He too gave tables of the relative proportions of various epochs and, like Brongniart, wrote of the physical constitution of the earth which would allow these relationships and no others. Thus in an 1834 article On the History of Fossil Vegetables he gave an amended version of Brongniart's table to show the number of species from certain botanical classes through the four geological eras which the latter had discerned. And again like Brongniart, Decandolle used this table and further figures of the same nature to support the thesis that the history of plant life on this globe was one of sequential floras each of which differed considerably from the last, and which together made up a series ever more closely approximating to the ratios of today's vegetation.

Since so much of this interpretation depended on the assumption that the predominance of ferns and their allies during the earlier

epochs indicated a hot and humid climate (and thereby 'proving' that the earth had at one time been much hotter than nowadays), the younger Decandolle devoted much of his attention to close examination of the Carboniferous fossils, and, in particular, the plants which made up coal deposits. Here instead of calculating the relative proportions of classes through time, he proceeded just as if he had a problem flora of the present day and worked out the ratio of classes to each other and to one hundred species. His intention was to discover through these proportions exactly what the climatic conditions must have been when coal plants were flourishing in an unfossilised state. From the table (Figure 12.) given here he concluded that the group he called Aetheogameae (arborescent ferns, lycopodia and equisetales) dominated to the extent that they formed upwards of five-sixths of the vegetation, whereas other cryptogamia are "wholly wanting at this epoch". More significantly he reasoned that none of these groups were marine plants, or, "at all events they are very rare, as none have hitherto been discovered"[66], which gave him useful ammunition for the current debate over a possible marine or brackish origin for coal[67].

Both these naturalists therefore used botanical arithmetic to substantiate not only theories which were far removed from 'normal' topographical studies, but also theories which were something of an issue within geological circles. They employed statistics to vindicate a particular geological theory about the earth. Further than this, it appears that yet other naturalists, notably John Lindley, author of a rival Fossil flora of Great Britain (1831), who totally rejected the doctrine of a directed improvement of vegetation, still used statistics to refute such theories. In an anonymous article contributed to the Edinburgh New Philosophical Journal, Lindley criticised the attribution of whole epochs on a few "miserable plant fossils" and effectively demonstrated how given proportions could equally well be the result of irregular fossilisation[68].

This last view was most effectively presented in the work of Charles Lyell. Lyell also did not believe in a progressive or directed history of life, and was indeed the most famous opponent of this popular view through the two decades following the publication of the Principles of Geology (1830-33). He too took statistical computations to justify his opposition to 'directionality' and, more expressly, to support his own theory of the self-balancing steady-state earth. In fact the use of

following page 156

Figure 11

The following Table presents a summary of the vegetation of the four periods. It is formed from the tables of the prodromus of M. Brongniart, at the same time placing the genera Stigmaria and Sigillaria amongst the dicotyledons, according to the opinion of Lindley; and by again reducing the six classes recognised by Brongniart to the four which we admit.*

| | 1st period. | 2d period. | 3d period. | 4th period. |
|---|---|---|---|---|
| CRYPTOGAMEÆ. | | | | |
| Amphigameæ, | 4 | 7 | 3 | 13 |
| Etheogameæ, | 176 | 8 | 31 | 9 |
| PHANEROGAMEÆ. | | | | |
| Monocotyledons, | 18 | 5 | 3 | 25 |
| Dicotyledons, | 52 | 5 | 35 | 117 |
| Total, | 250 | 25 | 72 | 164 |
| So, there is of Cryptogameæ, | 180 | 15 | 34 | 22 |
| And of Phanerogameæ, | 70 | 10 | 38 | 142 |
| Again giving totals of | 250 | 25 | 72 | 164 |

Alphonse Decandolle 'On fossil vegetables' p 97, in which he expanded on Brongniart's scheme for the history of plant life.

Figure 12

| | | | | Proportion in the 100 Species. |
|---|---|---|---|---|
| CRYPTOGAMEÆ. | | | | |
| *Amphigameæ.* | | | 0 | 0 |
| *Etheogameæ,* | Equisetaceæ, | 14 | | |
| | Filices, | 89 | 170 | 66 |
| | Marsileaceæ, | 7 | | |
| | Lycopodiaceæ, | 60 | | |
| PHANEROGAMEÆ. | | | | |
| *Monocotyledons,* | Palms, | 3 | | |
| | Canes | 1 | 18 | 7 |
| | Indeterminate, | 14 | | |
| *Dicotyledons,* | Sigillaria, | 41 | 49 | 19 |
| | Stigmaria, | 8 | | |
| Species whose class is doubtful, | | | 21 | 8 |
| | | Total, | 258 | 100 |

* Fossil Flora. Sciences et Arts, Juillet, 1834.
† Bibl. Univer. 1833. T. iii. (liv.) p. 259.

Alphonse Decandolle 'On fossil vegetables' p 87, in which he tabulated the flora of coal deposits.

statistical geology was fundamental to Lyell's understanding of, in particular, the Tertiary period, and may well have had more far-reaching influences than even that: as Martin Rudwick has recently pointed out Lyell possessed a grandiose "dream of a statistical palaeontology"[69].

This "dream" focussed on the role arithmetic could play in a geological science which was based on Lyell's steady-state earth. In this doctrine Lyell claimed that all geological activity was balanced to render the earth dynamic and its parts perpetually undergoing motion and counter-motion. Part of this thesis required Lyell to assert that since the earth had therefore experienced no directional change through geological time, so then the fossil record had presented no evidence for progressive improvement. Wearing his own heavily tinted spectacles Lyell claimed that the successive faunas and floras did not 'improve' with time[70], and emphatically denied that the fossil record presented a sequence of introductions of still better and better forms of life. Hence he was forced to assume that even the most developed animals such as mammals had existed (but not been fossilised) in the remotest periods.

In this setting Lyell's statistics of the fauna of the Tertiary era appear to be designed to draw attention away from any intrinsic quality of "highness" or complexity. His history of the earth was to be devoid of successive stages or 'steps' in perfection. He used only molluscs which, by virtue of their ready fossilisation and abundance in these deposits, were more or less ideal for a comparative study of formations[71]. Instead of assessing the relative ages of fossiliferous beds by the 'quality' of the product so to speak, and thereby complying to a doctrine of directional change, Lyell resorted to the simple expedient of an impartial enumeration of species which did, and did not, still exist in the present day. This was an easily determined property which gave rise to a purely arithmetical relationship between strata. He wrote in the Principles of the three sub-periods into which he proposed dividing the Tertiary:

> "The fossil remains which characterise each of the three successive periods above alluded to, approximate more nearly to the assemblage of species now existing, in proportion as their origin is less remote from our own era, or, in other words, the recent species are always more numerous, and the extinct more rare, in proportion to the low antiquity of the formation."[72]

Thus like his botanical contemporaries Lyell saw that a change in relative proportions from an original 'state of grace' through periods which approximated more and more closely to the present day, could

indicate a change in geological conditions. But unlike Brongniart and Decandolle he reasoned that he should not take the proportions which major classes held to each other and so provide an index of perfection approaching the present day, but should instead take a simple numerical estimate of species.

Under Lyell's scheme the distinctions between fossil formations would be merely a "necessary consequence of the existing laws of sedimentary deposition, accompanied by the gradual birth and death of species". Though most geologists stressed the strikingly characteristic forms of any one period, and statistical geology had been employed to demonstrate their peculiarities, here, Lyell was attempting to link each period with the next by an insensible transition from one to the other and so he emphasised how the ratio of extinct to extant species only gradually shifted in favour of the latter through the Tertiary. It was a scale which linked the earlier times of the period to those of the present, and hence a ratio could be obtained at any point along that scale. Only vagaries of deposition and fossilisation made the geological structures appear to fall into natural groups of strata. Central to this thesis was Lyell's proposal that species were created one by one, in a piecemeal fashion, and equally, that they were extinguished in a piecemeal way. And although his statistical evaluation of the Tertiary implied that Lyell believed in a constant 'life-span' for each form between its creation and extinction (so that the 'turn-over' was suitably regular for a systematic survey of different points on the scale) he did in fact go to considerable lengths to show that this was the case only because of irregular extinction and fossilisation.

Lyell's molluscan proportions were given in great detail in a catalogue at the end of the Principles compiled by the eminent conchologist Deshayes who had himself written of the proportions of living to extinct species in different formations[73]. Ratios such as these - more notably between classes - were not, as I have shown, really anything new within geology. What was new with Lyell's use of arithmetic was the theory behind it, which was in his case the driving force for so arranging the Tertiary fauna. Unfortunately for Lyell it proved to be very easy to accept his statistical technique without any corresponding acknowledgement of the steady-state earth. Within a few years the comparison of extinct to extant was a commonplace of geological practice, though men such as Charlesworth in 1836 found much to criticise in the method, and other naturalists such as Phillippi were fond of stating how complicated

the calculations really were[74]. Lyell's statistics were a very real and immediately fêted contribution to the study of geology. Yet it ought to be remembered that they were delicately constructed to defy on all fronts the directionalist point of view and to further his own steady-state earth.

## Conclusions

With these words it becomes obvious that both sides of the coin which represented specifically geological arithmetic - that is, the relatively widespread practice of calculation of ratios between classes, and Lyell's more idiosyncratic derivation of relationships between the past and the present - were strongly impressed with the theories which they were to support. Some were 'progressive' whilst there was one which was 'anti-progressive'. Yet both sides employed statistics to support their own points of view. It is this 'theory-laden' usage which is so foreign to the manner in which botanists and zoologists tabulated figures. Statistics in this latter, topographical, study were there to serve a rather different purpose,in that they were first introduced to make the discipline into a 'science' and later functioned as perhaps the only tool by which naturalists could organise their materials. Geologists, on the other hand, had no such need either to make their study properly scientific (for by the 1830's the science of geology was well established after a self-conscious start), or to find new methods by which to order their facts and thoughts. Here, statistics were surely more an accessory technique, seen to be useful for one or two particular topics such as the history of life on earth, or the relative age of Tertiary deposits, and consequently used in a precisely determined and regulated framework dictated by the beliefs of geologists themselves. And though botanists were no less laden with hypotheses about the distribution of life over the globe than geologists were with interpretations of the earth, botanists tended to treat arithmetical surveys as an end in themselves, so that once the proportions of major groups had been worked out there was nothing else - arithmetically speaking - that could be done with the data. Only a few naturalists like Decandolle and Hooker turned to reflection and explanation of the ratios they had thus determined.

So in other words, topographical statistics and tables set out the problems with which future naturalists were to concern themselves and

stated the issues which would have to be answered in any truly scientific study of distribution. On the other hand, geological statistics were brought into a fully developed science where they were utilised as a simple piece of interpretative machinery to confer validity on one or two specialised ideas. Natural historians used statistics to state the facts of distribution, whilst geologists took them to substantiate theories.

# Part III

# Chapter 5: Charles Darwin's Botanical Arithmetic, 1836-1857

## Introduction

It is a curious feature of Darwinian studies that no historian has as yet noticed that Darwin spent a great deal of his very valuable time on seemingly endless statistical calculations of the relationships between species, genera and varieties. His incessant ill-health and the detailed survey of nature which his theory was intended to present both conspired to make Darwin a busy man who could not sacrifice his working hours to anything other than the most essential subjects, and this point alone might warn scholars that there can be few items of Darwiniana which can, in truth, be deemed immaterial or even tangential to the construction of natural selection theory. But despite continued interest in Darwin's accumulated papers and the story they tell of his progress from a "very ordinary boy" to one of the great theorists of the modern era, historians have remained ignorant of an important - and certainly voluminous - part of this process. It is just such an ignorance that I now wish to correct.

Nonetheless the greater part of the blame (if blame there must be) for this unusual state of affairs must surely be heaped on the head of Darwin himself. For in the Origin of Species, the one volume where the full scale of Darwin's theory should be found, Darwin barely referred to his botanical statistics or the long sequence of calculations which he had undertaken from 1854 to 1858. Thus the evidence which he had derived from these activities was severely compressed and simplified into a few meagre paragraphs.[1] The Origin gave only six pages of statistical data which contributed to Darwin's discussion of the existence of "Variation under Nature", whereas, by an almost farcical contrast, he had devoted over seventy closely written folios with further supplementary notes and tables to the same theme in an earlier draft.[2]

From seventy pages to six was unquestionably an unsatisfactory truncation of his argument, and Darwin took pains to remedy the omission. He apologised to the readers of the Origin explaining that this was only an abstract of his larger work on natural selection, and that here was not the place to go into the mass of detail which had provided the meat of his "big book". On statistics in particular he acknowledged that "to treat this subject at all properly, a catalogue of dry facts should be given,"[3] and promised that these would appear in the future work.

Nevertheless, he continued, the data had been examined by independently minded scholars (as indeed it had) who conceded that the results were fairly drawn: "Dr. Hooker permits me to add" wrote Darwin, "that after having carefully read my manuscript, and examined the tables, he thinks that the following statements are fairly well established".[4]

In other words, Darwin here claimed that space and consideration for his audience would not allow him to go into the detail required of this topic, but in order to make these facts seem less like phantoms of his imagination, he cited the acquiescence of a noted scientist like Hooker. Evidently feeling that a semi-popular book was not a suitable vehicle for any sort of exposé of botanical arithmetic, he yet struggled for some sort of compromise which could adequately convey its very real significance, and, in the event, only managed a rather feeble attempt at providing an endorsement by saying that Hooker found it important too.

Anyway, it is certainly the case that the Origin contained only a very brief version of Darwin's considerable investigation into the numerical relations between varieties and larger groups. There is not much there for historians to go on. For this reason writers who rely on the Origin alone for an understanding of Darwin's ideas and theories before and around the year 1859 are missing a notable part of his thesis.[5]

So much is now made obvious from a quick glance at the recently published transcript of Darwin's long manuscript on Natural Selection,[6] composed from 1856 to 1858 and only halted when he was interrupted by the receipt of A.R. Wallace's letter from Ternate. This manuscript was the intended "big Species book" and the source from which Darwin abstracted the Origin for publication at the end of 1859. Scholars cannot now fail to note that there was a lot more to Darwin's thought than that which was made public in 1859, and that the arrangement of information in the long manuscript can add considerably to our comprehension of the final version.[7] And more than this, the sheer bulk of the contents of Natural Selection provides the facts which Darwin thought most telling for the substantiation of evolution before a scientific audience: here are all his closely reasoned and intricate examples of selection at work, his expectations and qualifications, and his references to contemporary authors. And here also is a long section entirely given over to botanical arithmetic.

Yet there is still more to Darwin's statistics of variation and varieties than even this intended chapter for Natural Selection.

Interpretations of this area of his thought can be additionally enlarged by considering the extant notes and jottings, the long sequence of calculations themselves, and, in particular, by referring to Darwin's correspondence with his botanical mentor, Joseph Hooker. Thus fully 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 and computation, the notes written to himself and to the schoolmaster at Downe village who helped tabulate Floras,[8] and to his anxious correspondence with Hooker about the philosophical considerations which could - and did - affect the inquiry.[9]

Darwin's papers and his interchange with Hooker can, in fact, be pieced together to provide a marvellously detailed picture of the man and the mind at work. Hooker supervised Darwin's efforts in this arithmetical direction and acted as an efficient sounding-board for most of his ideas and suggestions. In many instances Hooker was such a Jeremiah that Darwin had to abandon or revise some of his more circumstantial results. And Hooker also supplied Darwin with advice on how to proceed with the calculations and ready information on Floras or catalogues of plants which might be suitable for the venture. Indeed Hooker, well situated with his own private library and the collection belonging to Kew Gardens, was able to forward many of the books which his friend used for this exercise, and some of these remain still copiously marked by Darwin's pencil. In all, there are sufficient materials for a very thorough examination of this neglected issue of Darwiniana, and a hitherto unexpected opportunity to look closely at how Darwin actually worked.

For these reasons I shall give some attention in the present chapter to the initial stimuli which made Darwin take up numerical analyses of species and genera with their varieties, and what it was which led him to believe that such techniques could further natural selection theory. This will take me from his first contact with the study of proportions to his comprehension of a rather more complex and useful technique and so on to a <u>coup d'oeil</u> of his work from around 1855 to the middle of 1857.

And for reasons which will later become apparent I shall devote a subsequent chapter to Darwin's systematic investigation of large genera, dating from mid 1857 through to the eventual composition of the seventy-page tract on statistics for the "big Species book".

The whole will, I hope, provide a fair guide to what Darwin was doing and the motives which activated him at any one stage through these years. Such a chronological account is, I believe, necessary to understand the gradual transformation in Darwin's application of botanical arithmetic to the 'species question', and the accumulation of numerical evidence which progressively gave him more and more moral support as he went through the testing business of writing up his theory for some as yet undetermined publication.

However I am not invoking a purely Whiggish or 'tunnel' history of the development of Darwin's usage of this single technique, or even of the evolution of the particular concepts which he derived from statistical data. Instead I want to provide an illustration of how the content of his system - "descent with modification" - could, at any one time, influence the status and hence the application of an idea or procedure like arithmetic. So, by taking Darwin at certain moments in time I shall claim that his different modes of employing statistical reasoning were an effect of a shift in the construction of a well rounded evolution theory. As his ideas about nature matured and encompassed new fields of evidence, so his application of a useful method changed accordingly, and, in the event, provided much valuable information that itself contributed to this gentle transmutation. In particular, my contention will be that Darwin had not yet achieved the 'full' theory of evolution that was to appear in the Origin until the 'late' date of the middle of 1857, and that only with the discovery of a "principle of divergence" as Darwin called it did the complete system emerge. In some ways this "principle" was dependent on then current numerical investigations into large genera, and it is with this point that my second statistical chapter is occupied.

But here I wish to turn to Darwin's usage of botanical arithmetic during the years of 1844 or so, through to July 1857. For the sake of clarity I have divided my discussion into two, the first part being focussed on his concepts as put down in the Essay of 1844, and the second on the path of investigation which he took after completing an extended study of the living and fossil cirripedes, that is, after 1854. The differences which I see between these points well exemplify my argument that Darwin's concepts were themselves undergoing an evolution.

## I. The question of range, 1836 - 1844

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. In my last chapter I gave some idea of the richness and versatility of statistical natural history, and how men such as Decandolle the elder and Humboldt had established the practical value of numerical analysis of this kind. At Cambridge J.S. Henslow would not have neglected to teach his eager pupil the rudiments of this method, and, if this were not enough, Darwin's youthful enthusiasm for Humboldt's works would have ensured that he was made aware of the way in which naturalists were discussing distributional data.[10] Moreover, even if he rejected his early teaching as old-fashioned Darwin soon came up against Charles Lyell's careful and exciting use of the statistical method as a guide to the age of fossiliferous beds laid down in the Tertiary period, and, as a faithful Lyellian disciple, he espoused and even used the "proportional method" himself.[11]

Thus in the notes on specimens collected by Darwin during the Beagle peregrinations through South America, and in his short papers on the geology of that country given after his return in 1836, Darwin showed a good grasp of the statistical techniques required of him. Despite the fact that such calculations on the comparative numbers of species, genera and families depended on a precise identification of forms and sufficient leisure to work through previous collections for information about the whole flora or fauna, Darwin managed without these resources on board the Beagle to give a general view of the relations of the populations which he encountered. Though statistics was essentially an armchair exercise which had to be done after the collection and arrangement of specimens , Darwin nonetheless remarked on the ratios of animals and plants without recourse to arithmetical statements. He expressed interest in the range of species and the numbers of individuals encountered, and a lively concern for the extent and type of habitat in which his subjects lived. Hence writing on the bird life of South America he noted whether specimens were "common" or "exceedingly abundant" as was the Icterus, a type of starling found round Maldonado, or "shy, scarce, solitary" like the two Lanius species collected at Port Desire.[12] And Darwin plainly distinguished between these statements and further comments on the avian habits which might contribute to such a general impression, adding notes on whether birds like the Partridge "went generally in pairs" or "in small flocks of five or six", or like the Condor were to be considered "to a certain degree a gregarious bird".[12] These were all descriptions of the proportions which individuals held to each other and to the whole association in which they lived.

Again, in the four or five papers which he read to the Geological Society in the twelve months after disembarcation from the Beagle in late 1836, Darwin tacitly used the Lyellian percentage method for a reconstruction of the geological events which had overtaken South America. His first paper, Observations of proofs of recent elevation on the coast of Chili (1837),[14] undertook to provide evidence for a geologically very recent upheaval of the coast of Chile by considering the "numerous level and horizontal beds of shells" at a height of some 60 to 230 feet above sea level. Darwin asserted that these elevated shell beds contained various kinds of molluscs but that they were "in similar proportional numbers to those on the beach."[15] Turning to the parallel "roads" of Coquimbo he went further and demonstrated that these terraces possessed fossil remains in the ratio of extinct to extant species that Lyell had ascribed to the more recent deposits of the Tertiary.

He used more or less the same reasoning for his suggestion that the wide and "almost boundless plains" of the Pampas had, at one time, been a shallow estuarine region where the La Plata river had discharged the carcases of now extinct quadrupeds.[16] Using the evidence derived from the comparative "recentness" of the shells associated with these fossil bones, Darwin claimed that elevation of the sea bed had taken place "within a very recent epoch" indeed.

And in other papers on geology Darwin tried to use the Lyellian percentage technique wherever appropriate. Even the work on hillside terraces of Glen Roy during 1838, which was "one of the most difficult and instructive tasks I was ever employed on",[17] provided a small niche for Lyell's statistics in that Darwin expected to find differential ratios between marine fossils on each shelf or terrace above sea level. He never did, and nor did he even find evidence of any organic remains, but nonetheless he had made a note to remind himself to search for this phenomena before the field excursion.[18]

So Darwin seemed to have a good grasp of what was proper to a distributional survey be it through time or space; he simply didn't put things down in a numerical way.

But it is the species notebooks which really demonstrate that Darwin could produce the arithmetic when required. From July 1837 to July 1839 Darwin compiled the four notebooks now known as the "B", "C", "D", and "E" notebooks on the "Transmutation of Species", and a further book "full of Metaphysics on Morals and Speculations on Expression" - the "M" notebook.[19] Here he was concerned to understand how populations change and exhibit different proportions between their constituent parts in both a topographical sense and through geological time. In the "B" notebook he remarked

on points made by the paleontologist Brongniart about changes in the relations of major plant groups over time, and by von Buch that the flora of islands were "very poor", and drew the conclusion that insular floras present "species few in proportion to difficulty of transport".[20] To substantiate this suggestion Darwin then cited Humboldt's statistics that the Canary Islands, St. Helena and - oddly enough - Lapland all had small numbers of species in comparison with the number of genera in these areas: I:I.46, I:I.15, and I:2.3 respectively.[21] All these areas he supposed to be far removed from the source of new (or rather different) kinds of organisms, or, in the case of arctic "Laponia", to be an example which "agrees with late production of these regions and consequently not many [species] get multiplied".[22]

In the "B" notebook Darwin even developed a passing fancy for a purely mathematical account of the way in which populations at two moments in time were differently constructed. In cryptic vein he wrote:

> "...if we take a man from any large family of 12 brothers and sisters in a state which does not increase, it will be chances against any one of them having progeny living ten thousand years hence; because at present day many are relatives, so that by tracing back the fathers would be reduced to small percentage: - therefore the chances are excessively great against any two of the 12 having progeny after that distant period."[23]

Imagining a "fine family" of twelve brothers and sisters, and assuming that the number of individuals was always the same and not increasing or decreasing, Darwin pointed out that chance extermination and extinction could definitely account for the differences between the family at time $t_1$ and later at time $t_2$. It seems that Darwin was impressed by the fact that people living in a circumscribed area like England at the time of his writing, tended to be closely related to each other rather than distantly so, and that there were thus more near relations such as sisters, brothers and first cousins now existing than there were third cousins once removed. It seems an oddly parochial point for Darwin to have made though, of course, something which might be quite evident to any early Victorian born into and blessed with a large family. What he meant to express was an idea that the closeness of all living populations meant that the majority of possible distant relatives had been eliminated at the source, so to speak. If I took Darwin himself as an example of this reasoning, the case would be that Darwin had many immediate relatives such as his two sisters and elder brother, and a plethora of uncles and aunts from the distaff side of the family, but he had very few (if any) cousins emanating from the brother and sister of his great-grandfather Robert Darwin of Elston.

As it was he had only three cousins (including William Darwin Fox) who arose from this Robert Darwin himself. So his great grandfather had contributed more to the present generation than either his great great aunt or uncle.

By applying this notion to the animal world Darwin therefore suggested that out of twelve members of a family only one or perhaps two would carry representatives in subsequent generations; all the rest must have been rendered extinct because they had not reproduced their like. And by applying this metaphor of a "fine family" directly to the process of speciation he remarked that of thirteen past forms, "Twelve of the contemporaries must have left no offspring at all, so as to keep number of species constant".[24]

This idea formed the context within which Darwin drew a justly famous diagram of a branching line from point (1) to 25 "twigs", of which 13 had serifs. Usually taken as a drawing of speciation from one ancestral form, or alternatively as a visual representation of divergence between groups,[25] this diagram seems to be more concerned with the way any one species was capable of filling up all the places that a fixed nature could provide, so that if one form could produce all thirteen kinds of the next generation there had somewhere to be an elimination of the first generation's other twelve.

I introduce this hypothesis - not one that Darwin retained for very long - as a confirmation that he was at this stage quite capable of perfectly ordinary mathematics. Too many historians have taken Darwin at his own word that he was particularly inept at any sort of calculation.[26] So we find that these years of 1837 to 1839 show Darwin as able and willing to use either normal statistics or the more specialised technique of botanical arithmetic to further his views, however temporary they may then have been.

With the development of the theory of evolution which was set out as a sketch in 1842 and then as an Essay of 1844,[27] it seems to have been the case that Darwin found no useful role for arithmetical work of this nature and it was consequently dropped.

For Darwin's eyes had focussed on islands as the source of species and the mechanism by which newly modified forms could be kept isolated without the deleterious effects of belonging to a large and interbreeding population. He envisaged an island or archipelago already peopled with aboriginal species or occasional accidental migrants, in which variations would appear as the "constitutions of some of the insular species" were upset by geological changes such as elevation or subsidence. Natural

Figure 13

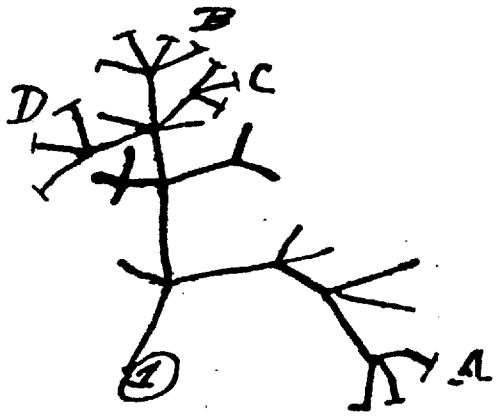



Fig. 3

From Darwin's "B" notebook on the transmutation of species.

selection would go to work and new species would be produced. Prolonged isolation on the one islet, coupled with the fact that such regions had few species to fill all the available "diversified districts", would lead to Darwin's contention that "an island would be a far more fertile source, as far as we can judge, of new specific forms than a continent".[28] The Galapagos archipelago, frequently cited, was clearly uppermost in his mind, and were islands where he assumed an original importation of South American finches had varied at random, only to be acted upon by natural selection to progressively adapt their habits and structures to the 'gaps' left in nature.

Moreover Darwin extended this theory to account for the origin of species all over the world and through all geological time. For, as he said, "almost every geologist will admit that in most cases [a continent] will have first existed as separate islands which gradually increased in size:

> "and therefore all that which has been said concerning the probable changes of the forms tenanting a small archipelago is applicable to a continent in its early state."[29]

In the Essay of 1844 Darwin went to considerable lengths to make his thesis quite clear. Following Lyellian dynamics he postulated an earth that was constantly shifting the local relations between land and sea, although maintaining these at an overall ratio which was constant. Islands were thus being formed and destroyed ad infinitum, and so species were appearing, dispersing and being rendered extinct in accordance with the new conditions that were thus made available by geological activity. After explaining how subsidence would make any continent appear as a series of large or small islands, he wrote:

> "As soon however as the continent became divided into many isolated portions or islands, preventing free immigration from one part to another, the effect of climatic and other changes on the species would be greater. But now let the broken continent, forming isolated islands, begin to rise and new stations thus to be formed... we shall have equally favourable conditions for the modification of old forms, that is the formation of new races or species. Let the islands become reunited into a continent; and then the new and old forms would all spread, as far as barriers, the means of transportal, and the preoccupation of the land by other species, would permit."[30]

If this process was repeated enough times - and indeed Darwin made the point that elevation and subsidence did go on and on in just such a fashion - then all the multifarious relations between the beings of separate countries could be explained. "The oftener these oscillations of level had taken place...the greater the number of species which would tend to be formed" asserted Darwin, and he went on to say that now

"we can obviously see why the number of species in two districts... should be in some cases as widely different as in New Zealand and the Cape of Good Hope",[31] or why areas like northern America and western Europe should possess many forms in common.

The crux of this elegant system was that organisms (either past or present) were supposed by Darwin to be capable of spreading virtually world-wide, given enough time and no ecological or physical barriers to stand in their way. Like Lyell he claimed that a priori, one family should be able to range over the entire earth "given enough time",[32] an idea which was to achieve its most sophisticated expression in the work of Edward Forbes but which had been floating around (as, for example, in the writings of de Verneuil[33], the French palaeontologist who accompanied Murchison in his search for the Silurian system in Russia) since the early years of the century. Forbes had written of the correlation between the "age" of a species and its "area", assuming that as species increased by reproduction from one point (the doctrine of "single centres of creation") so the range of that species would enlarge according to the number of individuals at any one time. Inverting the proposition, he followed de Verneuil and Lyell and reasoned that existing or fossil species which presented a very wide geographical range had therefore persisted for a long time and were thus "older" than contemporaries.[34]

Now Darwin, though he was rather anxious about this last aspect[35] of what was soon fêted as a general law of nature,[36] conformed to the basic concept that species spread, come what may, and that it was only barriers which stopped them.[37] Hence his theory of speciation as outlined above postulated that new and old forms would disperse from their island source only "as far as barriers, the means of transportal, and the preoccupation of the land by other species, would permit". He had a vision of a dynamic flux of living organisms being created, dispersing and dying, which superimposed itself on the equally dynamic movements of the earth to render the history of nature one interrelated whole.[38] Back in geological time, for example, America was part of the same biologico-geological region as Europe so the species which were then created subsequently experienced many eras of geological change and accordingly show (in the present) some similarities and some differences depending on the dispersive capacity of the original forms. Darwin wrote that:

> "We can see how the better chance of diffusion, from several of the species of any genus having wide ranges in their own countries, explains the presence of other species of the same genus in other countries; and on the other hand, of species of restricted powers

of ranging, forming genera with restricted ranges."[34]

In other words, assuming that an aboriginal rodent possessed the capability to range widely over the bits of land which now form North America and Europe, the present day faunas of both these countries should include species descended from that one kind but not now exactly alike. Such an interpretation would explain the vole, for instance. The longer ago that this first dispersal took place, then the less close the relationship in taxonomic terms. Conversely, a very restricted animal like the English robin, though it may have been created at the same time, was unable to spread and thus remains in the present day endemic to Europe.

This notion of dispersal is important for the historian because, were it possible to typify in one word Darwin's immediate and recurrent concern through the years 1844 to 1846 and beyond, it could be done by the term "range". His theory of evolution demanded that dispersion from insular regions be a common occurrence, dependent on the elevation of intermediary land to facilitate the spread of new and old forms, but further encouraged by inbuilt powers of the organisms themselves. Thus he occupied much of his time after the composition of the 1844 Essay with a delightful series of experiments designed to show that plants and animals could travel much further from their "centres of distribution" than was usually believed. He kept the seeds of many different sorts of plants, some of which were specially chosen because they lived on islands, in salt water tanks in the cellars at Down to prove that seeds could live for a certain number of days whilst being whirled about the oceans of the globe. He laboriously counted all the seedlings which grew up from a sample of mud collected from a duck's foot, or watched fish at the Zoological Gardens ingest worms and such like. His preoccupation with the subject was such that even on holiday on the Isle of Wight he was struck by seeing thistle-down being wafted out to sea.

Range was a property which required his attention. On the theory worked out in the Essay Darwin ought to have been able to state that every flora and fauna which presently showed affinities of some sort or another were once part of the same geologico-biological system. To circumvent having to suggest enormous continents, for example, in mid-Atlantic, Darwin tended to lay more and more emphasis on the sheer dispersive powers available. The marsupials of South America were clearly related to those of Australia, yet he was not sure that he could invoke enough geological changes of level to provide a land mass of sufficient extent to bridge the gap. Far better to rely on the ancestral opossum's power

of shifting for itself.

And it was with these thoughts uppermost in his mind that Darwin was exposed, in the fullest sense, to botanical statistics of the most philosophical kind. He began corresponding with Joseph Hooker, seven years his junior and recently returned from his own circumnavigation of the globe (with the Ross magnetic observatory expedition to the southern hemisphere), through the good offices of J.S. Henslow who had forwarded Darwin's Galapagean plant specimens to Hooker.[40] The young botanist was thrilled both with the collection as such and with the introduction to this "delightfully frank and cordial" naturalist who had so impressed him with the "variety of acquirements , mental and physical", which he possessed.[41] Their acquaintance soon ripened into a firm friendship which was to last until Darwin's death in 1882, and which never floundered despite their several irreconcilable differences. Darwin wondered if he and Hooker would ever be "public combatants" over the species question but reflected genially that "anyhow, I congratulate myself in a most unfair advantage of you, viz. in having extracted more facts and views from you than from any one other person".[42] And this was, I believe, a perfectly just assessment of the relationship between the two men: Darwin fired off question after question in his letters, and Hooker delighted in providing a medley of botanical detail for his sometimes unstructured answers. Though modern opinions may differ about the relatively trivial point, 'did they actually <u>like</u> each other?', I think that it is undeniably the case that Darwin and Hooker were definitely well matched, and that their correspondence has few peers in the question and answer genre.

Making the most then of his new acquaintance, Darwin put forward a series of tentative questions about the ranges of species in his first letters to Hooker.[43] On February 23, 1844 he wrote to ask if a point that he was introducing to the <u>Essay</u> had any botanical counterparts: he had been led to expect that the property of ranging widely could be an inheritable character and so wondered if there was any relation between the range of species and their genus. He explained:

> "In discussion with Mr. Gould, I found that in most of the genera of birds which range over the whole or greater part of the world, the individual species have wider ranges, thus the Owl is mundane, and many of the species have very wide ranges...Is it not so with Cryptogamic plants?"[44]

That is, did the species of a well dispersed genus have wide ranges themselves? Discounting the evident fact that any genus might have a far-flung kingdom through the mere juxtaposition of lots and lots of small

ranges, Darwin wanted to know if all the species of a group such as the voles or mice for example had wide ranges each in their country. And here it is important to remember that Darwin was looking for an inheritable facility to spread far and wide: a genus to Darwin was a collection of species all descended from the same aboriginal form, and so if this first one had the power to spread itself out over the immediate lands then available, so, on Darwin's theory its descendants ought to be able to do exactly the same. Taken in purely taxonomic terms of course the question seems rather odd. If one finds a certain species to be very wide ranging then one would expect its genus to be mundane, simply because this particular species belongs to that particular genus. Indeed how does the naturalist otherwise decide whether a genus is mundane or not save by estimating the range of its participant species?

But Darwin was arguing from the higher taxon to the lower as if a genus had an existence of its own apart from its several parts. In evolutionary theory this is in fact the case, for the 'genus' as such was once a single species before it started to diversify into further new forms. To Darwin, all willow trees had come from one aboriginal species of willow, so that he was quite entitled to speak of a genus of owls or cryptogams as if they were real bodies with properties of their own which could be "passed on" to successive generations of species.

Nevertheless Hooker was puzzled by this question. He did not know of Darwin's theory of descent and could hardly be expected to infer that a question superficially about ranges was really one concerning the continuity of generic characters. Although Darwin had in an earlier letter admitted that "species are not (it is like confessing a murder) immutable"[45] he had not gone so far as to explain the rudiments of his system, and he did not deem it useful for Hooker to receive the full account with this isolated query. Yet ignorance of Darwin's theory would not, I think, materially alter the way in which Hooker could have understood the inquiry, since it was almost de rigeur for early 19th century naturalists to attempt to answer questions or discuss phenomena without a prior hypothesis. Whether this valiant effort really succeeded or not is here beside the point; Hooker would not have felt that his unfamiliarity with any of Darwin's motives therefore disqualified him from posing a suitable reply. So under the norms of the science of the day, we should not be surprised that Darwin felt no need to express his proper aims to Hooker, or that Hooker did not require them in framing his answer.

But what is interesting about Hooker's response to Darwin's question on the ranges of genera and species, is that he misunderstood the actual query to include something which was patently not there. He introduced an extra quality to the problem which necessitated an answer couched in such different terms that Darwin was to find it virtually unusable. Hooker thus imposed his own interpretation and answered this his own reformulated question, not Darwin's. The subtle change is a valuable indication of the state of Hooker's mind and botanical affairs in general, and, as I shall point out later, a change which provided information that Darwin did not want, and which he consequently ignored in favour of his original inquiry.

Darwin had wanted to know if the species in a widely spread genus were themselves wide ranging; Hooker thought that he meant "whether the species of large mundane genera have so wide a range as those of small genera?"[46]

He thus introduced the idea of size into what was a statement relating entirely to range, and spoke of large mundane genera and small. The size of a genus was merely the number of species it contained, and the adjective 'large' might apply to say, eight species or more in any one genus, whereas 'small' would cover those groups which possessed only four or fewer. Both Darwin and Hooker were quite familiar with quantitative remarks of this kind, and indeed the size of genera was an interesting topic to each of them, but here, as Darwin reminded Hooker, it was entirely extraneous.

Why then did Hooker introduce it? It is unlikely that one so precise and conscientious would simply have misread the appropriate sentence or two. His undoubted admiration for Darwin would have ensured that he fully examined missives from Down, and a desire to do the 'right thing' in Darwin's eyes would have secured that questions were carefully considered and answered. It is far more likely that to Hooker range and size were more or less synonymous, and that wide ranging genera were thus assumed to have many species, and restricted ones few.

One particular facet of Hooker's thought substantiates this suggestion; his understanding of representative species hinged on the belief that since these forms were geographically mutually exclusive, then the more representative species there were in a genus so the wider the topographical area that genus must cover. A multiplicity of representatives of the azalea, for example, stretching out over Japan, eastern Asia and north America, and completing the global circuit with one species in the Mediterranean, would to Hooker be a phenomenon that firmly linked an

extensive range with a large number of species. Conversely, he might suppose the Kerguelen's Land cabbage to belong to a small genus of only one species, because it also enjoyed the very restricted habitat of one isolated Antarctic island.

In the event, Hooker replied to Darwin and stated the question in what he took to be its "simplest and boldest form". He asked "what species are common to the Old and New World?", and established a list of mundane forms that were suitable for analysis. Then he continued and asserted that "the following is then my proposition (theorem rather) -":

> "What proportion of the Ranunculaceae of the Old World including Greenland and N.W. America (W. of the Rocky mnts) is common to the American continent? - and secondly do the larger proportion of these plants belong to large genera or small?"[47]

Hooker rarely generalised if he could work with actual examples, but here this admirable characteristic seemed to take over. Darwin must have been surprised and gratified that Hooker found the point so complex and amenable to statistical analysis: Hooker proposed working out a proper proportional assessment of the ranges of both small and large genera, and proceded to do so in great detail. Evidently for Hooker the question was one that could only be answered by arithmetical means. He wanted to give an exact answer to this "philosophical naturalist" and to him exactitude was synonymous with arithmetic.

He listed the suitable mundane species that occured in the New and Old Worlds; he reduced this to a short list by eliminating all those which would disturb the equanimity of the results (as for example very large polymorphic genera like Rubus or Salix which could hardly be subdivided into species at all)[48]; and he compared the species to their genus to see whether it was the large or small genera that bore most of these widely ranging species. Thus he tabulated:

> "In Ranunculus proper the common are to the whole as 1:10.6.
> In as many species as Ranunculaceae contains together forming 10 small genera it is 1:56.3"[49]

That is, the small genera contained only one species in 56 or so that appeared in both the New and Old Worlds, whereas the proportion was closer to one in ten for the largest genus of that family, the namesake genus of Ranunculus. In the six or seven further examples that Hooker worked out, each one exhibited the same sort of proportional relationship (though none to the accentuated degree of Ranunculaceae) and he seemed to be justified in his conclusion that "Species of small genera have narrower ranges than the species of large mundane genera".[50]

Now some ten years later Darwin was himself to be deeply involved with exactly this kind of botanical analysis: not only were his techniques to be the same by virtue of the employment of the proportion of species to genus and the comparison of 'small' genera with 'large', but also his future aims were identical to these expressed by Hooker. Darwin later believed that range as an organic property was inextricably related to the number of species that any genus might contain for, as I shall in time explain, he decided that a supposedly successful genus ought to present many offspring (i.e. species) which demonstrated their advantages by ranging widely over a diversity of habitats. Therefore he would take it upon himself to calculate the numerical relationship between mundane and restricted genera and their species, in just the same way as Hooker had here, in 1844, attempted to do.

Yet Darwin's response to this remarkable adumbration offered by Hooker was at the time negative. He politely acknowledged the evident trouble which Hooker had undergone to work out these figures, but reminded him that "that was not the precise point which I was curious to ascertain". He coolly reiterated the original question and stressed that "it has no necessary relation to size of genus".[51]

Again Hooker misunderstood. From an unfortunate juxtaposition of query and illustration Darwin made it possible for Hooker to infer that the real problem lay in representative species and their ranges. He conscientiously tried to answer this new question which as he saw it attempted to establish links between the extent of each representative's range with the wide or narrow distribution of its parent genus. The genus of Linum (flax) he thought a fair example of such links, since each species was itself quite widely spread and the genus ranged all over the world. And in reverse, "the contrary may however be as often true" for in the Cacti "we have a parallel case to monkeys, their geographical range is small being confined to warm and chiefly to tropical S. America and Mexico. I have somewhere read that the species are remarkably peculiar to certain narrow limits".[52] In conclusion however he qualified these generalisations and said that though it was true to say that "species of local genera are themselves local", and that "in mundane genera many of the species have mundane ranges", it was not the case with representative species:

> "It is not proved in Botany that 'in mundane genera the representative species have a wide range each in its own country' to any remarkable extent".[53]

Hooker's remarks in both this letter and the one which preceded it

failed to interest Darwin. Apart from marking the original mistake in Hooker's calculations with a cross he did not even pencil in the customary aide-mémoires which usually litter his correspondence. Nor did he refer to the point in his subsequent communciations. He had not achieved anything like the sort of answer that he then wanted and so, simply, the question was dropped.

It seems clear then that Darwin was at this time only prepared to consider dispersal and range divorced from all extraneous connotations of size of genus. He was preoccupied with this faculty as an inheritable character which would explain why some species ranged more widely than others, and could disperse themselves over large areas as his theory of evolution required. Darwin was not then to be swayed from this important point by Hooker's admittedly pertinent and (with hindsight) provocative correlation of range with other features such as size, or his interesting red-herring of representative species and their ranges.

Furthermore, Darwin's next question to Hooker mirrored this entrenched position. Taking up one of the botanist's passing remarks on the elusive nature of a "typical" or "type" species, Darwin asked in the closing weeks of March 1844, did perhaps "typical genera have wide ranges?" and grumbled:

> "There is, however, so much vague in the meaning of 'typical forms' and no little ambiguity in the mere assertion 'wide ranges'... that I feel very doubtful, though some considerations tempt me to believe in this remark."[54]

Hooker had thus more or less 'fed' Darwin the idea of "typical forms" and Darwin responded by airing his absorption with dispersal: perhaps these forms at least would show some tangible correlation?

This then was the manner in which Darwin dealt with Hooker's communications on the subject of range. Turning now, for a moment, away from what we might call Darwin's public face, it appears to be the case that even in his own private jottings Darwin was endlessly circling around this same question. The idea of "typical forms" for instance found a home in the many-roomed mansion of his mind and on the very same day that he wrote to Hooker asking if types had wide ranges, he also composed a little note to himself reiterating and expanding on the point. In a characteristically elliptical passage he mused on the fact that "typical genera" were more successful than non-typical forms because they had more species and a wider range, and so, surely, ought not non-typical beings to be "less adapted" and consequently "less widely distributed?"

He wrote:

> "March 31/44... Swainson's statement (and Waterhouse independently to me) that typical genera...have wide ranges (converse may still hold good?) is important; for the genera which are not typical are only rendered so by the extinction of allied genera and that implies they are less adapted than other groups of genera to the world - and therefore one might expect they would be less widely distributed..."[55]

Despite the fact that this was not even a properly constructed sentence Darwin's message does get across: the thrust was that as he supposed typical genera to have wide ranges (a point more or less made by William Swainson[56] and George Waterhouse, the latter being one of Darwin's oldest entomological friends and a naturalist whose opinion he trusted), so he expected non-typical forms should have small ones. Concentrating on these forms alone Darwin reasoned with the full force of selection theory behind him that they might be atypical because all their relatives had been extinguished. A genus which had once been part of a series now stood in isolated peculiarity because its congeners had been eliminated. To Darwin this process indicated some inherent weakness or disadvantage common to the original series - in short a mal-adaptation to the surrounding conditions - which would be shared more or less equally with the one surviving genus. So non-typical genera would thus be "less adapted than other groups of genera" and consequently "less widely distributed".

There are difficulties here for the historian of evolution, and these will be returned to at greater length in the second half of the present chapter. In particular it is hard to see why Darwin thought the one surviving genus was "less adapted" when by the sheer fact of its survival it should be considered successful. But problems such as this will reappear in due time. Here, however, the most significant point to be drawn from Darwin's note is that yet again range was the determining factor and the quality which linked the two halves of the proposition together: 'typicality' with 'great extent', and its converse with 'restricted areas', were the hooks on which Darwin hung this suggestion about extinction.

So if we pause now to look back at the items which excited Darwin's greatest interest in and around the early months of 1844, it can be seen that these were - as could be expected - entirely related to substantiating and expanding the theory of descent which was put forward in the 1844 Essay. He sought confirmatory facts from the botanical kingdom through a recent introduction to Joseph Hooker and, imagining himself thwarted in that attempt, he barely considered the information which Hooker was in fact handing him on a plate. That is, Hooker presented all the aspects of one

of Darwin's subsequent theories to a Darwin who was not ready to accept them. In a determined vein Darwin even picked out the 'wrong' thing from Hooker's nicely reasoned remarks on typical genera and thus thought only about the way in which membership of such a group might alter the distribution patterns of species. The question of range was, without doubt, his guiding light at this time. It regulated the manner in which Darwin saw and understood the news that was offered to him. Moreover it is plain that Darwin was at this time well versed in the intricacies of separating populations into associations with different relations to each other, or, that is, with the general aims behind the technique known as botanical arithmetic. Historians cannot therefore assume that there was any unfamiliarity or novelty attached to Hooker's proposals and examples, which led to their rejection on Darwin's part.

To tie up the bouquet I can only repeat that here Darwin's concept of a dynamic and fluctuating earth-cum-life system naturally directed his thought to the issue of range, and that it was this question which dominated his initial response to other topics and, especially, the ideas put forward by Hooker in a statistical manner.

## II. The question of aberrance and the size of genera. 1854 - 1857.

For reasons best known to himself (and which have unfortunately escaped historians) Darwin took up the anatomical study of barnacles in the autumn of 1846, and subsequently devoted eight years of his supposedly precarious life to an extensive and thoroughly comprehensive account of living and fossil cirripedes. In his own view Darwin thought that perhaps so much time on the one study was regrettable ("I doubt whether the work was worth the consumption of so much time.") but this as in so many of Darwin's autobiographical statements must be taken with a pinch of historical salt.[57] He had, for instance, throughout this study used natural selection theory and the concept of descent with modification in order to understand the taxonomic relationships of form with form and the anatomical similarities of organs. He had shown to his own satisfaction that selection could explain complex morphological features like the separation of the sexes from an assumed primitive hermaphrodite into suitably characterised male and female barnacles. The pride of Darwin's work was his recognition of the peculiar sexual system of cirripedes where, when males are present, they are generally small and live attached to the females. "I proved" he remembered "the existence in certain genera of minute males complemental to and parasitic on the hermaphrodites"[58] which was a state of affairs intermediate between complete hermaphroditism and

bisexuality. It was his species theory that led him on to this discovery:

> "I never should have made this out, had not my species theory convinced me, that an hermaphrodite species must pass into a bisexual species by insensibly small stages; and here we have it, for the male organs in the hermaphrodite are beginning to fail and independent males ready formed."[59]

And in purely morphological terms Darwin managed to describe and make clear the arrangement of the external plates or valves which cover the sides of a typical barnacle, by referring to a decidedly developmental or evolutionary theory of their origins and subsequent modification. "The arrangement of external plates" with their various shapes, sizes and methods of interlocking with each other were considered in the light of ancestral species which might have diversified into a range of structures such as these.[60] Though the final printed results of these investigations did not explicitly introduce any such theory of development, Darwin made no bones that this was what had, at all times, motivated him and helped him.

Yet there was more to the barnacle work than "two thick volumes, describing all the known living species, and two thin quartos on the extinct species". From this extended and minute examination of one order he derived immense personal support for the existence of evolutionary processes in nature. For the first time he saw that natural selection could really work.

The cirripede study gave Darwin confidence and a vital confirmation that his ideas were not counter to nature. Contrary to T.H. Huxley's assessment of this period of Darwin's life,[61] historians now see barnacles not as a useful but merely technical introduction to the taxonomic minutiae of species, but instead as a significant 'testing of the theory'. In the words of Michael Ghiselin, who has made a special plea for a fundamental role for this study, Darwin used barnacles as a comprehensive trial for evolution and his work exhibited "Hypotheses about past evolutionary events...conjoined with equally hypothetical laws of nature, and both were tested by observations on the organisms themselves."[62] In other words, for better or for worse Darwin had proved to himself that evolution could be demonstrated in nature.

I think this view is well founded, and it explains why after finishing barnacles in September 1854 Darwin moved on to the topics that he did. He turned to extensive experimental work on the longevity of seeds, the disparity in weight and length of wing bones in the domesticated and wild pigeon, and the symmetry of flowers amongst other things, all of which I suggest were studies directed to finding further proof of

variation and selection in the living world. Moreover, after the barnacles were completed, on September 9th Darwin recorded in his Journal that he "Began sorting notes for Species theory" evidently in preparation for some as yet undefined period of writing up, and he turned straight away to a close examination of the grandest and largest topic that his theory would have to explain. This was the overall 'scheme' or apparent 'plan' of nature that philosophical naturalists had recognised and attempted to explain since Aristotle's time, which demanded a system that encompassed all the taxonomic, geographical, structural and metaphysical relations that were then held to exist between organisms. Descent with modification was 'invented' to cope with these questions and Darwin was now absolutely sure that it did so in a better way than any other scheme.[63] So he set to, to work his way through the current philosophies of nature and classifications with the intention of explaining every point within his own system.

Certainly Darwin had tried to account for the grades of complexity and the relations of life ever since he first wrote on the "transmutation of species" in 1837. But the cirripede exercise gave him a slightly different perspective on things in 1854. In line with other naturalists of the time Darwin turned to study the properties of 'type' genera and species and their counterparts, aberrant forms.[64] The existence and taxonomic position of these groups were then perhaps the most pressing issues of theoretical natural history, and men such as Richard Owen, Edward Forbes and before them W.S. MacLeay, William Swainson, and George Robert Gray in England, Henri Milne-Edwards and the two Geoffroy St. Hilaires in Paris, and Louis Agassiz, had had something to say about it.[65] Mostly influenced by the philosophy of the German romantic school, and most notably that of Schelling, these men postulated a variety of ideal types or archetypes from which organisms diverged in one or more respects to make up the panoply of nature. The type could be taken at any taxonomic level and could for example explain why vertebrates all had four limbs, or, on a more precise scale, the relations of the mouthparts of insects.

Except for the Swainson-Macleay philosophy of nature based on circles and the mystic number five, I do not think that aberrance - the converse of typicality - actually received much attention. Swainson, it will be remembered, thought that each circle of five groups contained one that was more typical and one that was more aberrant than the rest, and that in some respects all the other members of that circle had qualities which made them 'represent' these two ends of the scale. Swainson thought that

aberrance was the over-development of only one property common to the circle whereas typicality was a "union of many properties", and was led to an enthusiastic exposé of what aberrance was all about, where he concluded a purple passage with the words "They are, in short, symbolically the type of evil."[66]

Now to Darwin this short of remark was anathema. Ever since his youth he had striven to refute such metaphysical views with his own materialistic creation of natural selection. How then could he abstract the notion of type and aberrance from Platonic models or circles? This I believe was the motive which drew him into a consideration of the numerical method as a purely impartial way of characterising groups. By using the statistical method alone he could remove any sort of qualitative statement about the degree of peculiarity which a group presented.[67]

Darwin proposed that aberrance was merely a question of size: an aberrant genus was one that belonged to a family which had very few genera, and an aberrant species was one that belonged to a genus with equally few species to its name.

He wrote to Hooker in December that year (only three months into his investigation) to tell him that he suspected it was "extinction which has made the genus anomalous",[68] and thus reiterated his comments of nearly ten years before that "the genera which are not typical are only rendered so by the extinction of allied genera". But this time it was not range that excited his interest but the size of the genus. He returned to a view in which a supposedly complete set of genera was subjected to selective extinction so that just one or two now remained in existence. These groups, reasoned Darwin, must therefore stand alone with no near relatives in the taxonomic table and so appear to be aberrant when compared to more plentiful associations. For what is aberrance if it is not the absence of features in common with others?

Here of course Darwin had closed his eyes to the possibility of any inherent oddness in an atypical form, and as we shall see he soon became trapped in his own logic. But for the moment he thought it a marvellous idea. He had found with the anatomy of barnacles that most structures could be explained by supposing an aboriginal series of forms from which all the existing species were descended. Those which were now systematically isolated from the rest could be drawn into the scheme if he postulated the one-time presence of intermediary links that had later been rendered extinct. Applying this argument to aberrant forms of life Darwin suggested that a genus which now stood in isolated singularity only did so because its congeners had been eliminated.

Such a theory is, in fact, sound unless like Darwin one tries to apply the extinguishing process as an inherited disability which could be passed on from species to species and thus appear as a character which linked both the genus and its offspring species.[69] He explained to Hooker:

> "Now, my point (which I think is a slightly new point of view) is, if it is extinction which has made the genus anomalous, as a general rule the same causes of extinction would allow the existence of only a few species in such genera..."[70]

Darwin thus expected to find some proof of his supposed inherited disability in the actual numbers of species which aberrant genera managed to present in the face of imminent extinction. He therefore described to Hooker how he anticipated that a simple calculation of the number of species in each atypical genus should add up to an average which was considerably less than the usual figures, and asked Hooker to get his botanical associate George Bentham to compile a list of aberrant plant genera so that he do exactly this.[71] Bentham and Hooker obliged, and Darwin calculated the point, but not without inquiring whether Bentham had excluded any aberrant forms simply on the basis that they had many species which would then skew the results.[72]

This interest soon turned into a "hobby-horse" in his own words. He pestered his entomological friend Waterhouse for a similar list of aberrant insect groups, and persuaded him to mark all those odd genera which were catalogued in Schoenherr's Genera et species Curculionidum or weevils.[73] He told Hooker all about it:

> "In Schoenherr's Catalogue of Curculionidae, the 6,717 species are on an average 10.17 to a genus. Waterhouse...has given me a list of 62 aberrant genera, and these have on an average 7.6 species; and if one single genus be removed (and which I cannot yet believe ought to be considered aberrant) then the 61 aberrant genera would have only 4.91 species on average."[74]

In other words, using ordinary natural history statistics Darwin found that the usual number of species contained in any one genus of weevils was about ten. Working through Waterhouse's list of atypical forms the average was calculated as only 7.6, or with some judicious elimination only five species per genus. The aberrant genera had less than half the number of species possessed by normal genera.

Darwin was quite naturally excited by this apparent proof of his entirely materialistic understanding of aberrance, and went on to further calculations based on John Lindley's Vegetable Kingdom (third ed.1853) with cross-checks on Bentham's and Waterhouse's material, being particularly

interested to see whether the results still came out if he removed monotypic genera from the sample.[75]

It is as well at this point to note that Darwin never really got much further with this particular line of enquiry, although he did eventually put a small piece in the Origin about it.[76] The problems of so equating peculiarity with fewness of species were too manifest for Darwin to continue, when he knew that aberrant genera often did have quite substantial numbers of species, or that adding more would not make them any less odd. Grumbling about the platypus - everyone's favourite example of oddity - he remarked to Hooker that:

> "Ornithorhynchus and Echidna would not be less aberrant if each had a dozen species (I do not say 100, because we have no such cases in the animal kingdom) instead of one."[77]

The penguin, again a peculiar form, was blessed with at least eight genera and a richness of species which could not in any sense betoken a maladapted bird which had extinction staring it in the face. And further, if Darwin took this hypotheses one step lower on the taxonomic scale and applied the extinction of relatives to the number of individuals contained in any species, what then was he to do about the earwig? As early as 1844 he had noted that "The earwig is case of a genus in an abnormal group being very abundant in individuals and species".[78] This could hardly count as an unsuccessful form when it appeared to live everywhere in the world, and in large numbers at that.

Thus there did seem to be a case for the existence of some intrinsic quality of aberrance which was not reducible to a simple lack of numbers. And here we find Darwin using the gift which was to get him (with some style) out of many a tricky situation or intellectual cul-de-sac: with great aplomb he reversed the proposition and started looking for the opposite effect in "typical" genera. He mused: "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."[79]

Inverting the hypothesis Darwin therefore asked if typical forms were those which were more numerous in species than other genera, and which thus showed (by possessing many species) that they had not experienced a sustained extermination campaign such as aberrant genera had struggled through. In fact, had not "creation" - Darwin's euphemism for speciation - been taking place instead?[80]

This proposition I hold to be a crucial intellectual link between Darwin's notions about aberrance and the ideas which were soon to dominate

his thoughts. By a simple (if ingenious) reversal of the tenet which had been providing the stimulus for an arithmetical survey of odd and diminished genera, he arrived at a state where he could assert that no extinction (or rather more accurately,"creation") ought to be evident in their opposite numbers - typical genera. Virtually simultaneously he also suggested that if typical forms were as large as he supposed because creation and speciation were taking place, then was it not to the larger genera per se that attention should now be directed? He had reasoned from aberrance and small genera to typicality and large ones, and from the action of extinction to its opposite the existence of "creation", and so reached a point where he could effortlessly connect large genera with the facility for speciation.

So at the very beginning of 1855, only a few weeks after he had expressed his interest in aberrance to Hooker, Darwin devised a further arithmetical calculation to see whether "creation" had fallen on the larger groups in nature. By counting the numbers of what he called "closely allied species" and working out if there were more of these pairs or triplets in either large or small genera, Darwin thought that he would achieve results which demonstrated his point. "Closely-allied species" were, to him, forms which had only just (so to speak) reached the grade of species and were thus two or more very strongly marked varieties which still retained the closest of relationships with each other. But the crucial point about them was that extinction had not here worked its evil way and eliminated one or other of these close relatives. The existence of sets of closely allied species was therefore something akin to Darwin's supposed aboriginal series of forms from which modern barnacle species had descended, or from which only one aberrant genus had managed to survive.

Darwin consequently asked the American botanist Asa Gray, whom he had recently met at Kew Gardens during a visit to Hooker, and the irascible Hewett Cotrell Watson author of the magnificent compendium of British plants The London Catalogue, to mark for him their catalogues so that he could identify these closely-allied forms.[81] In the event both Gray and Watson were a bit confused as to what Darwin really wanted them to do and, for example, we find that Watson carefully marked all the varieties which other botanists at some time or another had ranked as species, and the species which occasionally featured as mere varieties in different works. This was nearly, but not quite, what Darwin was after, and by August of this year he was immersed in a philosophical correspondence with Watson over the nature of relationships between species and their sub-groups.[82] Asa Gray however provided splendid annotations for his Manual of the

Botany of the northern United States[83] although it appears to have been a rather complicated business. Darwin reminded himself that "Red cross means one or more species in genus having varieties. The red circles mean "close species" of A. Gray's MS, two circles mean 2, when many [,] number [of species] within circle".[84]

With this information to hand Darwin calculated the average number of species per genus for those genera which presented varieties of any description. This figure he took as a 'standard' against which he could compare the average species to genus ratio of genera which included the "closely-allied" forms of the problem. Thus Darwin computed:

> "Now Asa Gray has marked for me 115 genera with 733 close species... now these 115 genera have on average 115 [into] 733 = 6.37 [species to 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".[85]

His figures seemed to indicate that genera with closely allied forms amongst their species had more species per genus (6.37) than those genera which simply presented varieties (4.67). Darwin spent an enjoyable six months or so through the middle and end of 1855 working out many further variations on this theme all of which gratifyingly came out 'right' for his hypothesis that there should be species of a very intimate and near relationship in the larger genera. He extended the idea of closely allied forms to look also at the number of varieties in large or small groups, and, under H.C. Watson's unwitting encouragement, at varieties which had once been considered to be true species and were therefore of somewhat indeterminate rank.[86]

Now the most notable point about this unexpected side to Darwin's researches, is that he continued using the simple statistical method which he had employed for the calculation of the size of aberrant genera. He added up the number of species which belonged to the genera which contained his variable, and divided the one into the other to get an average number of species per genus for that sample. This was compared with a similar average derived from the genera which did not possess the variable, or, on some occasions with the whole flora or catalogue. It should be noted also that Darwin here indulged in a remarkably unsophisticated way of looking at the final figures, and this, I believe, was entirely due to the transfer of the technique from the study of aberrance to that of "creation" in an unchanged format. With aberrant genera he had obtained figures which represented a ratio of species to unity, that is they contained, say, four species per genus on average. This result was then compared with an average drawn from the whole sample which might work out as,

say, ten species per genus. Now Darwin took these as absolute results and talked of the difference between four and ten instead of between 4:1 and 10:1. This was certainly immaterial for the calculations with which he was then involved, but, with the advent of more complex relations to be discerned between groups, this practice led Darwin into a slightly simplistic view of large genera. This first way, whenever he obtained a result, he was happy as long as it was absolutely bigger than the standard with which it was compared: in the example cited on the previous page, 6.37 was bigger than 4.67 and Darwin had proved his point. But more than twelve months later he was to discover that there was, in fact, much to be made of the point that some genera were intrinsically large and others intrinsically small. That is, he could in the future calculate the same issues using genera with say, eight species and more, and genera with four species and less.

I shall return to this interesting point at the beginning of the next chapter for it determined the eventual course of Darwin's statistics through the most active and profitable phase that he was to experience from the exercise. But here it is really only necessary to note that he was still using the method of calculation which he had devised to account for the size of aberrant genera, and which was thus transferred unchanged to issues where size was indeed maintained as the prime question but where the data were of a different order of complexity.

When, in January 1855, Darwin had begun these calculations of the second kind he hardly expected to undertake more than a rapid glance at the numbers of species in large genera with desirable attributes like closely-allied forms and such. Yet he soon became fascinated with the multifarious issues which readily made themselves apparent and, I suggest, soon recognised that here he had stumbled on another way to prove the action of natural selection in nature. Explaining some results to Hooker he joked with more foresight than he knew, that this would be another barnacle job and that "All this has amused me, but I daresay you will have a good sneer at me, and tell me to stick to my barnacles".[87] Not only was Darwin to enter into statistical calculation with all the meticulous concern and enthusiasm that he gave to barnacles, he also was to derive some much needed moral support and confirmatory evidence of natural selection at work from this analogous investigation.

It was at this point, the first half of 1855, that various lines of thought therefore began to come together and gel in an uncertain way. Darwin saw how the larger genera with more species had, on his theory, experienced little or no extinction, and that they thus should present

many intermediate forms at the specific and varietal level. His preliminary computations seemed to confirm this assumption and he was poised to strike now at the heart of real evidence for speciation.

And here he experienced what can only be called historical coincidence.

Darwin read the very recently published tract on botanical geography by Alphonse Decandolle. Issued in May 1855, the Géographie botanique raisonnée[88] was in Darwin's hands by October and he soon wrote to tell Hooker how he was "reading Decandolle with interest" and discussed several points that the Swiss botanist had made about social plants.[89] But the most striking thing about Darwin's perusal of this cogent botanical treatise was the way it enlarged his vision of the statistical method.

As I have pointed out in an earlier chapter, Decandolle's work was devoted to the principle that botanical geography ought to be a statistical science, and ~~that~~ the book itself was almost entirely given over to table after table of data so arranged as to allow the inference of general laws about distribution. Decandolle had perfected the technique which Darwin had been applying in his own uncertain manner, and here, in the Géographie botanique raisonnée was page after page of calculations worked out in the most elaborate botanical arithmetic that Darwin had ever seen.

In particular the tables given on pp. 465-468 excited his attention for they seemed to substantiate Decandolle's notion that species with a large number of individuals belonged to the larger families which had both a greater number of species and covered a wide area. Darwin wrote beside these tables "It would be very curious to see what result would follow from genera calculated in this manner or by averages",[90] and puzzled over the fact that the relationship which he had discerned for genera seemed to extend all the way through to families. It did not seem quite right. "Can families include too great a range of adaptation to answer for such calculations?? The resemblance in Families may be due to Parentage?" he asked, and decided that yes, indeed these groups were too large and widely spread to give accurate results, since they encountered all sorts of diverse conditions and would, by necessity, therefore, present many adaptations.[91]

Below Decandolle's table on the number of "common" species (i.e. species with many individuals) presented in certain families Darwin noted that "the very small families have more than average!! quite opposed to my views."[92] In yet another example worked out by Decandolle from Furnrohr's Flora Ratisbonensis (1849) he noted that "This goes as it should do",[93] and made an aide-mémoire that "Before making any calculations...

skim over to p.519".[94] Between these sixty odd pages Darwin made extensive pencil comments and counter-claims to Decandolle's remarks on the properties of families, and at all times focussed on the irregular results that were obtained by Decandolle from calculations entirely based on these taxonomically high groups. Darwin preferred genera as his units, "but I cannot say why I think so" he complained.[95]

At the end of the volume he added a list of books to be acquired "to see whether frequency goes with genera, as it does in Families".[96] Darwin intended now to work through the same floras that Decandolle had used to find if the results were, in actuality, more pronounced when his method was employed. In his manuscript index to the work he considered this issue to be among the "chief points" and one which "bears on extinction".[97]

So we find Darwin at the end of 1855 anxiously asking Hooker for copies of the works mentioned by Decandolle. Hooker supplied him with Boreau's Flore du centre de la France and Furnrohr's Flora Ratisbonensis but could not obtain the third treatise by Miquel on the flora of Holland for some time;[98] it is perhaps a measure of the importance with which Darwin now regarded this exercise that he got quite testy with Hooker until he managed to forward the Linnean Society copy in early 1856 (Darwin was not a member and thus could not borrow books). More or less absorbed by the ideas that Decandolle had sown, Darwin occupied his time until the arrival of the books by working through the ones that he already possessed such as Watson's London Catalogue, Gray's Manual, a little catalogue of plants compiled by J.S. Henslow, and three of Hooker's own publications which had been presented to him by the author.[99]

In all these, and in the books mentioned by Decandolle, Darwin tried as many combinations of variables as he could muster. From the beginning of 1856 to the middle of 1857 he twisted and turned and looked at the question of large genera from all angles.

He began with a calculation derived from Decandolle's collation of the size of families with an abundance of individuals in each of their species, in which Darwin replaced families with genera believing that these 'lower' groups were more natural and discrete aggregations of species than the 'higher' grade. Working through Boreau's catalogue of the French flora which Decandolle had also used for this purpose, he counted all the species which were marked with the typographical symbol "C.C." for commonness or plenty of individuals, and all the genera which contained species so labelled. Dividing the one into the other he acquired an average number of species per genus for that section of the flora.

The figure so derived was then compared with a standard here drawn from the remaining species and their genera:

> "...with respect to plants marked CC as most common: of the 413 genera, 180 have one or more species marked CC and these 180 genera include 736 species and therefore each genus has on average 180 /into/ 736 = 4.08. Consequently, the remaining genera (413 - 180 =) 233 genera including (1156 - 736 =) 420 species, and each genus has on average 233 /into/ 420 = 1.80"[100]

So the calculation demonstrated genera with common species to number around four species (on average), whereas those genera without such forms presented only 1.80. Clearly four was more than 1.8 so the abundant species tended to occur in larger genera.

But Darwin tried other things as well. One of the most valuable features of these exercises was the way in which Darwin's attention was redirected to the phenomenon of variation and his often expressed idea that varieties were simply 'little' species or as he called them "incipient species". He devoted a great deal of time and energy to an extensive survey of the relative incidence of varieties according to the size of the genus which contained them, and found to his gratification that they seemed to appear more often - i.e. in greater numbers - in those genera which had a large number of species. Such a proof was important to him for it showed that varieties were akin to species in that where there were many species, so there were many varieties. In a curious metaphor in the Origin he was to explain this point further by remarking that "where many large trees grow, we expect to find saplings":

> "Where many species of a genus have been formed through variation, circumstances have been favourable for variation; and hence we might expect that the circumstances would generally be still favourable to variation."[101]

In other words his theory demanded that large genera should present above the average numbers of varieties. The fact that they seemed to do so was of enormous significance for Darwin and constituted his first really telling /arithmetical confirmation of evolutionary processes in nature. This was something which he could lay down in front of scientific audiences as 'proper' evidence for his notions.

So he spent perhaps more time on this one relationship than on any other. For instance, in working through Boreau's flora again Darwin tried three or four different ways of calculating by separating the sample from the body of the flora on various criteria. He tested the relationship in French monocotyledons, dicotyledons and in the whole flora.

Writing of the dicotyledons alone he calculated:

> "First with respect to varieties (and Boreau makes a distinction between varieties with greek letters and variable genera), of the 413 genera, 100 have one or more species with varieties and these 100 genera include 536 species. So they have on average 5.36. The remaining 313 (with no species having a variety) have consequently (1156 - 536 =) 620 species, or on an average only 1.98 species to each genus. Or if we take whole Dicotyledones we have 413 /into/ 1156 = 2.97."[102]

Thus he divided the dicotyledons into genera that had species with varieties (100 genera) and those that did not (the remainder, 313 genera) and compared the average number of species per genus in each (5.36 and 1.97). Alternatively an average drawn from the whole kingdom was 2.97. Either way varieties were connected to the larger genera.

Now with these figures in mind it is useful to stress again the technique which Darwin was using. We can see that however satisfactory the method may have been for a consideration of the size of aberrant genera, it was not really adequate for these more complex problems. Darwin had put himself in a position where his final figures always expressed what he wanted to say, even if the order of magnitude of the difference between quotient and standard was very small. The difference between five and three is minimal but it was enough for Darwin because the one was bigger than the other. And further, in the example worked out above the final total of 5.36 was not, strictly speaking, a number of species which Darwin's botanical contemporaries would have called belonging to a "large" genus. Five species were not a great number where perhaps eight or nine were more usual in the literature of the day.

Darwin however was unaware that his work lacked any criterion of <u>absolute</u> 'largeness', and happily continued throughout these calculations to consider <u>relative</u> 'largeness' as if it was truly a statement about real size. Thus in practice he defined 'large' as 'bigger than' whilst understanding his results to exemplify some intrinsic quality of bigness.

This discrepancy I suggest was in part due to the rush of enthusiasm for statistics which swept him on from the study of aberrance and extinction through to the investigation of large genera and the source of new species in varieties. He had hardly paused for a reconsideration of his method - which was simplicity itself - or for an examination of possible alternatives. Like an evolutionary process, this method had been there at the start and readily adapted to its new usage as the surrounding conditions changed. In the same way as the fins of a lung-fish made perfectly good legs when there were not any other legs around, so Darwin's

earliest statistical procedure was ready and available to be applied in a different context and to make a success of its new role in the absence of competing techniques.

This last point - the absence of any competing techniques - brings me to my second suggestion for Darwin's continued use of this single statistical procedure. I think that it was the evident 'success' of the old method that made him unaware of any need to revise or re-examine the tenets on which he was proceeding. These calculations were consistently producing the 'right' answers and he was gradually building up a powerful consensus from different floras and different kinds of questions about the relations between genera, species and varieties in terms of their numbers, ranges, and relative frequencies. By the middle of 1857 the mass of computations showed that the larger genera (large in Darwin's terms) were indeed the source of variation and "incipient species", and that they also tended to be more widely spread and abundant in individuals than the smaller ones. As he completed each new calculation the results went forward to the general body of information which made these points progressively more and more telling. The sheer weight of arithmetical evidence was going to prove the thesis in no uncertain terms.[103]

So I suggest that the gratifying success of Darwin's statistics was the major factor which regulated the way he regarded his method of calculation. Success blinded him to inherent weaknesses in the manner of presenting results, and blinded him to the fact that he was only working out a statement of relative size. And success encouraged him to continue his labours with little outside help or consultation, as, for instance, he might have asked for advice or an opinion from Joseph Hooker had the calculations not proceeded as he expected. In fact there is a surprising lack of communication with Hooker over this absorbing topic, apart from his initial discussion about the problems of aberrance and extinction. Was Darwin keeping his cards very close to his chest? Or did he - as I suspect - genuinely think that he was on the right track and that there was thus no need for external guidance? Certainly his response to Decandolle's botanical arithmetic as mirrored in his marginalia was one projected by a man who thought he had a technique which was better than the Géographie botanique raisonnée. Darwin had no need of Decandolle's sophisticated statistics when he already possessed a good method of his own, and he therefore took only problems not a methodology from the Swiss botanist. Nor did he consult with either H.C. Watson or Asa Gray who had provided him with information for the

earlier study of aberrance and closely related species.[104]

Therefore I contend that Darwin undertook these eighteen months of botanical statistics in virtual intellectual isolation. He had devised and applied with every hallmark of success a method of calculation which provided him with fundamental evidence for natural selection. Why then consult with others about the ways and limits of botanical arithmetic? It was not until these computations had almost run their course and Darwin was delicately constructing an interwoven hypothesis of size, range and frequency, that he decided to let his young friend the mathematical John Lubbock run his eye over the accumulated papers. And then he received an awful shock.

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# Chapter 6: Charles Darwin's Botanical Arithmetic, 1857-1858

## The Correction of Darwin's Calculations

On the 14th July 1857 Darwin wrote an extraordinary letter to his young friend and protégé John Lubbock.

> "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!"[1]

He thus simultaneously criticised his own foolish statistics and praised Lubbock's skill in detecting the faults. Although Darwin openly encouraged Lubbock in all scientific matters and often indulged in innocent flattery, this uninhibited enthusiasm was quite unlike the even tenor of his usual correspondence and, as such, undoubtedly 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, and Lubbock did certainly help him to "clarify my brains" by showing Darwin a more rigorous way of dealing with arithmetical data.

As if to spread the burden of this sudden revelation, Darwin fired off a similar letter to Hooker on the same day admitting that he was the "most miserable, bemuddled, stupid dog in all England", and was "ready to cry with vexation at my blindness and presumption". It was the "grossest blunder"[2].

To both his correspondents Darwin thus lamented his lack of mathematical prowess and congratulated Lubbock for showing him the "right way" and the "right principle" of calculation. Historians can only be thankful that he did not carry out his extravagant threat to tear up his manuscripts and "give up in despair".

We can therefore readily imagine that Darwin was indeed on the point of crying with vexation. He had spent nearly eighteen months and a great deal of intellectual energy on a thorough examination of the properties of large genera and had already convinced himself that the results were consistent with a theory of evolution by natural selection. For these months Darwin had been building up an impressive body of

arithmetical evidence of relationships between taxa, none of which could be satisfactorily explained by mystical cosmic forces or divine creation. He was additionally drawing up statistics to prove that variation - and hence the appearance of varieties - was a phenomenon frequently encountered in nature and of an extent more than sufficient to fuel selective processes. Furthermore, he had allowed himself to think that these large genera were the most active source of new species. The careful calculations and cross-links between them correlating size with range and abundance of individuals, were his statement to this effect.

And what should happen but that Lubbock told him that he had not proved anything: that the method was inadequate; and that the conclusions did not follow from the figures. Darwin's whole edifice was dashed to the ground.

Though we do not know for sure what it was that Lubbock actually said to Darwin on his visit to Down (that "most fortunate conversation" according to Darwin), we can infer the greater part of it from Darwin's rueful letter of the 14th. The elder man described a calculation that he had attempted "as you suggested" using the new method.

This new way was, on the face of it, clearly concerned with showing that large genera had more of whatever was under discussion than the small. Lubbock had inverted the proposal from its earlier Darwinian format of asking whether the genera that had the desired quality also presented large numbers of species.

To these ends Darwin now, in his sample calculation, divided the flora he was testing into two sections, one of which contained all the (absolutely) large groups and the other all the (absolutely) small. "I have divided the New Zealand Flora as you suggested", he wrote to Lubbock:

> "There are 339 species in genera of 4 and upwards, and 323 in genera of 3 and less"[3].

That is, he separated the genera of Hooker's catalogue of the plants of New Zealand into genera which had four species and more, or those with three or less. Each cohort possessed a sum of 339 and 323 species respectively, and the dividing line between them had been so positioned that there would be roughly equal numbers of species on each side. Then proceeding on lines normal to botanical arithmetic and on lines commonplace in proper statistical calculations Darwin estimated

from one set of ratios what he should expect to find in a second set.

By following the "rule of three", a simple proportional device which gave the fourth term of a statement from the other three, he arrived at a figure - in this instance the number of varieties - which ought to be found in nature if she was consistent. Then he compared this anticipated quotient with the number actually found in real life.

> "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."[4]

That is, as the 339 species of the larger genera are to the 323 species of smaller ones, so the 51 varieties of the first should be, by proportionality, to the 48.5 varieties in the second. The fact that the actual figure was only 37 indicated that small genera did not have as many varieties as predicted. And this in turn implied that there was less "creation" going on in these tiny groups.

Now Darwin, by rights, should have been relieved to find that the new method as here worked out did give the same sort of result that had been forthcoming from earlier calculations. But he exhibited some slight recalcitrance in acknowledging the superiority of Lubbock's technique; writing at the close of this specimen computation, Darwin confessed that "the case goes as I want it, but not strong enough, without it be general, for me to have much confidence in". Because the product was not as "strong" as he had come to expect on the basis of former work, he complained that unless the phenomenon was found to hold through many calculations (as his previous method had done) he would hesitate to use these figures.

Here perhaps we have to extend a bit of sympathetic understanding fully to judge the position that Darwin was now in. Evidently depressed, and certainly dismayed, he must have felt that all his work had up to now been in vain and so fell into a temporary pose of thwarted unreasonableness: everything else had been shown to be wrong, so why should these admittedly 'right' results be considered as anything other than a transitory fluke? It seems to me entirely probable that Darwin's extravagant language and unjust assessment of the end result of this his first new calculation, were symptoms of a feeling that Lubbock had struck right at the heart of a favourite theory and demolished it.

Possibly I am reading too much into this minor incident, but the point bears some examination for Darwin is now understood to be a man

who became intimately involved with his own theories, was reluctant to give them up in the face of conflicting evidence, and was even prepared to heap extenuating circumstances and ad hoc explanations on the frame of superseded hypotheses to keep them going. So much could be inferred from the tenacity with which Darwin kept natural selection to the forefront of his theory when tormented by philosophical considerations of absolute materialism, the status of man, the death and destruction that was to be the over-riding feature of nature, and the religious sentiments of his wife and closest friends. All these were enough to make less tenacious or less courageous naturalists opt for an easier answer. At a lesser level it is also the case that Darwin clung on to circumscribed precepts like his explanation of the origin of the parallel roads of Glen Roy when constantly presented with evidence and hypotheses which ran counter to his own. Martin Rudwick has demonstrated how he was blinded to the glacial phenomena of the glens of Lochaber by his preconceived theory of a marine origin for the shelves or "roads", and how, in later years, he disputed suggestions based on ideas of glaciers and outwash lakes. It was only with the greatest reluctance that he eventually washed his hands of the whole affair and tagged it a "gigantic blunder", and even then continued to make excuses for the "great failure" as, for example, in his autobiography[5].

And yet again, it seems to be the case that Darwin's ever-delicate health waxed and waned according to the relative state of his theories. When confronted with fundamental questions about God and life, and those which brought natural selection under a fiercely critical light, Darwin was stricken with bouts of nervous illness, rashes and boils, and a curious nausea that rendered him virtually incapable for days on end. The most telling instance of this association must surely be the events which surrounded the rapid composition of the Origin of Species after the receipt of A.R. Wallace's letter: for during the months between July 1858 when a joint paper was read to the Linnean Society and the publication of the Origin in November 1859, Darwin was constantly in and out of bad health and undergoing a variety of cures at different establishments.

To return to my original point, although there are no signs of Darwin here retiring to his studio couch under the stress of discovering his statistics to be inadequate, I think that there are indications of a broadly similar sort of response to Lubbock's suggestions.

He told Hooker that he was only going to lose some few weeks' work

in redoing all his figures - an uncharacteristic dissemblance on Darwin's part which might have been designed to cover up how significant these computations had been and how devastating was their loss. He never again discussed either statistics or the issues thus clarified in his letters to Lubbock, which, after Darwin's first response, was something that Lubbock might well have the right to expect. And, as I shall show, Darwin was soon to modify Lubbock's new technique into a revised version which incorporated his own personal preferences and made it more the product of his own mind.

However, be this as it may, after his letter to Lubbock and that to Hooker on the 14th July Darwin turned to a more extended examination of the suggested method. His rough notes for the calculation on Hooker's New Zealand flora show that he estimated not only the number of varieties that he should expect 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:

> "N.B. The plan would be to calculate as . . .
> 323:339::37: x = 38.5"[6]

His other tabulation had shown that the larger genera actually possessed 51 varieties, or some thirteen more than they should. Further than this, Darwin additionally worked out that the thesis still stood when he took only species and their varieties:

> "The above 339 species in large genera have 94 varieties,
> " 323 " in small genera have 76, they ought
> to be 89½"[7]

So everything seemed to be as it should be. It is therefore fairly reasonable to find that during the next few days Darwin experimented with this way of working out relationships. He worked through his old calculations on Babington's Manual of British Botany, correcting and marking these as "useless" and drawing new conclusions dated 18th July - only five days after Lubbock's visit[8].

What then was the significance of the new method for historians of Darwin's thought? Was it simply the case of an arithmetical error brought on by the special circumstances under which he began to calculate floras and which, when corrected, continued to give the same sort of results? Or was there more to the reconstruction of Darwin's methodological procedure than this change-over might indicate?

I believe in the first instance that Lubbock's suggestions altered the general tenor of the inquiry by focussing Darwin's attention on slightly different parts of the exercise, and that secondly he now hesitated to take any new or innovative steps without first consulting Joseph Hooker on the merits or disadvantages of so doing. The second point is one that will become apparent as I follow Darwin's later statistical work where he became more and more dependent on Hooker's advice and recommendations, and especially on Hooker's remarkable facility for seeing the flaws in any botanical argument that he might put forward. After the Lubbock revelation Darwin was to be twice shy.

The first point on the other hand requires a certain amount of elaboration, and it is to this that I now turn. Taking the method itself as a starting place, I see two important features which distinguish the Lubbock kind from the 'home-grown' variety.

Firstly, Lubbock had constructed a procedure that was plainly intended to answer the question 'do varieties (or commonness or wide range) occur in the larger genera?' This was indeed the question on which Darwin had been conducting his researches but, as I have shown, was not exactly the point which his answers were making. Darwin had, up to now, been asserting in practice that varieties (or the other variables) appeared in genera bigger than those genera which constituted the standard. He had not encompassed the idea that there could be an absolute 'bigness' or 'smallness' of genera, instead of his own notion of relative largeness.

Lubbock therefore abolished Darwin's standard - and with it all connotations of relativity - and substituted a division of the given population into two halves, one of large genera and one of small. With a certain amount of judicious counting the dividing line could be well situated at the point which separated say, genera with four or five species and more, from genera with three species and fewer. The advantage of so doing was that now any quotient simply had to be expressed in terms of belonging to either sized group and thus being either 'large' or 'small' in species numbers. Darwin, working under this scheme, could find that for instance there were 57 species with varieties in the one section and only 37 in the other, and hence ascend to an immediate correlation between these figures and the size of the group to which they belonged. On this method all the resultant numbers said something about the kind of genus which contained the variable.

Secondly, Lubbock added the idea that Darwin ought to reason by proportionality not averages. Here no doubt Lubbock's mathematical upbringing encouraged him to persuade Darwin that this was the more proper method, especially since Lubbock's father had devoted much of his own time to the composition of a little tract on the laws and application of probabilities[9]. He told Darwin to follow the principle that as (a) is to (b) so (c) is to (d), and demonstrated how this would produce an anticipated figure for the desideratum. Proportionality gave an expected sum from which the real numbers should deviate by a substantial margin. How much more scientific, Lubbock would have thought, to compare predicate with reality than to relate two averages by their size as Darwin had been doing. And further, this new method facilitated a rapid cross check by allowing other predictions to be made, as, for example, Darwin had attempted with his calculations on Hooker's New Zealand flora, by working out the 'lack' of varieties in small genera and the 'excess' of the same in the large.

Yet it was a measure of the personal significance with which Darwin had invested his previous efforts that he still felt uneasy with this new style, however much better it might seem to Lubbock. He completed Hooker's New Zealand flora and reworked Babington's treatise in this way, when soon after the end of July he turned again to Boreau's Flore du centre de la France and found that the new method did not provide the 'right' result. And apparently struck by this fact he devised an alternative where one had no 'right' or 'wrong' answer but rather a straightforward comparison of numerals, exactly as he had had before.

For his first test based on Boreau's flora he worked out the ratio of varieties for each group of large and small genera, having already divided the flora into two sections of those genera with five species and up, and those with three and down, whilst reserving a separate category for genera with four species. The bigger genera had 679 species of which 109 had varieties, the total number of varieties being 153. The small genera as a group had respectively 625 species of which 66 bore 100 varieties. Darwin calculated that:

> "Species 109: vars 153:: species 66: x = 92.5; but the real number is 100, therefore the small genera, which have species varying, present rather too many varieties."[10]

Thus the small genera did not conform to the pattern of having fewer varieties than predicted. So on the same sheet of paper he tried something else:

"Now if we consider the number of varieties themselves:
In the large genera with 5 and upwards then 153/679 = 225/1000
In the small genera with 3,2,1 species then 100/625 = 160/1000"[11]

Put this way the number of varieties for each group of species showed an encouraging differential between numerators. And if he repeated the same exercise with the species that bore varieties as its final term, there was a similarly felicitous gap between the final figures of 160/1000 and 105/1000. Darwin, in fact, had returned to the same position which he had occupied in his earlier statistical programme but now, under slightly different constraints, he was offering Lubbock's proportions worked out as parts of a thousand which could then be treated more or less as absolute numbers. 225 was more than 160, and Darwin was comfortably back with something which he knew all about; similarly, 160 was bigger than 105 and Darwin must have felt a glow of recognition creeping over him.

Of course this modification of Lubbockonian methods was really nothing more than a personal preference for results expressed as parts of some round figure which therefore enabled an immediate and easy comparison, instead of the slightly more demanding and consequently less telling set of figures conveyed by a double proportion. This preference was plainly demonstrated by Darwin's later habit of converting the statistics which Hooker sometimes supplied, from a state of a:b::c:d to numerators of 1000, and I do not think that historians need lay much emphasis on this change-over. What should be noted however is the way this transformation allowed Darwin to relapse into comparing two quotients with each other instead of one with an anticipated, and carefully predicted numeral.

With this revised methodology Darwin made haste to rework the floras which he had so thoroughly examined the year before. Darwin was now in the throes of writing up his big species book, and he was anxious to include the data so derived in his presentation. "The subject", he wrote, "is in many ways so very important for me."[12] He solicited Hooker for the loan of books from Kew ("I am at a dead-lock till I have these books to go over again"), and asked 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"). In August he told him which treatises had been done or were being done, and asked again:

"Has not Koch published a good German Flora? Does he mark

varieties? Could you send it me? Is there not some grand Russian Flora, which perhaps has varieties marked? The Floras ought to be well known."[13]

Most of his earlier sheets of paper had to be ignored and so marked "old and useless", "old" and "reworked". The new Lubbock-cum-Darwin method demanded a complete recount of genera, species and their varieties from the catalogues themselves, for he had to know which group of genera was going to fall on either side of his dividing line into large and small. By adding up the number of species in each genus he then summed up with a list of how many genera there were with one, two, three etc. species all the way up to ten or more. Then he added and subtracted each collection of genera until he arrived at a roughly equal division into two halves[14]. Naturally this was a most time-consuming process which delayed the actual calculations even more, and so, with some alacrity, Darwin sought the help of a willing and numerate associate. The man he fixed on was a Mr Norman, the village schoolmaster at Downe who is now an obscure individual only known for this his relationship with Darwin. Mr Norman received a small payment for his very considerable work, and his hand will soon become familiar to those scholars who look at the many tables of species which he wrote out for Darwin. He was so willing and able at the work that Darwin even had the gall to offer his services to Hooker, saying "is it not a pity that you should waste time in tabulating varieties? for I can get the Down schoolmaster to do it on my return, and can tell you all the results."[15] There are many notes to Mr Norman still extant in the Cambridge University Library, dealing with the mechanics of separating genera into large and small, counting up all the varieties and species on each page and adding them to a running total, and so on. Darwin himself however conducted the final calculations, now with some aplomb as the results again exhibited an accumulation of what he wanted to see.

This last is a point that bears repeating: with the modified way of presenting Lubbock's arithmetical method that Darwin had devised (or imposed), he had regained all the confidence in calculation that had been so wretchedly lost in July of that year. He saw that he could indeed get just as useful conclusions from the new method as he had done from the old, but now with the added advantage of knowing that he really was proving what he postulated. The subject was still important to him: it still provided the much needed evidence of variation and speciation; and it demonstrated an important correlation between the size, range and

multiplicity of genera which mere words could not adequately convey.

More than this I contend that now, after July 1857, Darwin had a further reason to continue botanical arithmetic in this fashion. He had discovered that these large genera were the epitome of success, and that they were therefore to be considered as truly dominant forms from which all the major advantages of life were to stem. On a par with the idea that 'winner takes all', Darwin now believed that his large genera were the source of each splendid innovation that the progress of life through time had experienced and that "the larger genera thus tend to become larger; and throughout nature the forms of life which are now dominant tend to become still more dominant by leaving many modified and dominant descendents."[16] He had found that success begets success, and that his botanical arithmetic was an excellent way to demonstrate exactly that point.

So from August 1857 through to March or April 1858 Darwin conscientiously worked through some eighteen floras tabulating and assessing a variety of issues for each one and constructing a series of general tables where the final figures could be laid out against each other. He developed an easy facility with these investigations and firmly stuck now to the method which had evolved from Lubbock's helpful remarks with his own stylistic alterations. Thus Darwin would go through each catalogue and effect some preliminary marking of varieties, and draw up a carefully considered set of instructions for Mr Norman. The latter then compiled tables and totals on which Darwin weaved his arithmetical correlations.

Hence, for example, in Asa Gray's Manual[17] Darwin studied the two sorts of varieties which Gray had distinguished, that is ordinary varieties and another sort which was considered to be very strongly marked and nearly of species rank. Darwin retained Lubbock's basic division into two cohorts of genera, one with species numbering x and above and one with y and below, yet set out the results as numerators of one thousand for easy reference:

> "Asa Gray N. U.States. August 1857
> Summary of all results . . . there are in (and it is not possible to divide species more equally):-
>
> | genera having five species and upwards .... | genera with 4,3,2, and 1 species |
> |---|---|
> | 1005 species | 917 species |
>
> Of these counting the two kinds of varieties marked by different types (viz. ordinary varieties and varieties which may

prove to be species):

| | |
|---|---|
| Species presenting such two sorts of vars.<br>97/1005 = 96/1000 | Species presenting such two sorts of vars.<br>65/917 = 70/1000 |
| Of the two sorts of vars themselves<br>138/1005 = 137/1000 | Of the two sorts of vars themselves<br>89/917 = 97/1000 |

Now for the undoubted slight varieties by themselves:

| | |
|---|---|
| Of species presenting such vars<br>61/10005 = 60/1000 | Of species presenting such vars<br>34/917 = 37/1000 |
| Such slight vars themselves<br>89/1005 = 88/1000 | Such slight vars themselves<br>46/917 = 50/1000"[18] |

In every case the larger genera (on the left hand side of the page) had the higher numerators ~~varieties~~. They had the "big-type" and the "slight" sorts in a preponderance, and they had more of all sorts taken together as a group. No wonder then that Darwin was to think these facts agreed "admirably with my views that flourishing tribes vary most"[19]. And no wonder that he continued to reckon with this useful technique. It was shortly to become almost second nature to Darwin as he produced page after page of calculations, all in the same format, and all providing the same happy conclusions.

The most interesting feature of this third phase of Darwin's statistics is the constant guidance which he sought and received from the hands of Joseph Hooker. Darwin was soon to be comfortably established in the routine of tabulation and calculation, with his aims clearly defined and the overall theoretical status of the work plainly allocated. The discussion on larger genera was intended to go in the middle of a piece already written on "Variation under Nature", his proposed chapter IV which was to provide the fundamental premises on which the rest of the work was to rest. So in general terms his approach to the question of botanical arithmetic had changed and solidified into one that was confident, capable and pleasantly expectant. This transformation meant that he was not to be shaken from the views that were now going forward, and this attitude was reflected in the kind of questions which he now pressed on Hooker. They were questions entirely related to the work in hand and mostly of a sort which brought up technical or merely mechanical problems for individual calculations.

Darwin, for instance, had great trouble in getting any 'right' results out of isolated volumes of the two Decandolles' Prodromus[20], and he solicited Hooker for advice on whether it was the truly gigantic

genera like Labiatae which were spoiling his case. In fact his computation told him that gigantic associations "have very few varieties - 90/100 - less than the genera with ten and under which have 104/100", or, in effect, that enormous genera had even fewer varieties than his supposedly meagre population of such forms in the smaller genera[21].

Again, Darwin asked Hooker what he should do about monotypic genera which happened to have varieties. By leaving them in he was, so to speak, stacking the cards against himself for they would bias the final figures towards a greater number of varieties in the smaller genera. But Darwin got some sort of vicarious satisfaction in so working 'against the odds', and against the most unfavourable circumstances which nature could give him, because his conclusions were thus made all the more 'right' when they came out in his favour.

Yet other problems of this kind cropped up. In his return to the old favourite Boreau, one calculation on common species ended up as a proof that they occurred more frequently in the small rather than the large genera, not something that Darwin wished to demonstrate[22]. In similar vein Gray's Manual let him down over close species which appeared to be more numerous in genera with fewer species, and Darwin even wrote to Gray to inquire how this could have happened[23]. But in all these cases Darwin managed to get round it - usually by changing the way he divided the sample in the first place - and these alterations (which gave 'better' results the second time around) all served to make him feel his ideas must be true.

Perhaps the most evident problem, and the only one which I am going to discuss in any depth, was the fact that Darwin was tabulating proportions from catalogues that could only be called local floras. Though individual treatises might have covered fairly extensive areas such as Ledebour's flora of Russia, the majority of them were concerned with the plants of quite circumscribed areas like Holland, New Zealand or the insects of Sweden. Even the northern United States is, in botanical terms, a fairly limited region. Hooker was very distressed with this evident lack of universality and could not see why Darwin was thus deliberately laying his results open to a charge of parochialism. "I am obstinately inclined", he wrote,

> " . . . to take general monographs for data in preference to local Floras, for the general works alone seem to me to give a fair chance of the species being uniformly treated . . ."[24]

He expressed his doubts to Darwin, claiming that there was no reason

to assume that because large genera exhibited more varieties in restricted and well-known regions like the British Isles, so they would continue to do throughout the world. Per contra, the small genera of a local flora might nevertheless range widely and present lots of varieties somewhere else[25]. And now that Hooker was thinking over the subject he overflowed with perceptive criticisms, and utterly damned the whole botanical genre:

> "Now as you increase your area the small local (ie invariable) genera do not reappear, but the small mundane genera do with an increased number of variations, and the large mundane genera with their variable species also relatively increase. Is this not so? . . . Again, if the species of small local genera are themselves local, it follows that we procure fewer specimens of the species of such genera than of large, and hence make fewer varieties. This any general Herbarium shows. A genus of one species presents only a single specimen much oftener than a genus of 10 species does only 10 specimens . ."[26]

But the most crushing point from Darwin's view of things was his suggestion that botanists were not strictly objective when they allocated species and varieties for either small and large genera, or for local and general catalogues. One botanist might make five species out of twenty specimens, where another would make only one and give the different forms the status of varieties. This reflected, of course, the perennial issue in taxonomy between taxonomists who were by nature 'splitters' or 'lumpers', and Hooker, who had devoted much of his career to amalgamating other people's varieties and species into large and consequently variable species or genera, was the 'lumper' par excellence of the nineteenth century. He fired off broadside after broadside in his Introductory Essays to the various colonial floras which he published, criticising the tendency for local investigators to make far too many species out of forms which were, to a more travelled botanist, quite plainly variations of a well spread being. But he forgave them because after all they did not possess the great collections and Herbaria of European taxonomists. Yet he could not forgive these latter when they made very 'fine' species out of well-marked or strong varieties. Babington was one such botanist who provoked some acerbity, and even Hooker's amiable and modest colleague George Bentham came in for private criticism until he redeemed himself with the manuscript for his Handbook to the British Flora (1858) where he "turned out as great a lumper as I am! and worse."[27]

Hooker's point was that these personal differences could add or

subtract varieties and species to or from a flora ad infinitum, and that systematic catalogues were thus idiosyncratic and frequently artificial lists of taxa. He told Darwin that a botanist of his acquaintance often felt that there ought to be more species and varieties in the large genera, and that he therefore was prone to make more of these when describing new specimens from big groups. And the same happened in the smaller associations where other, usually provincial, botanists were likely to make two or three species in a very small genus because the variations seemed to be more noticeable. He himself would have made proper varieties out of some of the species in smaller genera found in the Flora Indica ~~if he had not been conscious of his position as a 'lumper'~~, and thus would "render them equivalent to the varieties in Clematis and other big genera, and [have] confounded your statistics".[28]

How then did Darwin take these remarks? He certainly reviewed his own thoughts about the 'splitting' and 'lumping' question and mused on the effect it might have on his results:

> "This would be a great difficulty if species have real existence; but I look at varieties and species as running together; so that the facts given by 'lumpers' would apply only to forms more unalike."[29]

But Darwin reasoned that each flora was probably consistent with itself since it was usually composed by one naturalist alone, and the foibles of that one man would, at least, be reflected to the same degree in each genus. The varieties, species and genera should thus all bear the same rank in one volume. And since he was not actually comparing flora with flora, but a multitude of points within each catalogue, he saw no reason to switch from local to more general tomes. In fact in Darwin's eyes local catalogues had a positive advantage: the varieties were usually better known and thus given an ascribed rank in "well-sifted" floras, whereas in extensive monographs these forms were obscured by the vast number of species which had also to be described. Anyway, he said, "I should expect the same rules to hold in local and general floras".[30]

But something that Hooker had to say about botanical practice did worry Darwin to such an extent that he wrote to his other plant-loving friends to press them for an opinion. This was I think the only point which temporarily shook his conviction that his choice of treatises was perfectly adequate for the job in hand. He was roused in February 1858 to write to Gray:

"My last letter begged no favour, this one does; but it will

> really cost you very little trouble to answer me, and it will be of very great service to me, owing to a remark made to me by Hooker, which I cannot credit . . . Here is my question - 'Do you think that good botanists in drawing up a local Flora, whether small or large, or in making a Prodromus like De Candolle's, would almost universally, but unintentionally and unconsciously, tend to record (ie. marking with Greek letters and giving short characters) varieties in the large or in the small genera? Or would the tendency be to record the varieties about equally in genera of all sizes? Are you yourself conscious on reflection that you have attended to, and recorded more carefully the varieties in large or small, or very small genera?"[31]

In other words, as Darwin said, was there "a stronger or weaker tendency in the minds of botanists to record such [varieties] in large or small genera"? He had picked up Hooker's suggestion that some systematists described more varieties in large genera, where perhaps others might allocate extra ones in the small. This malpractice would indeed affect Darwin's statistics since he had no way of deciding which sort of botanist he had got, and the 'errors' did not, so to speak, cancel each other out. To Darwin's dismay both Gray and Charles Babington to whom he had also written answered in the affirmative, and claimed that yes, there was indeed a tendency to record more varieties in larger genera. Babington answered this "curious question" by telling Darwin:

> "I think that in the very small genera, where perhaps there is only one species, there is a general tendency to think and take for granted, that there are no more forms deserving of notice; but that in the others, where many nearly allied species are known to exist, the botanist is led to look more carefully and therefore to notice and record varieties and forms."[32]

Yet Darwin could hardly believe what his botanical friends were asserting, and could not credit the idea that published works were subject to these whims and fancies. "You give a poor picture of the philosophy of Botany", he wrote to Hooker, "I can hardly persuade myself that things are quite as bad as you make them." And it seems to be the case that he ignored the possibility that his chosen catalogues were a hotbed of false varieties, only pausing to chide Hooker as a "worrier of poor theorists"[33]. In fact I suspect that the information which Gray, Hooker and Babington had supplied suggested to Darwin that if botanists indeed erred in this way, then at least they all erred in the same direction and made more varieties in the bigger groups. So his calculations might be over-emphasised but at worst they were all consistent. And further, I think that since Darwin was nearing completion of his manuscript

section which was to explain the statistics in full and glorious detail, he probably put the question to one side, expecting that Hooker would soon see the force of his - Darwin's - argument when he read the complete piece.

For this long arithmetical effort was at last drawing to a close with the mounting folios of Darwin's final discussion of the whole subject. His letters to Hooker in the spring of 1858 include warnings that he hoped Hooker would read the draft and give him an honest opinion. On April 14th Darwin entered in his Journal the completion date of the section and, after a few weeks' retirement for hydropathic treatment at Moor Park in Surrey, he forwarded a fair copy to his friend on May 6th. After receiving an encouraging note from the vicinity of Kew, Darwin gratefully replied on the 8th June confessing how very important the subject had become to him:

> "You would laugh if you could know how much your note pleased me. I had the firmest conviction that you would say all my MS was bosh, and, thank God, you are one of the few men who dare speak the truth. Though I should not have much cared about throwing away what you have seen, yet I have been forced to confess to myself that all was much alike, and if you condemned that you would condemn all my life's work, and that I confess made me a little low; but I could have borne it, for I have the conviction that I have honestly done my best."[34]

Darwin's diffidence barely concealed the very real value which he placed on this piece of work and its significance for his overall theories. If this was not good enough then everything else, which was conducted along the same sort of lines of reasoning, would also have to go.

But further discussion was delayed by the sudden arrival of Wallace's letter on natural selection and Hooker's joint efforts with Lyell to secure fair recognition for both Wallace and Darwin. Only on July 13th could Hooker give his friend his considered approval:

> "I went deep into your MS on variable species in big and small genera and tabulated Bentham after a fashion, but not very carefully. After very full deliberation I cordially concur in your view and accept it with all its consequences."[35]

The two managed thereafter to exchange one or two letters on the topic, but it seemed to die a natural death as other relatively incomplete sections of Darwin's work were brushed up and made suitable for his Abstract, the future Origin of 1859. And in this publication, as I explained in the opening pages of the preceding chapter, the whole subject of botanical arithmetic received an unfortunate compression at the

hand of its composer so that it was reduced to a remarkably ineffective argument: a reductio ad absurdum indeed. Darwin did, of course, promise to publish the data in a future work, and certainly still intended to do so when he introduced his two volume work on The variation of animals and plants under domestication (1868) where he assured his readers that it would be followed by a companion work on variation under nature. But it never came about, and the history of Darwin's statistics remains one of manuscript and archival investigation alone.

* * *

At this last stage of Darwin's statistical work we find that whilst he was gratefully thanking his botanical colleague for his favourable opinion, Darwin also alluded to its very significant role in a setting which has hitherto been unmentioned by me. The manuscript on large genera which had been so carefully drawn up and extensively documented with arithmetical evidence, was itself destined for "the end of the long chapter on variation in a state of nature". But further implications arising from the calculations were to be left, as Darwin said, "till when I discuss the Principle of Divergence which with 'Natural Selection' is the keystone of my book". He therefore proposed another written passage on genera per se but one which this time would be devoted to their 'creation', growth and eventual 'demise', or, as he put it, "genera coming in and out" of the history of life. These ideas would interlock in a fundamental way with his crucial concept of natural selection. So much is clear enough from Darwin's letter to Hooker of June 8th[36].

But what was this "Principle of Divergence" that ranked in importance with natural selection? Some twenty years later Darwin was to recollect with chagrin that he had overlooked an important feature of nature, until ("long after I had come to Down") he invented or discovered this single principle. It was designed to account for the way organic beings appeared to 'diverge' from ancestral stocks as the history of life was unfolded through time, so that existing animals and plants seemed to be grouped in associations of lessening affinity, as in, for instance, species, genera, families and so on. In his autobiography Darwin recalled:

> "But at that time [1844] I overlooked one problem of great importance; and it is astonishing to me, except on the principle of Columbus and his egg, how I could have overlooked it and its solution. This problem is the tendency in organic

> beings descended from the same stock to diverge in character as they become modified. That they have diverged greatly is obvious from the manner in which species of all kinds can be classed under genera, genera under families, families under sub-orders and so forth; and I can remember the very spot in the road, whilst in my carriage, when to my joy the solution occurred to me; and this was long after I had come to Down."[37]

Darwin, like so many individuals in later and more rosy years, remembered the circumstances which surrounded this realisation in dramatic shades of black and white. That is, on his own reckoning, there was in his mind an absolute lack of any notions of divergence before he discovered the "principle" which explained it, and after which incident all was sweetness and light. In fact, of course, the solution did not materialise out of nothing and nor had Darwin been unaware of the phenomenon of divergence beforehand, but I do think that it is fair to say that Darwin, before this time, then thought that natural selection alone fully explained the appearances. Divergence (as it is convenient to call it) was a fact of nature of which Darwin had been conscious ever since he began compiling his very first notes on species in 1837, yet was a phenomenon he felt no need specifically to account for until this more or less sudden moment of recognition.

It is to divergence and Darwin's explanatory "principle" of it that I shall devote the closing pages of the present chapter. It is my suggestion that Darwin's realisation of such an idea - a "principle" - was closely linked with his work on botanical arithmetic and his understanding of large genera at that time, and I shall propose that his statistics held a notable position in the hierarchy of ideas that appear to have contributed to what Darwin meant by divergence. Other historians have passed opinions on this moot point but the bulk of modern comment on Darwin's views has tended to concentrate on demonstrating that, contrary to his own words in the Autobiography, Darwin <u>did</u> know of divergence before the Essay of 1844 and even wrote of it in his notebooks[38]. I think however that this will prove to be something of a wild goose chase. For there are here all the hallmarks of a scholarly confusion between an evident awareness of a fact or phenomenon on Darwin's part, and a recognition of a <u>cause</u> for it. Certainly historians are free to assert that Darwin knew all about divergence in his cradle if they so wish, but they should be prepared to acknowledge that his correspondence and papers substantiate his own claim that he only thought of an explanation rather late in the day, and definitely after the Essay of 1844. Thus I think

scholars are missing the real point in this issue. It is the delayed recognition of a cause for divergence, not the long series of observations of the phenomena, that strikes me as the interesting feature.

But we may well ask when and why did Darwin come to see the divergent arrangement of organic beings in a different light from that which had gone before?

The when of the matter hinges, in my view, on a close examination of Darwin's long manuscript on Natural Selection which was composed in the twenty-five months between May 1856 and June 1858[39], and a corroborative series of hints issued by Darwin to his correspondents over the same period. I shall argue that the long and complicated sequence of interpolations and corrections to the text and, in particular, to the chapter on natural selection itself emanate from his discovery of a "principle of divergence" in the interim.

But the why stems from his use of botanical statistics to illuminate the dominant and dominating features of large genera, and I therefore assert that it was the introduction of, firstly, Lubbock's new methodology, and then, secondly, Darwin's own modifications, which drew his attention towards their success and subsequent diversification.

These are of course closely linked and before I turn to a review of each proposal under separate heads, I should like first to point out the remarkable proximity which 'divergence' and 'large genera' enjoyed in Darwin's thoughts and writings. If we look briefly at the way Darwin composed and corrected the various parts of his long manuscript, and the dates of completion of each exercise which he carefully recorded in his Journal, it is not too hard to reconstruct the actual pattern of procedure. To these ends, the extensive editorial material which introduces each transcribed chapter of this "big book" presents a well supported body of evidence to fully chart the history of the manuscript itself, and I can only describe the results of this effort as an achievement on which I have drawn with few reservations. From these editorial comments it is clear that Darwin proceeded to work - and write - his way through a pre-designated plan adapted from the Essay of 1844. The table overleaf gives the bare bones of Darwin's programme with his own dates for the completion of each chapter, and it can be seen that he more or less worked his way through from start to finish just as his reader was expected to do. The titles and numbers are Darwin's own. The mysterious absence of any chapter I, and the physical absence of these pages and the whole of chapter II are assumed (by the editor of Natural Selection) to

## Table of the composition of the Natural Selection Manuscript

| | | | | | | |
|---|---|---|---|---|---|---|
| 1856 | May 14 | "Began by Lyell's advice writing Species Sketch" | | | | |
| | Oct 13 | finished | whole of | Variation under Domestication | chapter | II |
| | | " | first part | Geographical Distribution | " | XI |
| | Dec 16 | " | whole | Crossing | " | III |
| 1857 | Jan 26 | " | first part | Variation under Nature | " | IV |
| | March 3 | " | whole | Struggle for Existence | " | V |
| | March 31 | " | first draft | On Natural Selection | " | VI |
| | July 5 | " | whole | Laws of Variation | " | VII |
| | Sept 29 | " | whole | Difficulties on the Theory | " | VIII |
| | Dec 29 | " | whole | Hybridism | " | IX |
| 1858 | March 9 | " | whole | Mental Powers and Instincts | " | X |
| | April 14 | "Discussion on large genera & small & on Divergence & correcting chapter VI" | | | | |
| | June 12 | finished above | | | | |
| | June 14 | "Pigeons (interrupted)" | | | | |

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be an unfortunate corollary of Darwin's later use of these two chapters for the treatise on Variation under Domestication (1868).

The table indicates that in the spring of 1858 Darwin wrote first a long piece on "large genera" (some 70 folios) and then another on "divergence" (50 folios) which were then inserted into his completed chapters on Variation under Nature and on Natural Selection. In other words he returned to these two chapters to add very substantial passages into arguments which had before then been considered his last words on the subjects.

Now if the scholar looks at this curious fact with his antennae tuned to the history of Darwin's botanical arithmetic, some remarkable coincidences make themselves apparent. Lubbock, as we know, corrected Darwin's statistical technique on July 14th 1857, which caused him to repeat and extend his calculations on varieties and large genera from August or so through to the spring of 1858 when he wrote up the discussion. What then do we make of the circumstance that immediately after (or even at the same time as) this final assessment of his thoughts on large genera, Darwin composed a further fifty folios on "The principle of divergence" which he interposed between passages on extinction and causes favourable to natural selection, and this in the most crucial chapter of his book which dealt with natural selection itself? From the way he had not interrupted the programme before this time, it would appear that Darwin did not think of adding to chapter six until he had decided to add to chapter four. And we know that he had been intending to supplement this latter chapter ever since the middle of 1857 when he had been forced to change into a new statistical venture, but that it could not be done until he had worked through previous calculations and drawn in more evidence. I suggest therefore that April 1858 was just about the earliest time that Darwin could have paused to take stock of these new calculations and put them in a form suitable for publication.

Was it the new Lubbock type of arithmetic which Darwin modified into his own distinctive technique, that set Darwin on a course where he would eventually collide with divergence? The answer to this question is, I think, yes, but not necessarily because of the coincidence here outlined.

Dispensing with this chronological proximity of two areas of thought, I contend that the points which are important arguments for such a suggestion are twofold. I believe, firstly, that a "principle of divergence" per se did not exist in Darwin's manuscript until he

composed this special account of it in the spring of 1858, and that secondly, the botanical statistics of this late period (July 1857 to April 1858) enlarged the scope of Darwin's understanding of the "coming in and out" of genera through the history of nature.

Taking these points seriatim I shall therefore consider the place of divergence in the Natural Selection manuscript, and the changing role of large genera in evolutionary theory.

## Divergence in the Natural Selection manuscript

It is quite plainly the case that Darwin wrote a substantial piece in the spring of 1858 expressly on "Divergence and correcting chapter VI". Here at last is the appropriate place to ask what then was this "principle of divergence", and how did Darwin explain it in these additional passages? In his autobiography he was emphatic that the principle put forward a "solution" to the phenomenon of divergent lines of development in nature, and stated that it was because:

> " . . . the modified offspring of all dominant and increasing forms tend to become adapted to many and highly diversified places in the economy of nature."[40]

Or, as he had previously said in the Origin, it was the most diverse offspring which managed to live and contribute to the next generation simply because they could acquire or carve out for themselves a "place" in the "economy of nature" which was just that bit different from the others and which therefore gave them an edge over the rest. In the Origin he wrote:

> "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 diversified places in the polity of nature, and so be enabled to increase in numbers."[41]

And this was exactly what he also said in the 1858 manuscript version. It was the most different varieties which survived since they were the ones which could occupy and create as "many places as possible". Writing of "our so-called principle of divergence", he explained:

> " . . . 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 and the extreme species will have a better chance of surviving or escaping extinction, than the intermediate and less modified varieties and species."[42]

To make this idea clear he invoked the then well-known notion of the benefits of a division of labour between the various parts of an association. In Darwin's eyes this meant that absolutely more forms of life could be supported in one area if they all performed different roles which were distinctly demarcated from each other:

> "We may go further than this and . . . assert that a greater absolute amount of life can be supported in any country or on the globe when life is developed under many and widely different forms than when under a few and allied forms"[43]

Thus since nature was tending to produce many complex forms by natural selection so she was also tending towards a greater diversity within which they could be accommodated. The division of labour allowed many varieties to live only when they were all of a widely diversified nature and deviated enough from their parent species and from each other to permit a relatively peaceful co-existence for all.

So Darwin asserted that the major 'branches' of organic life could be explained by a little-and-often selection for differences and diversity among varieties. The one that was most different would be the one most likely to succeed. If there were many trying to live together then only the most diverse collection would actually manage to do so, for competition struck hardest at forms which were very similar and thus striving for the same 'goals' in life. It was diversify or be done for. Selection therefore favoured difference from the norm, and so lines of modification would be pushed on and on, gathering more accumulated peculiarities until, for instance, the form which was once a small dinosaur found that it was a bird.

In a word, then, Darwin had invented a principle which stipulated that a distinct variety was likely to be favoured by selection. But did this not beg the very question he here strove to answer? By invoking a principle of divergence to account for the dissimilarities found throughout nature and the fact that there were such diverse things as dinosaurs and birds, Darwin was surely explaining <u>difference</u> by saying that <u>differentiation</u> occurred? He had not described why divergent variations actually arose but merely stated that if they did, they were the ones to be favoured. Nor did he entirely avoid a certain circularity in reasoning that varieties were always different from their parents because they were varieties, a tautology if ever there was one.

And again he appears to have contradicted his own point that natural selection was supposed to work by infinitesimally small steps, for

here he claimed that it was in fact the most different forms which survived and reproduced giving rise to an unexpected vision of Darwin as a saltationist. However this last point was brought into the embrace of evolutionary theory as we now understand it, by virtue of the proposal that it was all done at the varietal level: the differences which were thought to make a form more suited for survival were only differences of a minute order, for too much deviation would assuredly lead to the death of the individual concerned or, at the very least, no offspring. A bird with three legs and one wing would not get very far in life. Darwin visualised a nice balance between variations of a greater and lesser extent, where the ones very close to the parent species did not 'turn into' permanent varieties and so died without propagating their like, and where the more marked variations - "the extreme varieties" - would have "a better chance of surviving or escaping extinction".

Nevertheless, with all these encumbrances which scholars have yet to answer in a satisfactory manner, this was the "principle of divergence" as expounded in the Natural Selection manuscript and after. It was accompanied by an important corollary in which Darwin stated that divergence could be seen only in the larger genera, for these were the very forms which presented most varieties and so 'fuelled' the process. Because the large genera had been shown by his former statistical work to be the source of a multiplicity of varieties and hence the site for the 'creation' of new species, Darwin reasoned that here too divergence would be manifest as all these varieties competed among themselves and only the most different would survive. He believed that the "genera now large in any area, are now generally tending to become still larger" since they were manufacturing more and more species as his calculations had shown. And, since there were evidently only very few gigantic genera now existing, Darwin suggested that these large ones eventually split into several smaller genera by the process of divergence.

> "Therefore, from the species of larger genera tending to vary most and so to give rise to more species, and from their being somewhat less liable to extinction, I believe that the genera now large in any area, are now generally tending to become still larger. But what will be the end of this? for we do not find in nature genera of indefinite size, with innumerable species. Here in one way comes in the importance of our so-called principle of divergence: as in the long run, more descendants 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 and the extreme species will have a better chance of surviving or escaping extinction, than the

> intermediate and less modified varieties or species. But if in a large genus we destroy all the intermediate species, the remaining forms will constitute sub-genera or distinct genera, according . . . to the degree of difference between the extreme species of the original genus. Nevertheless the modified descendants from the common parent-stock, though no longer forming what is called the same genus, may still go on becoming more and more numerous, and more and more diversified."[44]

This passage gave, in a roundabout way, all the essential points for Darwin's vision of divergence in action. He stipulated that large genera presented many varieties and that these, under the rule of a suitable division of labour, would survive only if they approached a certain level of diversification from the norm. And large genera almost by definition had more species than most, and the potential for yet further increases in numbers, so was it not reasonable to suppose that they - the large genera - at some point in time broke up into a series of smaller genera through the action of this diversification at the varietal level? All those forms which were not sufficiently different were doomed to extinction, by which process Darwin suggested that more or less 'artificial' gaps were made in the once continuous series of organisms belonging to large genera leaving only the more distinct forms behind. These 'left-overs' were thus called by naturalists 'sub-genera' and, Darwin asserted, they would continue to multiply and modify themselves in the direction that that line had initially taken until they ascended to the rank of genus. Such a "complex action", as he called it, was the "coming in and out" of genera through the history of life: a long continued growth, diversification and splitting of genera into many and unalike lines of modification. It was, in fact, what we now call evolution.

Darwin's ideas on this point were exemplified by preliminary drafts of the well-known diagram which accompanied the Origin and which showed a succession of varieties and the branching paths of modification they might be assumed to take[45]. After explaining to the readers of Natural Selection how he envisaged that natural selection could enforce the total replacement of one species by another modified form (viz. what we now call ~~orthographic~~ phylogenetic evolution), Darwin turned to a discussion of branching evolution and his chart with reference to diversification. "A little reflection", he wrote, "will show the extreme importance of this principle of divergence for our theory":

"Taking a modest glance into futurity, we may predict that

> the dominant genera, now abounding with common and widely diffused species, will tend to be still more dominant for at least some considerable lapse of time, and will give rise to new groups of species, always diverging in character, and seizing on the places occupied by the less favoured forms, whether or not their near blood relations, supplanting them and causing their extermination. The great and flourishing genera both of plants and animals, which now play so important a part in nature, thus viewed become doubly interesting, for they include the ancestors of future conquering races. In the great scheme of nature, to that which has much, much will be given."[46]

So it was evident that large genera and the ideas derived from his botanical calculations were here crucial to an understanding of divergence, and the way diverging lines arose in the history of life. Large genera - the "dominant" forms of the above passage - were to be the source of new branches in the tree of organic development.

With these points in mind it is now appropriate to return to the general theme of this section of my chapter, and to inquire whether Darwin had anything approaching these ideas in his first draft of the Natural Selection manuscript? Were the main features of the "principle of divergence" as put forward above, in evidence in the original chapter VI On Natural Selection, composed one year previously in the spring of 1857?

The most telling feature of any comparison between Darwin's initial writings on natural selection and its ultimate form which included his ideas on divergence, is that the first draft is obscure and woolly on points where the second bears a certain clarity of expression[47]. 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 thus attempted to explain his own conviction that selection could be directional and that favoured varieties gradually became species in their own right.

Without any explanation of divergence Darwin did two things. He emphasised the role of competition and the availability of suitable "places in the polity of nature" (or what we would now call niches) for every step from varietal to specific rank. He did not assume that each successive modification appearing along this line served initially the same purpose which it eventually fulfilled, as, for instance, he well knew that modification of the tail feathers of a pigeon could have been encouraged by selection because the feathers were perhaps useful for aerial stabilisers and not for courtship displays. But nonetheless he

stated that selection was directional and had the appearance of being directed towards certain aims, just as the pigeon's fan-tail got more and more pronounced with successive generations.

He fell back in the Natural Selection manuscript on the phrase "expression of variation in a right direction" to indicate this process, but never, as far as I can see, intended it to convey a sense of progress or notions of internally or externally guided forces which made forms either 'better' or more complex in their organisation. This is an important point, for two recent scholars have proposed that Darwin's ideas of divergence were born out of a desire to explain the progress that the fossil record indicated, and furthermore that he was happy to do so in plainly progressive terms[48]. I find no evidence for such a view.

So Darwin used the phrase "expression of variation in a right direction" as a convenient (if cumbersome) expression for the phenomenon he was later to call divergence. In this first draft of chapter VI he did not even employ the word 'divergence' to describe the branching relationships of life. To emphasise, however, that there was plainly some sort of directional selection he contrasted the results of natural selection by competition with the unstructured and non-directional 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 Ch. 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" to the isolated organism which had it. He wrote in a passage immediately following the last:

> "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 quite an effective argument, yet it laid the onus on natural selection and competition to provide the directing momentum and the availability of 'places' to regulate the speed. So in the longish section on Causes favourable and unfavourable to Natural Selection he worked his way through all the possible changes which could affect or increase the number of ecological nooks or crannies into which a modified variant could slip. This was the only way he could account for the facility with which "modification might thus be added to slight modification in any given direction useful to the animal".

Now contrast this usage of competition and "places" with Darwin's counterpart in the Origin where all is explained by diversification:

> "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 diversified places in the polity of nature, and so be enabled to increase in numbers."[51]

This late (1859) sentiment is perfectly mirrored in his eventual section on the Principle of Divergence, composed some twelve months after he had grappled with the points given above. With a "principle" in 1858 he could now say that it was different modifications which survived:

> "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 and the extreme species will have a better chance of surviving or escaping extinction, than the intermediate and less modified varieties and species."[52]

With a notion of divergence, as in this last passage taken from the 1858 supplement to chapter VI, Darwin did not have to talk of there being a ready-made number of ecological niches waiting for the newly modified variant to come along and occupy it. Instead 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. Hence diversification was a process which would make new niches as and when they were required, with no need for Darwin to labour over an explanation for the phenomenon.

In summary then, I think that Darwin's primary draft of this sixth chapter was focussed on the question of explaining diverging lines of evolution - a "right direction" - without any idea of a principle which might invoke selectional advantages accumulating from a differentiation

from the ancestral stock. To these ends he therefore emphasised competition for a limited number of places and supposed that a "right" modification would fill these places more adequately than other purely random fluctuations. He had no concept of the divergence of varieties and no principle to explain it.

So I now contend that Darwin thought of these points in the interval between draft one and draft two, that is in the period between March 31, 1857 and June 12, 1858. At some time between these two dates he experienced a more or less sudden recognition of the phenomenon and its "solution".

And here there are two telling pieces of substantiating evidence from Darwin's correspondence which give greater weight to my assertion.

Darwin wrote to Hooker on August 1857 describing some more results from botanical calculations, and requesting the loan of further Floras. The reader will remember that this was at a moment in time almost immediately after John Lubbock had encouraged Darwin to change his method of procedure, and that Darwin was therefore anxious to rework Floras which he had previously tabulated. He explained the importance which these results bore to his general theories and added some words on the "principle of divergence" in all its glory. He wrote:

> "If it will all hold good [viz. his botanical calculations] it is very important for me; for it explains, as I think, all classification, ie. 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 . . ."[53]

And that was all he said on the matter. Nevertheless I think these remarks certainly show that Darwin was in August of 1857 bearing down on the very same ideas, and with the same conclusions about them that he was to present in the additional piece on divergence in 1858.

Further corroborative evidence can be derived from his letter of one month later to Asa Gray in which he effortlessly epitomised the whole theory of evolution by natural selection (and which epitome was to be put forward later as part of Darwin's contribution to the Linnean Society paper of July 1858), and included a closely argued paragraph on "one other principle, which may be called the principle of divergence". But to Gray, Darwin preferred to describe the notion not as one which explained large genera increasing and splitting up, but as one grounded in the division of labour which must ensue when so many forms of life

were struggling to increase in numbers. He said:

> " . . . 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."[54]

Both these passages then, the one in August to Hooker and the other to Gray in September 1857, gave the two sides of Darwin's understanding of divergence and how it came about. They were neither of them quite so sophisticated as the ultimate description of this topic, which might perhaps be most easily explained by the mere constraints of letter-writing. However there is, in my opinion, a further reason for this apparent unsophistication and quite real brevity. I believe that Darwin had only just thought of the whole complex notion.

To conclude this sub-section with a resumé of my main points, I would like to remind the reader that Darwin saw fit to revise his chapter dealing with natural selection in the light of his "principle of divergence". Many years later he confessed that this principle had come as something of a revelation to him and at a time well after he had arrived at Down House. In the preceding pages I have therefore tried to show that Darwin had indeed no principle of divergence in his writings at least up to the completion date of the first draft of chapter VI On Natural Selection, March 31, 1857. As his notions of divergence were evidently absent where they could have been useful, and then present some twelve months later in the same context, I feel it fair to infer that he thought of them in the interim. Some substantiating evidence from his correspondence with Hooker and Gray shows Darwin talking of a "principle of divergence" which tallied in general respects with the one put forward in the spring of 1858. And his letters to Gray and Hooker were framed in August and September of 1857. What then was it that helped Darwin to comprehend this concept? Was it perhaps the new method of statistical procedure which Lubbock had demonstrated to Darwin on July 14, 1857? It is to this assertion that I now turn, and to an examination of the significance which large genera held for selection theory.

## The significance of Large Genera for selection theory

Before July 1857 Darwin had available to him all the component parts of the notion that he was to dub the "principle of divergence". His private papers indicated a clear awareness of the three primary elements which went towards such a concept - that is, the branches in all organic nature, the idea of a division of labour, and the importance of large genera in contributing more species - and he even possessed a set of explanations for each of them. These were the ideas which came together and fused with Darwin's recognition of a principle, and which became transformed into something which both explained and dictated the circumstances under which divergence could act.

This was the synthesis which constituted his "principle". For in June 1858 Darwin was to stipulate that divergent branches in existing and long-gone realms of nature were definite and discrete lines of modification because, at the level of species and varieties, the benefits of a suitable division of labour required that only the most diverse or different forms could survive. In turn this view demanded that there were many varieties in existence, for what else was there for competition and a subsequent apportioning of labour to work on, if there were no variations? For these reasons Darwin drew in the results of his botanical statistics to show that it was large genera which supplied the raw material which his theory needed, and demonstrated that these genera were the 'manufacturing house' for varieties. Again in turn, this notion supported his claim that it was the larger and more dominant forms of life which contributed the next array of beings to the world at large, because it was here that more diversification and hence divergence were taking place.

These latter thoughts, so neatly interlocking with each other, were in a nutshell the main thesis of the principle as it eventually came out in the Natural Selection manuscript. Nonetheless despite their evidently close relationship after Darwin had recognised divergence (for what he later took it to be), these three elements were beforehand quite separate concepts each with their own panoply of Darwinian explanation. It is to these three that I now briefly turn to recapitulate the thoughts with which Darwin invested each one.

The first and over-riding element of this triptych was, of course, the notion that life was readily sub-divided into different classes, orders and families which indicated a hierarchy of relationships that

evolutionary theory had to explain. Now Darwin, as I have shown in this and the previous chapter, was always perfectly aware that such a hierarchy was a feature of nature, and, moreover, a feature which had to be accounted for. In his earliest notebook on the transmutation of species in 1837 he even drew a little diagram to portray the various lines of modification, and their arrestment by extinction, which could arise from a single form and so contribute rather different forms to the next generations. Again, after he had finished working on barnacles in 1854 the first thing that Darwin turned to was a detailed study of what it was that made classification systems the way they were. And in the long manuscript that was to be eventually abstracted for the Origin he equally devoted a great deal of attention to the same problem, although now he tended to call it the "expression of variation in a right direction". He even occasionally used the word 'divergence' to describe the phenomenon of branching evolution, as, for example, in 1854 he noted:

> "Nov. 1854. It is indispensible to show that in small and uniform areas there are many Families and genera. 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 tree-like appearance to the natural genealogy of the organised world."[55]

More than this I think is probably here unnecessary, for as I have already pointed out these words, and others like them, do not indicate that Darwin actually understood or professed to ascribe a cause to the phenomenon. But the case still stands that he was writing notes to himself like this which exhibited a clear recognition of the way natural beings were grouped together, from 1837 onwards.

The second element which I hold to be significantly important to the whole idea of divergence, was the so-called rule of the division of labour. The economic philosophy of Adam Smith was here applied to the natural kingdom and many of its protagonists drew striking analogies from this study and social ideals to further their work on the differentiation of, say, the embryo (von Baer) or the physiology of organs or systems (Milne-Edwards) from a primitive and unspecialised structure to one with many parts each adapted to its own specific function. Things could get along more satisfactorily if every merchant, social class, embryonic germ layer or set of cells had a job to do and a job which each did well. The whole would benefit from the diversification of its parts into separate and self-sustaining individual pursuits.

Now Darwin was certainly not unaware of this notion, as indeed he too compared his ideas on diversity with the striving of people against each other[56]. But he tried at first, and especially in 1855 when the idea of a division of labour seemed to excite him most, to relate this evidently beneficial diversification to a combined process of competition and absolute abundance of resources in any one area. He did not therefore have the same sort of idealistic or altruistic opinion that each part was thus 'ordered' or 'put' into the most appropriate place which would serve the community most efficiently. And nor did he suppose that his diversification would lead to the progress that others' would. It was all firmly based on the theme of competition for resources and the struggle between individuals. In January 1855 he wrote on the problem:

> "Now in considering amount of life supported in given area, besides size as an element, as in Trees and Elephant, 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 heath, 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 not final cause but mere results from struggle (I must think out last proposition). Heath, Pine woods, Lakes, Arctic regions many individuals few species. It follows that if there be few species there be many individuals, as compared to the individuals of species, when many exist, in an equal area. So we have to account for fewer species, when not much means to support life, which perhaps is almost self-evident."[57]

Thus in characteristically elliptic vein Darwin mused on what it was that made some areas present a diverse population and others a strikingly poor association of species but yet with seemingly plentiful individuals. He was struggling with the idea of an index of diversity which in modern terms we call the 'biomass' of an area, and suggested that this was primarily the result of competition between different organisms. He noticed that there was a sort of symmetry in the fact that areas which had many species had only few individuals in each one, and conversely that areas with only few species had numerous individuals, and related this latter phenomenon to the possibility that there were "not much means to support life". So between them, competition and the physical environment accounted for the "amount of life supported in given area". There was here no talk of selection actually favouring the most diverse[58].

And the final element of the three which were to go towards Darwin's theory of divergence was that concerned with large genera. As I wrote in a former chapter this topic had been occupying Darwin's thoughts and pencil for many months before July 1857: he had been investigating the incidence of varieties and other factors like commonness and range in the larger genera ever since the beginning of 1855, and by now, in the summer of 1857, was quite convinced that these were groups which dominated the history of life because they presented more of everything. Large genera were seen to be blessed with all possible advantages, as in having more varieties and species to their name, a greater range, and many individuals, and were thus, in Darwin's eyes, most likely to be the source of new species. And in most of his writings about how he envisaged large genera influencing the course of evolutionary processes he put forward a nice little statistical explanation for his point that extinction did not "fall" on these forms as readily as it did on the smaller genera with fewer species. I have referred to this notion in greater detail in the preceding chapter.

In short, Darwin thus possessed all the component parts of the theory that he was to call the "principle of divergence". He was aware of the fact of divergent lines of modification for as long as he had been studying evolution; by 1855 if not before he was familiar with the notion of the division of labour; and he had spent some eighteen months working over the idea that large genera were the "manufactory" of new species.

What then caused these thoughts to fuse? Why did Darwin suddenly realise that they were intimately related and mutually self-explanatory concepts?

I suggest that it was John Lubbock's visit to Down and his revision of Darwin's statistical method which set Darwin on a path different from that which he had previously been following. On 14th July 1857 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". Within a few days Darwin was girding his loins to start again but, this time, properly equipped with a "right" method which he had devised from Lubbock's example.

The changes which Lubbock encouraged Darwin to make led the latter to realise that in regard to results from his statistics, it was not really a <u>relative</u> largeness of genera that counted but, instead, the

crucial point was one of absolute largeness. I have already spoken of Darwin's first attempts at botanical statistics in the preceding chapter, and would now remind the reader that these were essentially directed towards extinction in the small aberrant genera and the lack of it in the large. Here he had been content to put forward results as statements of size where 'largeness' was dependent on being bigger than the standard. Hence he was content to call any genus large as long as it possessed more species than the standard. Now, however, in July, Lubbock made him contrast absolutely large genera of a predetermined size with correspondingly small ones: thus Lubbock told Darwin to compare figures derived from genera with, for example, five species and more, and with four species and under.

I contend that this change in emphasis from a relative to a real bigness of genera forced Darwin to shift his gaze from the interesting problems of extinction and the lack of it in certain genera, to something far more potent. That is, Darwin now looked at the success which big genera so evidently enjoyed and saw that they were the forms favoured in the struggle for life.

And this notion of success in the place of his previous ideas about an apparent lack of extinction in large genera, provided the link which allowed him to collect and fuse the three elements of a principle of divergence. All at once things fell into place. He recognised that large genera had more advantages than most and that their varieties too were superior, so that the successful forms of today were in the very middle of producing the successful forms of tomorrow. What would happen to all these wonderful varieties that the large genera were producing, but that they would diversify and create new niches for themselves as yet more and more advantageous modifications arose? In time this process would contribute new lines of development to the course of life, and divergent branches would split off from the root-stock.

It is my proposal then, that it was, in a word, the success of large genera - so rudely brought to his attention by Lubbock - which permitted these concepts to mesh with each other. Now, when he looked at a large genus its size was a definite statement about its advantages in life: the bigger the better. This was not a maxim that could have arisen spontaneously from Darwin's earlier comprehension of relative size, for there Darwin tended to find just the slightest degree of difference to be sufficient for his purpose. It was as if looking at a finely graduated scale had clouded his eyes to the markedly extreme

qualities which the two ends of it displayed.

The notion of success rather than an apparent absence of extinguishing forces was the 'trigger' which enabled Darwin to conjoin large genera with the idea of the diversification of labour. For here he assumed that large genera produced many successful varieties and that these could only live with each other if there was a suitable division of the resources and organisation available. Formerly, when he was more concerned with the hypothesis that large genera were large because they experienced little or no extinction, he had not needed to ask himself what it was that allowed so many varieties to exist since it was the number of "places in the polity of nature" which determined their coexistence. But now, with these new eyes, he saw that varieties went out and made their own niches through the process of adaptive diversification to different roles in nature. The rule of a division of labour positively encouraged a diversity of populations and the divergence of varieties from the norm. Here then was Darwin's "principle".

## Conclusions

In conclusion, and drawing both this and the previous chapter to a close, I think we can see several interesting points emerging from Darwin's botanical statistics. Insofar as one can decide what historical figures may have been thinking and why they may have thought it, my suggestions for the origins of Darwin's principle of divergence tally well with the development of his ideas on the size of genera - large and small - and the more generalised and less tangible shift in the content of natural selection theory itself. I have here shown that there was more than a simple coincidence in time which linked Darwin's statistics with his recognition of divergence, for botanical arithmetic had a considerable part to play in the actual 'discovery' of this last important addition to his system before its exposition in the Origin. But in these last two chapters I have also shown that Darwin's statistics themselves changed according to the various ways in which he saw the subject to relate to natural selection and evolution. In 1844, in 1854 and in 1857 he worked at transmutation in three rather different ways, and these have here been described each with their characterising features.

At first Darwin concentrated on the dispersal and range of organisms because the then current theory relied on an isolation of forms to

stimulate and preserve new modifications and thus new species. For these reasons he had to provide some means to get both the aboriginal form to the isolated spot and, in turn, the new species away from it if it was ever to play any further role in nature. Here then, in 1844, statistical calculations could not really help or hinder the demonstration. They were not used despite the fact that he seemed to know all about them.

Secondly, in 1854, Darwin decided to work on philosophical problems of classification and taxonomic relationships. Here he wished to remove the topic from the realms of mystical and metaphysical speculation and hit upon a purely arithmetical explanation for the contemporary and problematic issue of aberrance and typicality. He suggested that the former forms were characteristically few in species and individuals, and the latter more numerous. Though this idea did not 'work', so to speak, he was led on to consider the size of genera as a more general feature of the effects of extinction, or its opposite number the lack of extinction. Moreover, he was by now busy writing up his intended book on the whole system of natural selection and consequently saw that botanical arithmetic could also provide valuable evidence that variation did occur in nature to the extent which his theory required. So statistics were carefully employed to further Darwinian ideas in this more mature and extensively documented stage of exposition.

Thirdly and finally, in mid 1857, Darwin was brought to a point where a 'gap' in his notions made itself apparent and - virtually simultaneously - he thought of a principle to fill it. After this happy event Darwin believed that the content of natural selection theory was changed and he consequently returned to certain sections of his work to supplement them with his new precepts. This 'last' stage in the life of his hypotheses was the one destined to see the light of day as the Origin, and was thus the theory that became known to Darwin's contemporaries and his successors as the 'true' natural selection.

One can only wonder what would have happened had Darwin been allowed to finish and publish his big species book in his own time. Would he have uncovered yet another major omission and invented further principles of the same order of magnitude as divergence? But perhaps the real point which we should here notice is that Darwin in his time possessed three - possibly more - distinct approaches to evolution. In the same way as he proposed a gradual transformation of one organism into

another by a sequence of stages, not one of which may be assumed to have served the same purpose as would ultimately prevail, so we historians might profit by remembering Darwin's theories before the Origin to be explanations collected together to account for then current problems of natural selection in the most advantageous manner possible. Darwinists speak of the 'origin' of the Origin; now perhaps we should talk of the 'natural selection' of Natural Selection?

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## Conclusions

In the opening pages of this thesis I asserted that of all the naturalists who were attempting to order and render coherent a jumble of data relating to the distribution of living beings over the globe, it was the geologist or the man sensitive to the aims and methods of geology who achieved striking generalisations and who established lines of research that subsequently came to dominate the science of biogeography. These were themes which centred on giving historical causes for present day distribution patterns, on the dynamic movements of floras and faunas in conjunction with geological change, and the obligation to provide explanations which reflected above all the parallel between distribution in space and in time. In the preceding pages I have attempted to describe what it was that Lyell, Forbes and Darwin brought to the study of today's organisms which helped them to account for their arrangement in the manner just outlined, and I have also provided information relating to the way in which natural historians and systematists regarded the same phenomena. Now it is appropriate to recapitulate the most significant factors which contributed to this apparent difference in understanding.

In examining the problem of arctic and alpine floras I touched on several notable elements which went towards this seeming dichotomy in thought. Firstly there was the way in which both Darwin and Forbes believed that each assemblage of species found in high latitudes or on mountain summits in Europe had had a history, and had thus experienced a succession of events over time. These were brought about by geological effects such as the elevation or subsidence of their usual haunts, which encouraged and regulated the extension or retreat of the whole body of plants into different regions. Further historical events or changes were wrought by successive acts of creation (on Forbes' part) and by continued speciation (on Darwin's part) which gave rise to a constantly shifting and changing organic and inorganic system.

This view may profitably be contrasted with the belief held by natural historians (outlined in chapter three, The investigation into biological provinces) where floras and faunas were thought to be essentially static associations which had been placed on the earth when and where God had intended them to remain for evermore. In this respect, though men such as Hewett Cottrell Watson had a clear idea of the vast length of time which had elapsed since the Creation and assiduously sought

the laws which regulated the creation of today's beings, organisms were understood to have maintained the same morphological form and the same topographical range from the moment of their origin to the year of Waterloo and beyond. Even increasing evidence to the contrary such as the ready introduction of foreign species to the populations of Great Britain (e.g. the rabbit), Ireland (the common frog), or South America (the horse), and philosophical considerations about the limits of species arising from breeding experiments and classical systematics, did not alter this static view of nature in any fundamental way. Watson, for instance, absorbed all contrary evidence with panache and decreed that it only went to show how the subject of distribution was more complex than usually supposed and how little was known about it.

The reason for the possession of a historical sense hinged in the first instance on the very nature of geology in the earlier years of this century. Forbes and Darwin were completely steeped in the comparative study of strata and systems and so thought of geological structures in terms of a succession of changes in state. When they regarded discrete populations of animals and plants they saw each of these to represent by analogy a sort of 'living' stratum and to change its boundaries and its relations with other 'living' strata over time. Moreover, at a detailed level, their espousal of Lyellian gradualism made them especially aware of the manner in which every geological occasion blended into the next by a gentle shift or transmutation of the natural forces then in action. This made it possible for them to think of a world which was constantly in motion and always in the throes of changing from one state of affairs to another, and hence of a world where the past was indissolubly linked to the present.

Thus our two geologists comprehended living associations to be part of a continuous process of change and wrote of the fluctuations of one or many specific ranges according to land movements. Arctic plants were held to have increased their area far to the south when suitably cool temperatures were combined with particular topographical configurations, and to have retreated at a later time in response to different conditions. The tendency within natural historical circles, however, was to ascribe disjunct ranges such as these to a multiple creation of some sort or another. Joseph Hooker, although never irretrievably fixed on the latter notion, was too much of a topographical botanist to accept certain features of either Darwin's or Forbes' proposals. This reluctance, I suggested, was due to his inability to fully appreciate

the stratigraphical and historical assumptions on which Darwin and Forbes proceeded.

Yet Forbes did not go as far as Darwin did in his espousal of geological and biological changes over time. When they both came to explain the existence of similar but not absolutely identical populations of arctic and 'arctic-like' plants they diverged according to their own personal preferences: Forbes for a section of his theory of "representation" through space and time which stipulated that God had created two geographically separated floras with analogous or "representative" forms of life; and Darwin for a section of his evolutionary theory which enabled him to extend his account of arctic and alpine plants to encompass ideas about a trans-tropical migration of species from the northern hemisphere to the south. Nevertheless, these explanations were both historical ones that can be seen to have differed only in degree when compared to more 'topographical' or natural historical suggestions to account for the same phenomena.

Turning to look at the two theories of nature proposed by Forbes and Darwin, these too support my thesis. Both men recognised the importance of understanding purely spatial phenomena so that the sequence of fossil organisms which came into and went out of the geological record could also be elucidated. They studied distribution in space to find out about the occurrence of living beings over time and the facts discerned from their topographical studies were fully integrated into wider and more general schemes for nature. This point is in itself valuable for historians since it explains why, in the first instance, geologists were bothering their heads over geographical distribution at all. With their heightened appreciation of the actualistic method they conscientiously investigated the living world to explicate the fossil, and the arrangements of organisms existing in the modern epoch were held to be vital clues for understanding the succession of extinct species with which they were preoccupied.

But these remarks bring me to another important reason for a seeming difference in comprehension between geologists and systematists. Forbes and Darwin quite evidently possessed well worked out and comprehensive theories of nature in all her diversity and separate dimensions. Forbes' ideas on "representation" explained, to him at least, the fact that there were analogous forms of life which replaced each other in a topographical sense and in a geological sense also; these notions were developed to support an assertion that there was in the natural world an all pervading "principle of polarity" which regulated the

appearance and disappearance of ancient forms of life. These ideas formed the substance of chapter two, The problem of representative species. Darwin's theory of evolution is, of course, better known to historians and I therefore refrained from describing it in all its complex rotundity in favour of a system whereby his explanations for precise points are given. Hence his theory is touched on in chapters one and two, where he accounted for the origins of arctic floras and 'representative' species, and in chapters five and six, Charles Darwin's botanical arithmetic 1836-1857, and the same, 1857-1858.

Here it can be seen that Lyellian geology encouraged its two enthusiasts to formulate their own views about the history of life and to propose grandiose schemes which embraced all natural phenomena. Even though these views were designed in antithesis to those which Lyell had set out in the Principles, and claimed that the fossil record was a record of serial not cyclical change, they were quite plainly theories of nature. By contrast, botanists such as Hooker and his zoological contempories were either struggling to articulate the basic axioms on which similar but essentially topographical schemes might be erected, or remained content to merely collect and describe distributional data with few speculations about its origins. Hooker, despite his contact with geological thought and his own desire to make a science out of spatial biogeography, could not ascend to some generalised explanatory model or system because, to him, there always seemed to be important exceptions to every statement. His knowledge of botanical fact was so great that he would not allow himself to pursue one explanation to the exclusion of all others, and so we find (chapter two) that although he was in a particularly advantageous position to solve or to make clear the problems which surrounded the existence of geographically 'representative' species, he was unable to do so.

The distinction which I am making here between a propensity, on the one hand, for geologists to theorise over the distribution of life and the neglect, on the other hand, of this faculty by natural historians, was more subtle than this first characterisation might suggest. In chapter three, The investigation into biological provinces, I described how natural historians were deeply concerned to understand the scheme of nature and how, from the time of Linnaeus, the study of geographical distribution and the delineation of the characteristic features of biological provinces was taken to be one of the prime routes towards an answer for the ultimate nature of the animate and vegetable kingdoms.

Hence botanists and zoologists were just as interested in the overall plan for living beings as were geologists. And in the following chapter (on Statistics in distribution studies), I showed how Hooker and Alphonse Decandolle attempted to put this inquiry onto what was then regarded as a scientific footing by the employment of botanical arithmetic, and by proposing that a proper collection and analysis of statistical data would ultimately lead to the revelation of the grand laws of nature and creation. Naturalists therefore thought that the best way to uncover God's plan was to collect more and more facts about it and to collate these in such a way that regularities must eventually be discerned. It would perhaps be accurate to say that their theory was that they should have no theory, at least until such a time as more evidence was available. This quasi-Baconianism dominated natural history to such an extent that even when oddities of distribution were made apparent through the use of botanical and zoological arithmetic and statistical tables of the sort described in chapter four, very few naturalists profferred an explanation for them.

It will be remembered, however, that when geologists adopted statistical techniques these arithmetical methods were employed solely for the vindication of theoretical statements about the history of the earth and its organisms. Both members of the Brongniart family, for instance, and Lyell used statistics of floras and faunas through time to support different accounts of the successive forms of life which had occupied the world and the series of environments under which they had existed. Furthermore, Darwin too used statistical methods gleaned from natural history to justify and expand on his system of evolutionary change.

The significance of having a theoretical scheme to direct one's thoughts is here demonstrated in two ways. Firstly, in terms of sheer results, geologists managed to produce explanations for distributional phenomena where natural historians omitted to do so. But secondly - and more notably for historians - it meant that scientists were not hamstrung by their own methods. To men such as Darwin statistical procedures were only a useful tool to uncover internal consistencies in nature which were explicable by some larger hypothesis, or a device by which ideas could be tested and further confirmatory evidence be drawn in to a more substantial body of facts. Thus in Darwin's statistical work (chapters five and six) we see him using this technique only where he thinks that it might be useful, and in a manner whereby many different facets of nature were investigated and correlated together. He had no

compunction about discarding practically all his botanical calculations when composing the Origin because there they would not materially advance his thesis. Alphonse Decandolle on the other hand, devoted the whole of his Géographie botanique raisonnée to the tabulation of data equivalent to Darwin's, as an end in itself. Darwin put in the results and left out the data where Decandolle did just the reverse.

In retrospect we can see that naturalists such as Hooker were, by contrast, more or less confined by their self imposed methodology. He and Decandolle were committed to supplying ever more information and to encouraging a proliferation of data which could be ordered by statistical conventions but not theorised over. However, although neither of these eminent naturalists would have denied that the eventual purpose of all descriptive detail was to enable the identification of one or more great laws of nature, they were plainly set upon a path which was not leading them directly to the desired goal. Of course, at the time, botanical arithmetic seemed like the perfect answer, for it was a method which clearly brought mechanical and intellectual order into a discipline which was then fuelled with a plethora of unarranged and confusing data, and it was, additionally, a method which was in tune with the mathematical tenor of nineteenth century science. But this immediate gain was, in a historical sense, to be offset by the disadvantages inherent in an approach to nature which so emphatically disavowed speculation and explanation.

Why then, we might ask, did such a situation come about? Why, when natural historians possessed just as much interest in the study of distribution and an equally strong desire to reduce the phenomena to general laws and to make it into a proper science, did the formative influence come from geological quarters?

Looking at these questions from our twentieth century vantage point, the reason for the apparent 'success' of geologists in the field of biogeography centres on the fact that they came to examine associations of living beings fully equipped with ideas about how and why organic nature disported herself the way she did, and primed also with a set of notions about the geological structure of the earth which provided immediately useful analogies and models for understanding the distribution of modern forms of life. Not surprisingly, the complementary 'failure' of natural historians to come to grips with distribution through time and space depended on their notions and the presuppositions

which they too brought to this study. Natural history was traditionally a descriptive and comparative science which was interlaced with similarly descriptive social and economic spheres of thought, and when individuals of the late eighteenth century turned to investigate distribution they - like geologists - took their metaphors and analogies, and particularly in this case, their methods of analysis, from past experience and from these familiar partners.

But discarding any evaluation of comparative success and failure with reference to modern biogeography, what else can be discerned from the patterns of geographical inquiry which I have described in this thesis?

What I find surprising is that distinct attitudes such as these two lines of thought can have existed at all in such a closely circumscribed area of investigation as biogeography. After all, this is merely the study of the distribution of animal and plant life and, as such, would hardly suggest to the historian that it was a subject composed of a variety of traditions and attitudes relating to the data concerned. Yet this seems to be the case. Along with many modern historians I believe that the biological sciences in the earlier half of the nineteenth century were much more complex than popularly supposed, and that each discipline or field of study was an intricate mixture of many lines of inquiry, diverse attitudes, approaches and aims. Without a due appreciation of this complexity it is easy to overlook the richness and high degree of sophistication which the natural sciences of that century presented. On my part, I have described the composite nature of early biogeography and pointed out the diverse threads which can be drawn out of this one subject. And in particular, I have outlined a historical situation where personal preferences, professional experiences and intellectual traditions played an important role in inducing different ways of thought.

In this last respect, scholars are only too familiar with the personal prejudices and preconceptions which affect the manner in which scientific phenomena are perceived and understood. But here I think we have something more fundamental to take note of. Extrapolating from my study of the early years of biogeography, it seems that nineteenth century naturalists, far from advancing fearlessly into the uncharted territories of future knowledge equipped with methods appropriate for the task of discovery which lay ahead of them, proceeded to investigate nature with the tools which were immediately to hand. These, more often than not, had been drawn from the intellectual heritage of each subject

and modified in an almost ad hoc fashion to supply whatever was required.

Darwin, for instance, unthinkingly transferred a tried and trusted method of statistical calculation from one problem to another - barely related - one. In a similar fashion, naturalists used their professional experience and the collective wisdom of their forebears to elucidate new fields of study such as the geographical distribution of organisms. Thus, when confronted with fresh and unexplored areas of natural inquiry, men of the nineteenth century ordered their researches according to what they already knew and applied their knowledge in the manner to which they were accustomed.

So much is perhaps obvious to the historian of science. What I want to say, however, is a little more subtle. The important point is that the past history of a subject, whether it be only recent as in the case of nineteenth century geology, or of long standing as in that of natural history, had a notable effect on the content of biological science in the years 1840 - 1860. This is shown particularly effectively in the growth of composite disciplines such as biogeography where the traditions of its two 'parent' sciences continued to exist as more or less separate enquiries for a number of years.

Can we therefore talk of the procession of events which make up the story of science as a kind of evolutionary process, where every occurrence has to be considered not only in its immediate context, but also in terms of its own past?

An organ such as the eye is believed to have passed through many graduated steps from a single light sensitive ganglion to the complicated structure which enhances the mammalian senses. We know well that Darwin, and others after him, stressed that every stage in this process was caused by adaptations to prevailing conditions and not through a development towards some predetermined goal. Modern historical scholarship reflects this view through portrayals of the intellectual and social milieu which surrounded individual figures and their ideas. However there can be no adaptations without something to adapt, and Darwin also emphasised that each stage in a series was a modification of the structure which preceded it. Historians can yet find much to interest them in 'developmental' accounts of the growth of science.

## Notes

Full details of all works mentioned in the notes may be found in the Bibliography. Conventional contractions are used for the titles of Journals, and a few abbreviations are used consistently throughout:

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| Darwin, Charles | On the Origin of Species by Natural Selection, or the preservation of favoured races in the struggle for life. London, Murray, 1859. A Facsimile of the First Edition with an Introduction by Ernst Mayr. Cambridge, Mass., 1964. Referred to as Origin. |
| Darwin, Charles | Charles Darwin's Natural Selection, being the second part of his Big Species Book written from 1856 to 1858. Edited from manuscript by R.C. Stauffer. Cambridge University Press, 1975. Referred to as Natural Selection. |
| Darwin, Francis | The Life and Letters of Charles Darwin, including an Autobiographical Chapter. London, Murray, 1887. Referred to as Life and Letters CD. |
| Darwin, Francis and Seward, A.C. | More Letters of Charles Darwin. A record of his work in a series of hitherto unpublished letters. London, Murray, 1903. Referred to as More Letters. |
| De Beer, Sir Gavin | Charles Darwin and Alfred Russel Wallace. Evolution by Natural Selection [A Transcript of the Sketch of 1842 and the Essay of 1844]. Cambridge University Press, 1958. Referred to as Sketch and Essay respectively. |
| Huxley, Leonard | Life and Letters of Sir Joseph Dalton Hooker ... Based on materials collected and arranged by Lady Hooker. London, Murray, 1918. Referred to as Life and Letters JDH. |
| Lyell, Charles | 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, 1830-33. Referred to as Principles. |

Manuscripts from the Darwin Archive, University Library, Cambridge are given as catalogued in the Handlist of Darwin Papers at the University Library Cambridge, and are referred to as 'Darwin MS . . .'. Many notes allude to material which is inconsistently paginated, if at all: Darwin's letters are here given as 'letter number . . .', and Hooker's letters are referred to by the page number of the first leaf.

## Notes to the Introduction

1. Darwin MS 114, letter 27, 10th February 1845.

2. Good, Ronald The Geography of the Flowering Plants (fourth edition). London, Longman, 1974, p 10. I was surprised to see, however, that Good uses the same quotation for the half-title of his work.

## Notes to the Prologue

1. Whewell, William The Philosophy of the Inductive Sciences, founded upon their history (second edition). London, J.Parker, 1847, p 638.

2. Porter, Roy The Making of Geology. Earth Science in Britain 1660-1815. London and Cambridge, CUP 1977; Davies, G.L.The Earth in Decay: A History of British Geomorphology, 1578-1878. London, 1969; Rudwick, M.J.S.The Meaning of Fossils. London and New York, 1972. See especially Porter, 91-111.

3. Whewell op cit note 1, 645-5.

4. Lyell, Charles 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, 1830-33.

5. Smith, William Strata identified by organised fossils, containing prints on coloured paper of the most characteristic specimens. London, 1816. See also Porter op cit note 2, 112-27, 160-83.

6. Rudwick, M.J.S.'The Strategy of Lyell's Principles of Geology'. Isis 61 (1970) 5-33; Bartholemew, Michael 'Lyell and Evolution: an account of Lyell's response to the prospect of an evolutionary ancestry for Man'. Brit. J. Hist. Sci. 6 (1973) 261-303. See also the various works on Lyell by Leonard Wilson, and the volume of the British Journal for the History of Science devoted to the papers delivered at the Lyell Centenary Symposium, 1975, Brit. J. Hist. Sci. 9, part 2 (1976).

7. Darwin, C.R.'Geological notes made during a survey of the east and west coasts of S. America, in the years 1832, 1833, 1834 and 1835, with an account of a transverse section of the Cordilleras of the Andes between Valparaiso and Mendoza'. Procs. Geol. Soc. 2 (1836) 210-12; 'Observations of proofs of recent elevation on the coast of Chile, made during the survey of HMS Beagle . . .'. ibid. 2 (1837) 446-9; 'A sketch of the deposits containing extinct Mammalia in the neighbourhood of the Plata'. ibid. 2 (1837) 524-44; 'On certain areas of elevation and subsidence in the Pacific and Indian oceans, as deduced from the study of coral formations'. ibid. 2 (1837) 552-54; 'On the connexion of certain volcanic phenomena, and on the formation of mountain-chains and volcanoes [sic] as the effects of continental elevations'. ibid. 2 (1838) 654-60.

   These, as well as Darwin's other papers, are reprinted in Barrett, P.H.

## Notes to the Prologue

The Collected Papers of Charles Darwin. Chicago, Chicago University Press, 1977.

The quotation comes from Darwin, Francis More Letters of Charles Darwin. A record of his work in a series of hitherto unpublished letters. London, Murray, 1903, volume II, p 117. Hereafter cited as More Letters.

## Notes to Chapter 1

### The Problem of Arctic and Alpine Floras

1. As described in Rowlinson, J.S. 'The theory of Glaciers'. Notes and Records Roy.Soc. 26 (1971) 189-204.

2. Reprinted in De Beer, Sir Gavin Charles Darwin and Alfred Russel Wallace. Evolution by Natural Selection. Cambridge, 1958. Hereafter referred to as Sketch and Essay respectively. The original manuscripts are Darwin MSS 6 and 7 respectively.

3. Forbes, Edward 'On the distribution of endemic plants, more especially those of the British Islands, considered with regard to Geological changes'. Report to the British Association for the Advancement of Science 1845 (1846) 67-8; and 'On the connexion between the distribution of the existing Fauna and Flora of the British Isles and the geological changes which have affected their area, especially during the epoch of the Northern Drift'. Mem. Geol. Survey London I (1846) 336-432. The latter is hereafter referred to as 'On the connexion etc.'

4. Darwin, C.R. On the Origin of Species by means of natural selection, or the preservation of favoured races in the struggle for life. London, Murray, 1859, pp 365-80 and especially pp 366, 372. Hereafter referred to as Origin.

5. See for example Gmelin, J.G. Flora Siberica sive historia plantarum Siberiae. St Petersburg, 1747, where he deduced from this fact that the same species had been created on diverse spots of the earth's surface.

6. Watson, Hewett Cottrell 'Observations made during the summer of 1832 on the temperature and vegetation of the Scottish highland mountains'. Edin. New Phil. J. 14 (1833) 317-23; and also Outlines of the geographical distribution of British plants belonging to the division of Vasculares or Cotyledones. Edinburgh, privately printed, 1832, and Remarks on the geographical distribution of British plants; chiefly in connection with latitude, elevation and climate. London, Longman, 1835.

   It is perhaps hard to remember that the flora of Scotland was still relatively unfamiliar to botanists of the 1830's. Robert Graham spent much of his publishing career devoted to detailed lists and descriptions of new species discovered in Scotland. vide Graham's many contributions to the Edinburgh New Philosophical Journal through that decade.

   Apropos of Watson's unfortunate experiences of Scottish weather, see his Cybele Britannica; or British plants and their geographical relations. London, 1847-59 and subsequent volumes, volume I, 21-2, for a delightful description of the hardships of botanical excursions.

7. Discovered by Forbes whilst accompanying Capt. Graves on his surveying voyage of the Aegean Sea in 1841, but first mentioned by him in his 1846 memoir as in note 3.

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8. Humboldt, Alexander von Essai sur la géographie des plantes; accompagné d'un tableau physique des régions équinoxiales. Paris 1805 [1807]. There is a facsimile edition of the first part of this work issued by the Society for the Bibliography of Natural History, Sherborn Fund Facsimile No. 1.

9. De distributione Geographica Plantarum secundum coeli temperiem et altitudinem montium Prolegomena. Paris, 1817. This was an extensively revised edition of the Essai as in note 8.

10. Principles II, 169-72.

11. Huxley's own description of Forbes as in Huxley, Leonard Life and Letters of T. H. Huxley. London, Macmillan, 1900, volume I, 94, 116, and Huxley's obituary of Forbes in the Literary Gazette & Journal of Science and Art No. 1975 (Nov 25, 1854) 1016-18.

12. Mills, Eric L. 'Edward Forbes, John Gwyn Jeffreys and British dredging before the Challenger expedition'. J. Soc. Biblphy. Nat. Hist. 8 (1978) 507-36.

13. Allen, David Elliston The Naturalist in Britain: A Social History. London, Allen Lane, 1976. My citations are from the paperback edition from Penguin Books, 1978, pp 84-7, 130.

14. An unlikely but notable source by which to gauge his senior standing is to be found in the famous lithograph of eminent scientists partaking of a banquet inside a model of a dinosaur created for the Great Exhibition of 1851. Alongside Murchison, Buckland and Owen sits Forbes.

15. Since I do not intend to describe these 'laws' in the text, I can epitomise them here. Firstly, Forbes proclaimed that the depth to which a marine species could range was proportional to its geographical extension in a horizontal direction: that is, "the extent of the range of a species in depth is correspondent with its geographical distribution". See his 'Report on the Aegean invertebrata', B.A.A.S. 1843 (1844) 130-93, p 171. Secondly, in the same paper, he asserted that as there were zones on a mountain side so there were zones of depth on the sea floor, and each one contained a flora and fauna analogous to its latitudinal parallel: "parallels in latitude are equivalent to regions in depth, correspondent to that law in terrestrial distribution which holds that parallels in latitude are representative of regions of elevation" ibid p 175.

16. op cit in note 15.

17. 'On the light thrown on Geology by Submarine researches . . .'. Edin. New Phil. J. 36 (1844) 318-27, and reprinted in Ann. Sci. Nat. 4 (1845) 117-29.

18. Horner, Leonard 'Anniversary address to the Geological Society of London for 1844'. J. Geol. Soc. 2 (1846) 145-221, p 161, and the same, 1845, J. Geol. Soc. 3 (1847) xxii-xc, p xxxviii. There is a

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copy of Forbes' paper which carries Horner's manuscript queries and appreciations in the British Museum (Natural History) General Library L 6 o F(3).

19. For his election to the chair of Natural History see the other contender's diary where he complained about the powerful backing that was being brought to bear in Forbes' favour: Traill papers, National Library of Scotland No. 30 (1852) and No. 31 (1853). Traill was heir apparent to Robert Jameson and the man who stepped in to complete Jameson's course of lectures during his long illness and after his death.

20. Autobiography of Charles Darwin as printed in Darwin, Francis The Life and Letters of Charles Darwin, including an Autobiograpical chapter. London, Murray, 1887, volume I, 26-107, p 88. This work is subsequently referred to as Life and Letters CD.

21. Principles II, 121.

22. Especially from Darwin and Hooker who wrote a fairly vitriolic series of letters to each other in 1845-6 on the subject. See More Letters I, 51, 55, 412; Life and Letters CD II, 38; Darwin MS 100, pp 25, 30, 69 and MS 104, pp 208-9 (misbound), 205, 188. See also D'Archiac, A.'Examination of Prof E.Forbes's views on the Geographical Distribution of British Plants'. Edin. New Phil. J. 48 (1850) 23-34 for a further critical opinion.

23. 'On the connexion etc.', p 350.

24. See for example Rudwick, M.J.S.'The Glacial Theory'. Hist. Sci. 8 (1970) 137-57; Hansen, Bert 'The Early History of Glacial Theory in British Geology'. J. Glaciol. 9 (55) (1970) 135-41; and North, F.J.'The Centenary of the Glacial Theory'. Procs. Geologists' Assoc. 54 (1943) 1-28.

25. After Lyell had proposed the term "Pleistocene" it seems that Forbes was one of the few geologists who adopted it in preference to the term 'newer Pliocene', vide 'On the connexion etc.', p 343.

Agassiz's contributions were as follows: Agassiz, Louis 'Upon glaciers, Moraines and Erratic Blocks; being the Address delivered at the opening of the Helvetic Natural History Society at Neuchatel on 24th July 1837', reprinted in Edin. New Phil. J. 23 (1838) 364-83; and 'On Glaciers, and the evidence of their having once existed in Scotland, Ireland and England'. Procs. Geol. Soc. 3 (1840) 327-32.

26. 'On the connexion etc.', p 345.

27. loc cit in note 26.

28. He was supported by considerable geological evidence, and by a map appended to Lyell's Principles which illustrated all the regions which had recently been under water during the Tertiary. Here, Europe was swathed in sea. Principles II, 304.

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29. 'On the connexion etc.', p 351.

30. Murchison, R I 'Presidential Address to the British Association 1846' B.A.A.S. (1847) xxvii-xlii, pp xxxiii-xxxiv.

31. Horner, Leonard 'Anniversary Address' to the Geological Society 1845, as in note 18, p lv.

32. Especially when others were hot to vindicate Lyell's claims for priority. See Horner ibid pp lxv-lxvi, and Hooker, J.D. Introductory Essay to the Flora Novae Zelandiae. London, 1853-55, pp xxii-iii.

33. op cit in note 3.

34. More Letters I, 408.

35. Sketch p 66. I might here add that in the manuscript the three paragraphs with which De Beer continues this passage were secondary interpolations by Darwin. They were added by Darwin on the verso and marked with his usual symbol for such insertions. This is probably why the printed version appears disjointed. The passage here quoted is, in manuscript, immediately followed by that of note 40.

36. Principles II, 169-76.

37. ibid 141.

38. ibid 170-71.

39. ibid 173.

40. Sketch 67.

41. Essay 180.

42. ibid 181.

43. Transcribed and printed by R.C. Stauffer as Stauffer, R.C. Charles Darwin's Natural Selection: being the second part of his Big Species Book written from 1856 to 1858. Cambridge, 1975. Subsequently referred to as Natural Selection.

44. ibid 535, 536, 544.

45. ibid 540. For other equally clear statements see pp 535-6, 537.

46. ibid 542.

47. ibid 544.

48. ibid 549. "All the intertropical productions would be in some slight degree distressed."

49. More Letters I, 437.

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50. Darwin recollected in 1858 that Hooker had read his 1844 Essay "some dozen years ago", Life and Letters CD II, 117. He was more or less right as evidenced by letters written to Hooker at the end of 1846 and beginning of 1847, vide Darwin MS 114, letters 78-83.

51. More Letters I, 95.

52. Perhaps only because Forbes himself had attempted to correlate the distribution of boreal molluscs with the glacial sea. See Forbes 'On the connexion etc.', pp 361-403, especially pp 376-93.

53. Darwin MS 50, glacial sequence folio 9, and transcribed in Natural Selection 531.

54. More Letters I, 437. The reference for Darwin's letter of the 4th November as mentioned is ibid 435.

55. ibid 438.

56. ibid 439.

57. ibid 439-40.

58. Darwin MS 100, p 111, 22nd November 1856.

59. Life and Letters CD II, 86-7, 23rd November 1856.

60. As in note 58.

61. Principles II, 57. Useful works relating to nineteenth century ideas about time are: Toulmin and Goodfield The Discovery of Time. New York, 1965; Whitrow, G.J. The Natural Philosophy of Time. London, Nelson, 1961; Berry, W. The Growth of a Prehistoric Timescale. np, 1968; and Buckley, Jerome H. The Triumph of Time: A Study of Victorian Concepts of Time, History, Progress and Decadence. Cambridge, Mass., 1967.

62. On the MS Darwin has written a firm "No" beside Hooker's remark. See note 58.

63. Life and Letters CD II, 87.

64. Forbes, Edward 'On the Manifestation of Polarity in the Distribution of organised beings in Time'. Proc. Roy. Inst. London 57 (1854) 428-33, p 432.

65. Horner, Leonard op cit note 18, p xxxvii.

66. One need only cite the Murchison and Sedgwick controversy over the age of deposits on the chronological boundary between Murchison's Silurian and Sedgwick's Cambrian systems, or that which raged over the supposed contemporaneity of the Old Red Sandstone and Devonian shales. Much of the first geological work undertaken in north America by European geologists was directed towards establishing that this region possessed the same sequence of beds and hence the same

geological time scale as in Europe.

67. Principles III, 53-8. See also p 22 for Lyell's statement that there is no periodisation and all blends gradually.

68. Horner op cit note 18, p xxxvii. I might here note that Forbes too considered geological periods to be 'parcels' of time. See his 'On the connexion etc.', p 402.

69. Royal Botanic Gardens Kew, JDH Antarctic letters 1839-43, no foliation but see letter 1st June 1842 from Hooker to Chas. Lyell senior, from the Falklands, where he writes that he has seen huge icebergs up to five miles long and assumes that blocks of stone must be frozen into its structure. However, he added, these are rarely exposed to view:

> "It is doubtless from this cause [surface snow] that among the many thousands of icebergs encountered, so few seemed to be transporting fragments."

But see also letter 90 to the same recipient 3rd April 1843, off the Cape of Good Hope, where he saw recently calved floes "transporting boulders of rock from the adjacent shores".

70. Natural Selection 536 where Hooker's notes are given as footnotes to Darwin's text and marked appropriately.

71. ibid 575, Hooker's Note A. And in an unpublished letter Darwin MS 100, p 105 he reiterated, "If icebergs are to be so powerful why did they bring no Greenland, American or other plants to these islands [Iceland, Faroes and Spitzbergen] which are so well situated for this purpose".

72. I must add however that Hooker never neglected the fact that there were also species on islands that were undoubtedly either remnants of some earlier flora or the products of special creation. The colonists were recognised to be relatively recent introductions. It was only Darwin - and perhaps von Buch - who suggested that all island floras were derived from accidental migration coupled with some subsequent change of form. For von Buch's views and their relationship with Darwin's earliest (notebook) theories, see Kottler, Malcolm 'Charles Darwin's biological species concept and theory of geographical speciation: the transmutation notebooks'. Annals Sci. 35 (1978) 275-97, pp 284-7.

73. Introductory Essay to the Flora Novae Zelandiae 1853-5, p xxiv footnote.

74. loc cit note 73.

75. Map immediately after Note A Darwin MS 100, p 109 et seq. This is not reproduced in Natural Selection with the rest of Hooker's comments. The quotation comes from the same passage as in note 71.

76. Principles I, 97-130. The climate theory formed an essential part

of Lyell's thesis for by these local changes in land and sea he could account for all previous climatic conditions, usually considered to be the result of a progressive and unidirectional cooling of the globe. By removing directional cooling, Lyell was obliterating one of the most powerful arguments against his doctrine of a steady-state earth. For a detailed discussion of Lyell's overall aims for such a climate theory see Ospovat, Dov 'Lyell's theory of Climate'. J. Hist. Biol. 10 (1978) 317-39.

77. Introductory Essay to the Flora Novae Zelandiae pp xxiii-v.

78. Trans. Linn. Soc. London 23 (1862) 251-348.

79. I am here speaking loosely of two ideas as if they were really one - as, in effect, they were. There is a difference between a flora that is spread out to the full extent of its range, and a flora that is gradually diffusing from one central source. The latter usually ends up as the former, and in modern evolutionary biology we assume that the former is the result of the latter. But it was not always so in the nineteenth century. However I feel that I am justified in amalgamating the two views in this discussion for both Forbes and Darwin believed in the diffusion of a whole floral assemblage from a single centre to the full limits of its range. The difference between these two ends of the scale was thus one of degree only and correlated with the length of time that a naturalist was to allow in the construction of his theories. The Pleistocene was here certainly long enough to permit a full diffusion of arctic plants from their source to the areas they were to occupy for the rest of the period.

## Notes to Chapter 2

### The Problem of Representative Species

1. Origin 399-403.

2. For modern appreciations of the differences between geographical races and representative species see: Good, R. The Geography of the Flowering Plants (fourth edition). London, Longman, 1974, pp 250-3; Mayr, Ernst Populations, Species and Evolution. Harvard University Press, 1970, especially chapters on 'Geographical variation', and the 'Polytypic species of the Taxonomist', pp 186-213; Polunin, Nicholas Introduction to Plant Geography and some related sciences. London, Longman, 1964, pp 201-4.

3. Egerton, F. N. 'Studies of Animal Populations from Lamarck to Darwin'. J. Hist. Biol. I (1968) 225-59, and his PhD thesis Observations and Studies of Animal Populations before 1860; A Survey concluding with Darwin's Origin of Species. University of Wisconsin, 1967. See also Richardson, R.A. The development of the theory of geographical race formation: Buffon to Darwin. PhD thesis, University of Wisconsin, 1968; Stauffer, R.C. 'Ecology in the long MS version of Darwin's Origin of Species and Linnaeus' Oeconomy of Nature'. Amer. Phil. Soc. Procs. 104 (1960) 235-41, and his 'Haeckel, Darwin and Ecology'. Quart. Rev. Biol. 32 (1957); Limoges, Camille La Sélection Naturelle. Presses Univ. de France, 1973, chapter 2; Kottler, Malcolm 'Charles Darwin's biological species concept and theory of geographical speciation: the transmutation notebooks'. Annals Sci. 35 (1978) 275-97.

4. Lacordaire, Theodore 'On the Geographical distribution of Insects'. Edin. New Phil. J. 27 (1838-9) 94-111, 333-51, and ibid 28 (1839-40) 170-83, 224-38, p 97.

5. Agassiz, Louis Essay on Classification, sections I-XVIII, from Contributions to the Natural History of the USA 1857, quoted from Davenport, Guy The Intelligence of Louis Agassiz. A Specimen Book of Scientific Writings, Boston, 1963, pp 68-9.

6. Milne-Edwards, Henri 'Scientific Intelligence, Zoology'. Edin. New Phil. J. 22 (1837) 397-9, p 398.

7. Lacordaire op cit note 4, pp 182-3.

8. Forbes, Edward 'Presidential Address delivered at the Anniversary Meeting of the Geological Society of London'. Quart. J. Geol. Soc. 10 (1854) xix-lxxi, especially pp lxxvii - end.

9. Forbes, Edward 'On the manifestation of Polarity in the distribution of organised beings in Time'. Procs. Roy. Inst. London 57 (1854) 428-33.

10. ibid 428.

11. MacLeay, William Sharp Horae Entomologicae London, 1819-21. See also Windsor, Mary P. Starfish, Jellyfish and the order of Life. Issues in

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nineteenth century science. New Haven and London, 1976, pp 82-97.

12. Galloway, D. J. 'The botanical researches of William Swainson in Australasia 1841-55'. J. Soc. Biblphy. Nat. Hist. 8 (1978) 369-79.

13. As defined in Swainson, William A Treatise on the Geography and Classification of Animals. Lardners Cabinet Cyclopaedia, 1835, pp 237-43, and in more detail in Swainson, W. and Richardson, J. Fauna Boreali-Americana; or the Zoology of the northern parts of British America. London, Murray, 1831.

14. Forbes op cit note 9, p 428.

15. Forbes, Edward 'On the connexion between the distribution of the existing Fauna and Flora of the British Isles, and the Geological changes which have affected their area . . .'. Mem. Geol. Survey G.B. 1 (1846) 336-432.

16. ibid, p 336. See also p 350 for a definition of his aims.

17. A doctrine which can be broadly characterised as the relation between 'age' and 'area' and which attempted to define the a priori statement that as numbers of a species increase, so does the area covered by the individuals. In this way range could be taken as an indication of the geological age of a species - as long as a single point of origin was assumed. Indeed this correlation was the first line of defence for naturalists who were anxious to prove that species - like Adam and Eve - arose in pairs and not in great numbers.

    Before Forbes took up this idea in his 'Report on the Mollusca and Radiata of the Aegean sea . . .' Report to the B.A.A.S. 1843 (1844) 130-93 especially p 171, naturalists such as the Parisian de Verneuil and his colleague d'Archiac had postulated the relationship between age and area to be a 'law'. Under R.I. Murchison they had discovered that the palaeozoic fauna of Europe and Russia exhibited a few absolutely identical species. Verneuil noted that the most widely spread forms were also those which persisted longest in the fossil record, and even, in some few cases, were found in two formations. See his 'Fossils of the older deposits in the Rheinish Provinces'. Trans. Geol. Soc. 6 (1842) 303-410, especially p 335. I quote the appropriate passage in footnote 33, chapter 5. Lyell too found much to interest him in this principle and in Principles III, pp 48, 56, he clearly connected range of species with their age. See also vol. II, pp 121, 176, where he used the common example that given enough time one family should be able to spread worldwide. Perhaps his views were derived in antithesis to the Italian geologist Brocchi who believed in a 'life-span' of pre-determined age for each species, just as if they were individuals, although Lyell discredits Brocchi's opinion in Principles II, 128. Nevertheless, much of Lyell's history of geology was taken from Brocchi, as P. J. McCartney has recently shown. See his 'Charles Lyell and G. B. Brocchi. A Study in comparative historiography'. Brit. J. Hist. Sci. 9 (1976) 175-189.

18. Forbes op cit note 15, p 351.

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19. ibid, p 351.

20. ibid, p 351.

21. ibid, p 352.

22. Forbes Anniversary address op cit note 8, p lxxix, "An appearance of such a law in many instances that has led over and over again to erroneous doctrines about progression and development". He reiterated this point in a review article of Lyell's A Manual of Elementary Geology, titled 'Life development, Geology, and Religion' for the Literary Gazette and reprinted in Lovell Reeve's Literary Papers of Professor Edward Forbes. London, 1855. ". . . every day we are approaching nearer and nearer the conclusion, that if there ever was a gradual progression, whether through development or special creation, of organised beings in time, the lower types regularly preceding the higher, the proofs of such a succession are not to be made out of the assemblage of fossils that has been preserved in sedimentary strata . . . Geologists and palaeontologists are too apt to fancy that they have been favoured with a sight of the world in its swaddling clothes." pp 36-7.

23. Forbes Anniversary address op cit note 8, p lxxx.

24. ibid 46. See also ibid 8, 21 for Forbes' remarks on Buch and Barrande.

25. Appended to Leonard Horner's copy of Forbes' Report on the Mollusca and Radiata of the Aegean sea, op cit note 17, in the B.M. (N.H.) General Library.

26. Allan, Mea The Hookers of Kew 1785-1911. London, 1967 and Huxley, Leonard The Life and Letters of Sir Joseph Dalton Hooker. London, 1918. W.B.Turrill has written two accounts of Hooker which extract a large amount from his writings: see Joseph Hooker botanist, explorer and administrator. London, 1963; and Pioneer Plant Geography: the Phytogeographical researches of Sir J.D.Hooker. The Hague, 1953.

27. In fact he was very opinionated.

28. Introductory Essay to the Flora Novae Zelandiae. London, 1853-5, p viii.

29. Darwin MS 100, p 12, dated 5th April 1844.

30. Introductory Essay to the Flora Novae Zelandiae pp xii, xiv, xix, xxvi; and Introductory Essay to the Flora Indica. London, 1855, pp 8-9, 14-19.

31. Introductory Essay to the Flora Indica, p 10.

32. Hooker, J.D.The Botany of the Antarctic Voyage of HMS Erebus and Terror . . . 1839-1843. London, 1844-60, which included Flora Antarctica 1844-7; Flora Novae Zelandiae 1853-5; and Flora

Notes to Chapter 2

Tasmaniae 1860. All these were introduced by Introductory Essays, as was his joint work with Thomas Thomson Flora Indica . . . volume I. [all published] London, 1855.

33. Hooker, J.D. 'An enumeration of the plants of the Galapagos Archipelago'. Trans. Linn. Soc. 20 (1851) 163-233, and its sequel 'On the vegetation of the Galapagos Archipelago as compared with that of some other Tropical Islands and of the continent of America'. ibid 235-62. Oddly enough Hooker nowhere in these papers actually explains what he means by representative species; he sticks to the facts of distribution alone.

34. Darwin MS 100, p 43, nd probably 1845, consisting of 3 pp in Darwin's hand and (verso) 3 pp in Hooker's. Hooker was answering Darwin's question "I presume there must be a good many cases where a genus (whether confined to the Galapagos or not) has a different peculiar Galapagean species on different islands:- for if it not be so, the genera must be wonderfully different on the different islands".

35. See, for instance, Introductory Essay to the Flora Novae Zelandiae, pp xii-xix, and that of the Flora Indica, pp 11-13, 24-36.

36. Darwin MS 100, p 12, dated 5th April 1844. This letter was the final one in a series of six or seven spanning the early months of 1844 in which Hooker misunderstood Darwin's initial question about ranges and answered in terms of representative species. Later in the year (Dec. 1844, Darwin MS 100, p 32) he again discussed representative species in endemic genera of the Sandwich and Society Islands: "The Sandwich Isld. Flora is by far the most peculiar and the least tropical, perhaps the most allied to the American. . . . As far as materials go, the several islets of the Sandwich present numerous instances of representative species".

37. Darwin MS 100, p 12, 5th April 1844.

38. See, for example, Hooker's letter to Darwin of late February/early March 1844, Darwin MS 100, p 4, where he drew up a table to show that widely ranging species were more plentiful in genera which had a large number of species. This he certainly demonstrated, and the table forms an important point in Charles Darwin's understanding of botanical arithmetic. This will be returned to in Chapter 5. Here, the significance of Hooker's answer lies in the fact that his data are drawn from type species of families, as, for example, the Ranunculus for a wide ranging species in a mundane family Ranunculaceae.

39. Although of course this obsession with having no theory to support determined his behaviour just as strongly as if he had had something to vindicate.

40. Hooker 'On the vegetation of the Galapagos Archipelago'. op cit note 33, p 236. The paper was read in 1846 but not published until 1851. This was one of the reasons that made Hooker anxious to reform the publishing policy of the Linnean Society, a change which came about under the Presidency of Thomas Bell in 1855.

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41. ibid 258.

42. ibid 259.

43. Meyen, J. 'Comparative remarks on the distribution of vegetation on the greatest heights of the Himalayah and of upper Peru'. Edin. New Phil. J. 23 (1837) 34-45, p 44.

44. Gray, Asa 'Statistics of the flora of the northern United States'. Amer. J. Sci. second series, 22 (1856) 204-32, and ibid 23 (1857) 62-84, 369-403.

45. ibid 78, 79.

46. ibid 79-80.

## Notes to Chapter 3

## The Investigation into Biological Provinces

1. Foucault, Michel The Order of Things. An archaeology of the human sciences. London, Tavistock, 1970, takes 'natural history' to be a way of doing things instead of the subject. His "Classical" period of the renaissance to the late eighteenth century was a time when naturalists pursued a "natural history" type of investigation, and so concentrated on an external description of nature. See also Albury, W.R.and Oldroyd, D.R. 'From Renaissance mineral studies to Historical Geology in the light of Michel Foucault's The Order of Things'. Brit. J. Hist. Sci. 10 (1977) 187-215.

2. Wallace, Alfred Russel The Geographical Distribution of Animals. London, Macmillan, 1876, volume I, 54.

3. Aristotle The Works of Aristotle. Translated into English . . . Volume IV Historia Animalium by D'Arcy Wentworth Thompson. Oxford, Clarendon, 1962, book VIII, 19, 28.

4. Pliny Natural History Book VIII, XI, 32, Loeb Classical Library volume III, p 25.

5. Natural History Book III, V, 78-9. This translation from Philemon Holland's version published and edited by the Wernerian Club 1847-8.

6. Yale, H.The Book of Marco Polo, the Venetian . . . London, Murray, 1871, pp 145, 196.

7. Bartholomew the Englishman On the Properties of things. John Trevisa's translation of Bartholomaeus Anglicus De Proprietatibus Rerum. A critical text edited by M.C.Seymour, Oxford, 1975, p 598.

8. Turner, William A Newe Herball Part I, London 1551, Part II, 1562, Part III, 1568. With part three was issued a revised edition of the earlier parts. The quotation comes from the title page. See Callery, B.F. 'Ancients, Moderns and reliable friends: stated sources of some English Herbals'. J. Soc. Biblphy. Nat. Hist. 8 (1978) 435-44.

9. Ms Callery in the paper cited in note 8 goes into a revised estimate of Gerarde in some detail, p 440.

10. Parkinson, John Paradisi in Sole Paradisus Terrestris, or a garden of all sorts of pleasant flowers which our English ayre will permit to be noursed up . . . London, 1629.

11. Foucault calls this earlier period one of signatures, and charts the change from this attitude to nature to one in his "Classical" period where organisms took on a meaning of their own. In the seventeenth century he tells us that the study of taxonomy was a specialised application of the "natural history" method of describing purely external and surface parts of the body. Because plants, for instance, have a quantity of visible structures like petals, stamens and leaves the botanist could classify them more readily than, say, geological specimens. Hence Foucault suggests an interesting cause for the

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pre-eminence of botanical classification in this era. Vide Foucault's chapter 5 op cit note 1, 125-62, and Jacob, Francois The Logic of Living Systems: A History of Heredity. New York, 1973.

12. Raven, C.E. English Naturalists from Neckham to Ray: a study of the making of the modern world. Cambridge, CUP, 1947, pp 1-4.

13. Linnaeus, Carl Systema Naturae 1735, facsimile of the first edition with an introduction and translation of the 'Observationes' by Engel Ledebour, M.S.J. and Engel, H. Nieuwkoop, 1964, p 18.

14. ibid, p 18

15. Klein, Jacob Theodor Mantissa Ichthyologica de sono et auditu Piscium. Leipzig, 1746.

16. Gould, William An account of English Ants . . . with many other curiosities observable in these surprising insects. London, Miller, 1747.

17. Smellie, William Natural History, general and particular, translated with notes and an introduction . . . Edinburgh, 1781. This passage from a new edition of 1812, volume 5, p 1.

18. Farber, P. L. 'The Type-concept in Zoology during the first half of the nineteenth century'. J. Hist. Biol. 9 (1976) 93-119.

19. Hooker directed the greater part of his Introductory Essay to the Flora Novae Zelandiae 1853-5, to a criticism of provincial naturalists who thought that their local forms were 'new' species. Vide pp xii-xix.

20. Link, H.K. 'Contributions to the botanical geography of southern Europe'. Edin. New Phil. J. 22 (1837) 304-9, p 304.

21. See, for instance, Farber's discussion on this topic op cit note 18.

22. Decandolle, Augustin-Pyramus Géographie botanique article in the Dictionnaire des Sciences naturelles edited by F C Levrault, volume 18, 359-436, and reprinted separately as Essai élémentaire de géographie botanique. Strasbourg, 1820. My citation is from the dictionary article, p 392.

23. Watson, H.C. Cybele Britannica; or British plants and their geographical relations. London, 1847-59, volume IV (1859) 375.

24. Hooker, J.D. Introductory Essay to the Flora Indica. London, 1855, p 37. See also Introductory Essay to the Flora Novae Zelandiae, p viii for his remarks about the "mystery" of species.

25. Lacordaire, Theodore 'On the Geographical Distribution of Insects'. Edin. New Phil. J. 27 (1838-9) 94-111, 333-51; 28 (1839-40) 170-83, 224-38. My quotation comes from volume 27, p 109. This article, contributed anonymously, is a translation of Lacordaire's Introduction à l'Entomologie, comprenant les principes generaux de l'anatomie

et de la physiologie . . . Paris, 1834-7, which formed part of the Suites de Buffon.

26. Sclater, P. L. 'On the general geographical distribution of the members of the class Aves'. J. Proc. Linn. Soc. London Zool. 2 (1858) 130-45, p 130-31.

27. Clift, W. [and Jameson, R. editor] 'Report by Mr Clift . . . in regard to the fossil bones found in the Caves and Bone Breccia of New Holland'. Edin. New Phil. J. 10 (1831) 393-6. A pair of papers on the organic remains of Australia followed shortly afterwards under the authorship of William Pentland, see Pentland, W. 'On the fossil bones of Wellington Valley, New Holland or New South Wales'. ibid 12 (1832) 301-8; and 'Observations on a collection of fossil bones sent to Baron Cuvier from New Holland'. ibid 14 (1833) 120-1. William Clift was to continue his work in this vein and discovered that the fossils of South America were also 'designed' on the same plan as its living residents, see 'An account of the discovery of portions of three skeletons of the Megatherium in the province of Bueons Ayres in South America'. Procs. Geol. Soc. 1 (1832) 403-4. Richard Owen, Clift's associate and son-in-law, was later to claim the discovery of this apparent law of nature for himself. I have also seen it stated that Charles Darwin was the first to describe such a phenomenon.

28. Agassiz, Louis 'On the primitive diversity and number of animals in geological times'. Edin. New Phil. J. 57 (1854) 271-92, pp 286-7. This debate over the uniformity or diversity of organic life before the present day is well chronicled in the pages of the Edinburgh New Philosophical Journal. It was a crucial point to establish for it bore on the doctrine of a progressive history for the earth itself: most geologists such as Alexandre and Adolphe Brongniart, Alcide D'Orbigny and Francois Pictet were anxious to demonstrate greater uniformity in previous epochs so that they could state that life was progressively approaching the present state of affairs. See, for instance, Brongniart, Adolphe 'General considerations on the nature of the vegetation which covered the surface of the Earth, at the different epochs of the formation of its crust . . .' ibid 6 (1828-9) 349-71; D'Orbigny, Alcide 'General considerations regarding the palaeontology of South America compared with that of Europe'. ibid 35 (1843) 362-72; and Pictet, F.J. 'Distribution of fossils in the different formations and succession of animals on the surface of the globe'. ibid 40 (1846) 255-80. In his book on Fossils and Progress, 1976, Peter Bowler touches on this specialised debate in places, pp 22-5, 79, 108-9.

29. Lacordaire recognised this point, Edin. New Phil. J. 28 (1842) 182-3, as did Henri Milne-Edwards, ibid 22 (1837) 398.

30. Watson, H C Remarks on the geographical distribution of British plants . . . London, Longman, 1835, p 44.

31. Decandolle, Alphonse Géographie botanique raisonnée, ou exposition des faits principaux et des lois concernant la Distribution Géographique des plantes de l'époque actuelle. Paris et Geneve, 1855,

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chapters on Habitation, Frequency, and Area, pp 419-606.

32. Hooker, Introductory Essay to the Flora Novae Zelandiae pp xix-xx.

33. See for example Glass, D.V. Numbering the People. The eighteenth century population controversy and the development of census and vital statistics in Britain. np, D.C.Heath, 1973; and his 'Some aspects of the development of demography'. J. Roy. Soc. Arts 104 (1956) 854-69. Other useful works are Cullen, M.J. The Statistical movement in early Victorian Britain. Hassocks, 1975, and Pearson, E.S. and Kendall, M.G. Studies in the History of Statistics and Probability. Griffen, 1970.

34. Watson, H.C. Cybele Britannica. op cit note 23, volume I, 12.

35. Balfour, J.H. Class Book of Botany. Edinburgh, 1852, part II, 996.

36. Altick, R.D. Victorian People and Ideas. London, 1973, chapter 7 'Machines and the Spirit of Man', pp 238-46. For a good description of statistics in ethics (moral arithmetic) and in political economy during this period, see Cullen, M.J. The Statistical Movement in early Victorian Britain, 1975.

37. Cannon, W.F. 'History in Depth: the early Victorian period'. Hist. Sci. 3 (1964) 20-38, and the same but updated and expanded in Cannon, S.F. Science in Culture. The early Victorian period. London and New York, 1978, pp 225-62.

38. Westergaard, H. Contributions to the History of Statistics. Mouton, 1969.

39. Essai sur la géographie des plantes [1805] 1807, p 30. There is an interesting paper by Erwin Ackerknecht on Humboldt and the Göttingen school of thought generally, Ackerknecht, E.H. 'George Forster, Alexander von Humboldt and Ethnology'. Isis 46 (1955) 83-95.

40. Principles II, 116-21.

41. ibid III, 31-2.

42. A fact which reflected his ideas about a relatively 'fixed' life span for species. See Rudwick, M.J.S. 'Charles Lyell's dream of a statistical palaeontology'. Palaeontology 21 (1978) 225-44 for a full account of Lyell's statistics and his ideas about numerical proportions as, at first, an ecological indicator (i.e. for distinguishing biogeographical provinces), and, secondly, as an indicator of geological age.

43. Watson, H.C. Cybele Britannica I, 10.

44. Principles III, 32.

45. Natural Selection 146.

## Notes to Chapter 4

### Statistics in Distribution Studies

1. Cannon, W.F. 'History in Depth: the early Victorian period'. Hist. Sci. 3 (1964) 20-38, and recast and expanded in Cannon, S.F. Science in Culture. The early Victorian period. London and New York, 1978, pp 225-62.

2. Darwin MS 104, p 219.

3. More Letters I, 403.

4. Decandolle, Alphonse Géographie Botanique raisonnée, p xvi.

5. ibid, p xvii.

6. ibid, p xvii.

7. Rudwick, M.J.S. 'The Strategy of Lyell's Principles of Geology'. Isis 61 (1970) 5-33; Porter, Roy 'Charles Lyell and the Principles of the History of Geology'. Brit. J. Hist. Sci. Lyell Centenary Issue, volume 9 (1976) 91-103; McCartney, P.J. 'Charles Lyell and G.B.Brocchi: A Study in comparative historiography'. ibid 175-89.

8. Humboldt, Alexander von Essai sur la géographie des plantes accompagné d'un Tableau Physique des régions équinoxiales. 1805. This volume formed the fifth section of Humboldt's Voyage aux régions équinoxiales du Nouveau Continent fait en 1799-1804. Paris, 1805-34 in thirty-four volumes.

9. ibid, pp 41-2.

10. Humboldt 'Géographie des plantes' as given by Decandolle (Augustin) in his Essai élémentaire de géographie de botanique in the Dictionnaire des Sciences Naturelles edited by F.C.Levrault, volume 18, 1820, p 424.

11. Essai, op cit note 8, 24-30. Humboldt was fond of linking human and natural histories together, see p 30.

12. Willdenow, K.L. Grundriss der Krauterkunde. Berlin, 1792, and English translation (anonymous, but perhaps by Graham or Jameson?) as Principles of Botany. Edinburgh, 1805. See pp 371-408 of this last for the "History of Plants".

13. ibid, 402-7.

14. Humboldt Nova Genera et Species plantarum . . Prolegomena. Paris, 1815 [1816] - 1825. NB that this Prolegomena is not the better known Prolegomena to the De Distributione Geographica plantarum . . . Paris, 1817.

15. ibid, xiii. I am grateful to Professor A.R.Hall for translating this passage for me. The Latin reads as follows:

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> "Sic haec fundamenta Arithmetices botanicae ulterius prosequamur, patebit plantas monocotyledones et dicotyledones annuas praesertim zonae temperatae proprias esse, in qua sextam partem omnium Phenerogamarum conficiunt, quum, observante Decandollio, in plaga aequinoctiali vix vigesima pars sint, in Laponia trigesima."

16. ibid, the table on p xiv.

17. ibid, xviii.

18. See W.T.Stearn's biography of Brown in the Dictionary of Scientific Biography.

19. The travelogue in which Darwin's Journal of Researches was to appear as volume III: King, P.P. and Fitzroy, R.Narrative of the surveying voyages of HMS Adventure and Beagle etc, London, Colburn, 1839.

20. In Flinders, M.A.Voyage to Terra Australis . . . 1801-3 in HMS Investigator. London, 1814, and then as Brown, Robert General remarks, geographical and systematical, on the botany of Terra Australis. London, 1814.

21. General Remarks, pp 35-6.

22. ibid, 55.

23. Essai élémentaire, op cit note 10, p 392. Decandolle defined the study of "habitations" to include "l'origine même des êtres organises". Many naturalists used the word 'origin' to mean a history of the introduction of, say, several floras to England, rather than the study of their creation. The moment of creation was one that was to remain clothed in mystery, whereas the subsequent travails of species could be elucidated. It may be too obvious to remark that naturalists thus did not always mean what we mean when they used the word 'origin' of species, but we might take heed from Peter Bowler's paper, Bowler, P.J.'The changing meaning of Evolution'. J. Hist. Ideas 36 (1975) 95-114, and additional note ibid 367.

24. Essai élémentaire, op cit note 10, p 400.

25. Darwin notebook 'B', July 1837 to January 1838, pp 156, 158. In the British Museum (Natural History) Historical series transcription these citations are pp 60, 61 respectively.

26. Willdenow op cit note 12, p 373.

27. Translated by C.König from Beytrage zur Naturgeschichte. 1801, in König, C. Tracts relative to botany translated from different languages . . . and occasional remarks. London, 1805, pp 27-74.

28. ibid, p 44.

29. Giraud-Soulavie, J-L.Histoire naturelle de la France méridionale 1780-84, Tome I contenant les Principles de la géographie physique

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du règne végétal 1783.

30. Lavy, Jean État générale des végétaux originaires moyen pour juger . . . de la salubrité de l'atmosphère, de la fertilité du sol etc. Paris, 1830.

31. Translated by Schouw himself as Grundezuge einer allegmeinen Pflanzengeographie. Berlin, 1823.

32. Danish edition of 1822, as in the text, pp 258-9, 272-3, 294-7.

33. Allen, David Elliston. The Naturalist in Britain. London, 1976, is very informative about provincial natural history and gives many details on the development of the field club and printed guides for excursions. See, for instance, his chapter 8 'The Field Club', pp 158-75 in the Penguin edition.

34. Wagner, Rudolf 'The numerical relations of animals from Linnaeus to the present day'. Edin. New Phil. J. 15 (1833) 221-7. I might point out that this was Johann Christian Fabricius (1745-1808) to whom he was referring, not Fabricius of Aquapendente.

35. Allen, D E, op cit note 33, p 107.

36. Edin. New Phil. J. 14 (1833) 317-23.

37. Watson, H.C. Outlines of the Geographical distribution of British plants . . . Edinburgh, privately printed, 1832. In 1835 Watson revised and extended this work in his Remarks on the geographical distribution of British plants etc. London, 1835.

38. As in note 36, p 323.

39. Throughout the first half of the nineteenth century "natural orders" was the common term for what we now call families, and was used to signify a natural group rather than a Linnean division.

40. i.e. Rosaceae formed 1/14; 1/5; 1/16 of the floras at each elevation whereas Ericeae only constituted 1/27; 1/20; 1/40 at the same heights.

41. Watson's 112 vice-counties are still the primary floral divisions of the British Isles, as evidenced by the Ray Society's 1969 North Sheet of the British Isles.

42. Cybele Britannica I, 42.

43. As an aside it is interesting to discover that Watson called this work Cybele as a substitute for the over-worked term Flora. She - Cybele - was a goddess who presided over the productions of the earth and, as Watson reasoned, her name belonged more properly to the study of distribution than any of the other unwieldy terms hitherto proposed. It should be added that here in my thesis I have ignored the various shades of meaning which went into nineteenth century names for the study of distribution, for (like many of the

naturalists concerned) I think that the subtleties of attempted distinctions between what we now call ecology and biogeography are mostly a waste of time. Decandolle, for instance, tried to demarcate between 'botanical geography' (i.e. ecology or distribution on the small scale) and 'geographical botany' (the overall comparison of floras). Watson hoped to transcend these distinctions by the all-embracing designation Cybele.

He thought that distributional surveys should be called Cybeles as catalogues of plants were called Floras. Unfortunately - though not unexpectedly - the term never caught on, and Watson became convinced that there was a conspiracy against him because botanists refused to use it. He remained adamant in his proposal and introduced the topic into every preface of all five volumes of the work, even giving detailed instructions as to the proper pronunciation (Sy-beel-lee) in case that was what was hindering its adoption.

44. Cybele Britannica IV, 379.

45. Meyen, F. J. F. Grundriss der Pflanzengeographie . . . Berlin, 1836, and translated by Johnson, Margaret Outlines of the Geography of Plants with particular enquiries concerning . . . . the principle cultivated plants on which the prosperity of nations is based. London, Ray Society, 1846.

46. But in later years Darwin was to confess that he was glad the Ray Society also published new tracts, for otherwise how could he have had his two volumes on Barnacles issued? See More Letters I, 94.

47. Meyen, F. J. F. op cit note 45, English version, p 260.

48. ibid, 270.

49. First published as Introduction à l'Entomologie . . . Paris 1834-7 as part of the Suites de Buffon, and translated and published anonymously in the Edinburgh New Philosophical Journal as 'On the geographical distribution of Insects'. Edin. New Phil. J. 27 (1838-9) 94-111, 333-51; ibid 28 (1839-40) 170-83, 224-38.

50. ibid 27, p 346, which also included Table I.
Table II ibid 28, p 171.
Table III ibid 28, p 177.
Table IV ibid 27, p 349.

51. Forbes, Edward 'Report on the Mollusca and Radiata of the Aegean Sea, and on their distribution . . .' Report B.A.A.S. for 1843 (1844) 130-93, especially pp 171-2, 174.

Forbes, in his position as paleontologist to the Geological Survey, appears to have had a batch of printed sheets run off and distributed around the country for the tabulation of dredging results. These consisted of ready drawn columns with depth headings into which naturalists were supposed to insert the appropriate names and numbers. They were thus evidently designed to facilitate rapid comparison between zones.

These sheets are still in use as rough paper in the Institute of

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Geological Sciences, the modern successor of the Geological Survey.

52. Dana, James 'Geographical distribution of Zoophytes'. Edin. New Phil. J. 43 (1847) 41-5. Table from p 44.

53. Balfour, J H Class Book of Botany. Edinburgh, 1852, p 996.

54. Cybele Britannica IV, 441.

55. Rudwick, M.J.S. 'Charles Lyell's dream of a statistical palaeontology'. Palaeontology 21 (1978) 225-44.

56. Bowler, P. J. Fossils and Progress etc. New York, 1976.

57. Bowler would have us call the 'improvement' doctrine 'progressionism'. Under his view the only people who believed in this, the gradual unfolding of a prearranged plan of development from primitive to advanced, or, alternatively, the manifestation of some internal force like Lamarck's sentiment intérieur, were Louis Agassiz and Lamarck himself. In his review article on Bowler's book Roy Porter points out that there were other naturalists who could be subsumed under this admittedly restricted label, such as Robert Chambers. I would add Richard Owen. See Porter, Roy Brit. J. Hist. Sci. 11 (1978) 83-5.

58. Cuvier, Georges Recherches sur les ossemens fossiles du quadrupèdes ou l'on rétablit les charactères du plusiers d'espèces animaux. Paris, 1812. For example, the fossil elephant - the mammoth - was special to the period which for Cuvier preceded the "northern drift" or, as we would have it, the Ice Age.

59. Buckland, William Reliquiae Diluvianae. London, 1824.

60. Cuvier, G. and Brongniart, Alex. Essai sur la géographie minéralogique des environs de Paris. Paris, 1811, included in Cuvier's Recherches op cit note 56 and then issued separately as Description géologique des environs de Paris. Paris, 1822.

61. Brongniart, Adolphe 'Tableau des genres de végétaux fossiles considerés sous le point de vue de leur classification botanique . . .' [extrait Dictionnaire universel d'histoire naturelle] Paris, 1849, p 93.

62. Brongniart, Adolphe Prodrome d'une histoire des végétaux fossiles. Paris, 1828, p 181.

63. ibid 177.

64. ibid 219.

65. Decandolle, Alphonse 'On the history of fossil vegetables'. Edin. New Phil. J. 18 (1834) 81-102, p 97.

66. ibid 87.

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67. Nicholas Rupke at Oxford is at present working on the history of the Carboniferous debate, and hopes to publish some of his findings soon. Other than that, it is evident from Darwin and Hooker's correspondence that the origin of coal was both intriguing and arguable. Darwin suggested a marine origin which Hooker vehemently disputed, see More Letters II, 217-20.

68. Lindley, John 'On the mode of determining fossil plants'. Edin. New Phil. J. 13 (1832) 221-28. His major work, cited in the text, was written in conjunction with William Hutton: The fossil Flora of Great Britain, or figures and descriptions of the vegetable remains found in a fossil state in this country. London, 1831.

69. Rudwick op cit note 55.

70. See Rudwick, M.J.S.'Caricature as a source for the History of Science: De La Beche's Anti-Lyellian Sketches of 1831'. Isis 66 (1975) 534-60 for a reproduction of the sketch from which this metaphor is derived. Lyell is here caricatured proffering a pair of spectacles to the uncomprehending geologist at his side.

71. Principles III, 47-8.

72. ibid 21-2.

73. Deshayes, G.P. Description des coquilles fossiles des environs de Paris. Paris, 1824-37, in which he divided the Tertiary into three periods where the first (oldest) carried 3% living species, the middle period 19%, and the most recent 52%. See the article on Deshayes in the Dictionary of Scientific Biography.

74. Charlesworth, E. 'On some fallacies involved in the results relating to the comparative age of Tertiary deposits, obtained from the application of the test recently introduced by Mr Lyell and M. Deshayes'. Edin. New Phil. J. 22 (1836) 110-6; and Philippi, A. 'Comparative remarks on the recent and fo-sil mollusca of the south of Italy, and more particularly of Sicily'. ibid 38 (1845) 202-12.

## Notes to Chapter 5

## Charles Darwin's Botanical Arithmetic 1836-1857

1. Origin pp 53-8.

2. Natural Selection pp 134-64. The manuscripts are in Darwin MS 15, and include a fair copy of 42 folios on large genera varying which was sent to Hooker in May, 1858 and bears his notes. Stauffer's transcript is taken from the fair copy (despite what he states to the contrary) and includes Hooker's additions as footnotes.

3. Origin 53.

4. ibid 53.

5. Though of course this only applies to historians who are concerned with the workings of Darwin's mind. I would not pretend that interpretations of the Origin itself or the reception of Darwin's arguments should be revised in the light of this new material.

6. As in note 2.

7. See for example Hodge, M.J.S.'The structure and strategy of Darwin's "Long Argument" Essay review of Natural Selection etc.' Brit. J. Hist. Sci. 10 (1977) 237-46. Hodge compares the structure of the sketch of 1842 with that of Natural Selection and the Origin as a case study of Darwin's command of current philosophy of science.

8. Darwin's papers on these topics are contained in Darwin MS 15 (ii), 16 (i) and (ii), 45, and several portfolios in Box B, such as C 40 b to e, and i to j inclusive.

9. His letters to Hooker 1843-58, Darwin MS 114, and copies in box 150; Hooker's letters to Darwin 1843-62, Darwin MS 100, plus a few in 104, and an incomplete set of copies in box 152. There is a set of copies of Darwin to Hooker letters at the Royal Botanic Gardens Kew, given to Hooker by Francis Darwin in return for the originals. For a full account of the history of the manuscripts themselves, see Browne, E.J.'The Darwin-Hooker correspondence: an analysis of manuscript resources and their use in biography'. J. Soc. Biblphy. Nat. Hist. 8 (1978) 351-66, given as an appendix to this thesis.

10. Allan, Mea Darwin and his Flowers. London, Faber, 1977, especially the first few chapters explaining Darwin's knowledge of botanical theory. See also Barlow, Nora Darwin and Henslow: the growth of an idea. London, 1967; Autobiography in Life and Letters CD pp 26-107, especially pp 52-5 for his friendship with Henslow, and pp 55-6 for his enthusiasm for Humboldt.

11. Lyell's percentage method as explained in Principles III, 47-58.

12. Barlow, Nora 'Charles Darwin's Ornithological Notes, edited with an introduction, notes and appendix . . .' B.M. (N.H.) Bulletin Historical Series 2 (1963) 201-78, pp 214, 229.

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13. ibid 212, 218, 242. On p 220 Darwin states that a genus was "both numerous in individuals, as well as in species" and on p 233 the Caracara "is a very common bird and has a wide geographical range". Frequency of individuals, the number of species and the extent of topographical range were three items which were to be linked in his mind some ten years later through the agency of botanical arithmetic.

14. Darwin, Charles 'Observations of proofs of recent elevation on the coast of Chile . . .' Procs. Geol. Soc. 2 (1837) 446-9. This is not strictly speaking his first paper, but is rather the first which he presented himself.

15. ibid 447.

16. Darwin, Charles 'A sketch of the deposits containing extinct Mammalia in the neighbourhood of the Plata'. Procs. Geol. Soc. 2 (1837) 542-4.

17. Darwin, Charles 'Observations on the Parallel Roads of Glen Roy . . with an attempt to prove that they are of Marine Origin'. Phil. Trans. part 1 (1839) 39-81. The quotation comes from Darwin's Journal, edited by Sir Gavin De Beer B.M. (N.H.) Bulletin Historical Series 2 (1959) 1-21, p 8. This was Darwin's only paper presented to the Royal Society and he went to a great deal of trouble to get it just right, especially on philosophical grounds. It may well have been a trial run for the construction of his arguments pertaining to natural selection and "descent with modification", as is suggested by Rudwick, M.J.S. 'Darwin and Glen Roy: a "Great Failure" in scientific method?' Stud. Hist. Phil. Sci. 5 (1974) 99-185.

18. Rudwick op cit note 17, Appendix A, pp 179-80, gives a transcript of Darwin's Agenda for the field excursion. Points (2) "organic remains", and (11) "the relative preservation of the shelves", imply that Darwin would look for marine fossils and partially decomposed shells, and try to assess whether these were differentially preserved as he moved from shelf to shelf. I do, however, acknowledge that Darwin might just as easily have meant to remind himself to search for mineralogical or structural differences between shelves.

19. Darwin MS 121-6 inclusive and transcribed by De Beer, Sir Gavin 'Darwin's Notebooks on the transmutation of species'. B.M. (N.H.) Historical Series 2 (1959) numbers 2-6, and ibid 3 (1963) number 5. See also an alternative transcription by Barrett, P. H. 'A Transcription of Darwin's first notebook on "Transmutation of Species"'. Bull. Mus. Comp. Zool. Harvard 122 (1960) 247-96.

20. Darwin MS 121, pp 156, 158, or De Beer pp 60-61.

21. ibid p 157, or De Beer p 61.

22. ibid p 154 (excised) or De Beer, Sir Gavin 'Pages excised by Darwin' op cit note 19, number 3, p 135.

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23. ibid p 41, or De Beer p 46.

24. ibid p 37, or De Beer p 46.

25. See especially Sandra Herbert's PhD thesis The Logic of Darwin's Discovery. Brandeis University, 1968 (copy in the Cambridge University Library), her chapter on Darwin's understanding of divergence and the function which this diagram supports. I believe that Professor Herbert is soon to publish on this problem. Equally, Dov Ospovat of the University of Nebraska has considered this diagram in conjunction with the idea of divergence (personal communication), as has Silvan S Schweber of Brandeis University (personal communication and in press), and Sir Gavin De Beer.

26. More Letters I, 336, and for his criticisms of mathematicians ibid I, 315. But see also Autobiography in Life and Letters CD 46 where he states that although mathematics was "repugnant to me", still he regretted that he had not pursued his studies. David Hull has fallen into the trap of taking Darwin at his own word, as evidenced by his remarks in Charles Darwin and his Critics . . Harvard University Press, 1973, p 12: he writes that "on occasion Darwin had to make some simple computations. When these proved too much for him, he asked for help. In later life his son Francis took over this duty".

27. As transcribed by Francis Darwin in The Foundations of the Origin of Species . . Cambridge, 1909, and by Sir Gavin De Beer Darwin and Wallace. Evolution by Natural Selection . . Cambridge, 1959. Neither of these publications are fully adequate for the demands of modern scholarship, although they are invaluable in the face of exceedingly complex manuscripts. The MS of the Sketch of 1842 is so intricate that one recent scholar has claimed to have found a 'mini-sketch' lurking within its pages. See Vorzimmer, P. J.'An early Darwin manuscript: the "Outline and Draft of 1839"'. J. Hist. Biol. 8 (1975) 191-217, which includes a complete transcript. This claim is shortly to receive a refutation from R.C.Stauffer and a counter-claim that the date should be between 1842 and '44.

28. Essay p 200.

29. ibid p 200.

30. ibid p 200-1.

31. ibid p 201.

32. Principles II, 91 (as numbers increased so area covered increased until stopped by barrier), 121 (given enough time one family should spread worldwide), 176 (the relationship between age and area).

33. Verneuil, P. E.de and D'Archiac, A.'Fossils of the older deposits in the Rhenish Provinces'. Trans. Geol. Soc. 6 (1842) 303-410. The law ran as follows: "The species which are found in a great number of localities and in very distant countries, are almost always those

which have lived during the formation of several successive systems". p 335.

34. See Forbes, Edward 'On the light thrown on Geology by Submarine researches'. Edin. New Phil. J. 36 (1844) 318-37, "Animals having the greatest ranges in depth have usually a great geographical, or else a great geological range or both . . . The cause is obvious: such species as have the widest horizontal and vertical ranges in space, are exactly such as would live longest in time, since they would be much more likely to be independent of catastrophes and destroying influences, than such as had a more limited distribution". pp 324-5.

35. For Darwin this law implied that the species which have ranged the furthest have longest remained immutable. In the Essay p 165 he tried to answer this by supposing that not all forms had to change according to his views, and in Natural Selection p 138 by turning the proposition around and stating that the species which had lived longest were evidently the ones which were going to spread furthest.

36. Horner, Leonard 'Anniversary address of the President'. J. Geol. Soc. 2 (1846) pp 211-12, and by Darwin in Natural Selection 138. In the fair copy of the manuscript version of this Hooker has altered the word 'law' to read 'fact'. See Darwin MS 15 (i) Fair copy f A8.

37. Essay pp 169-72.

38. Described in detail in Essay pp 195-204 "An attempt to explain the foregoing laws of geographical distribution, on the theory of allied species having a common descent". In the Sketch of 1842 Darwin provided a summary of the views he was trying to put forward: "Effect of climate on stationary island and on continent, but continent once island. Moreover repeated oscillations fresh diffusion when non-united, then isolation, when rising again immigration prevented, new habitats formed, new species; when united free immigration, hence uniform characters. Hence more forms on the island." Sketch p 70.

39. Essay p 202.

40. Henslow had been wondering what to do with the collection ever since the plants had begun arriving in England from the various ports of call of the Beagle. Darwin was relying on him to provide the identification of specimens, and asked for information on his return to be included in his Journal of Researches, 1839. Henslow tried to get W.J.Hooker (Joseph's father) interested in the job, but he politely declined. Subsequently, he managed to deter Robert Brown from commandeering the collection for the archives of the British Museum, at Darwin's request, since Brown had not yet got round to examining the specimens sent home from the Beagle's first voyage under Phillip Parker King (1817-22). After some consultation with Henslow the fungi were sent to the Rev. Miles Berkeley, and Henslow himself began to look at the Keeling Island plants of which there were only 22. From these he produced a short report, 'Florula Keelingensis. An Account of the native plants of the Keeling Islands'. Annals Nat. Hist. 1 (1838) 337-47, to join the previous paper he had written on Darwin's Opuntia spp., 'Description of two new species of Opuntia

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(O. darwinii and O. galapageia) . . .' Mag. Zool. & Bot. 1 (1837) 466-9. With some relief both Darwin and Henslow gladly agreed to let Joseph Hooker have the specimens for the analysis of his own collections garnered on the Ross expedition. It appears that W.J. Hooker solicited Darwin's collection, vide Darwin's reply 12th March 1843, More Letters II, 242.

41. Hooker's reminiscences as in Life and Letters CD II, 19-20. The mysterious shipmate who introduced Darwin and Hooker in 1839 (though only Hooker was subsequently to remember this meeting) was the irascible naval surgeon Robert M'Cormick and not a man called Davis as usually supposed. M'Cormick had joined the Beagle as surgeon and naturalist (vide Gruber, J.W.'Who was the Beagle's Naturalist?' Brit. J. Hist. Sci. 4 (1969) 266-82) only to leave in disgust at St Jago when it became clear that Darwin was receiving all the favours. M'Cormick went on to experience a frustrating career with little of the promotion which he believed to be his due, and, after much pleading with the Admiralty, was eventually appointed as Surgeon-naturalist to the Ross expedition of 1839-43. This was the voyage which Hooker was also to accompany, and he, in turn, was disappointed by being deprived of his position as official naturalist, see Life and Letters JDH I, 40-46.

42. More Letters I, 47. Francis Darwin dated this as [1845] when it is in fact an answer to Hooker's letter of July 1st 1846. See Darwin MS 100, p 60 for Hooker's letter, and Darwin MS 114, letter 54 for Darwin's reply.

43. For an account of the correct sequence of letters to be exchanged during these early months, and for the notice of a hitherto unpublished and unrecognised 'first' letter, see Browne op cit note 9.

44. Life and Letters CD II, 25. See also Essay pp 172-3.

45. Life and Letters CD II, 23 (in part) and More Letters I, 39 (remainder).

46. Hooker's reply nd (between 23 February 1844 and 9 March) Darwin MS 100, letter 4.

47. ibid letter 4.

48. Such an elimination was common practice in botanical calculations. These exceedingly large groups, such as Carex, Salix, Rubus, Hieracium and others, are now known to be ~~polymorphic~~ apomictic and highly interhybridised collections. It only goes to show that nineteenth century naturalists possessed a sixth sense about the abnormality of these genera.

49. As in note 46. It is interesting to note that Hooker had pencilled out a draft of this table on the back of Darwin's letter. Darwin MS 114, letter 3.

50. As in note 46.

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51. More Letters I, 402-3. In between Hooker's letter as discussed (note 46) and this letter there were one or two others.

52. Hooker to Darwin, 5th April 1844, Darwin MS 100, letter 5.

53. ibid.

54. More Letters I, 403.

55. Darwin MS C 40 e, unfoliated slip. This piece of paper has undoubtedly been added to over the years, but the passage here quoted is an integral whole and belongs to the date given.

56. It is possible that Darwin got Swainson's remark not from his book, A Treatise on the Geography and Classification of Animals. London, 1835, but from a review article which he cited on the verso of the slip of paper quoted in note 55: "Linn. Trans. 18, p 417," where the anonymous author asserted that Swainson's idea was not true. Apropos of Waterhouse, the latter had, according to Darwin, published on aberrant forms having few species. Although I cannot trace this paper, it is the case that Waterhouse and Darwin were very close friends and so Darwin probably received the information via personal communication.

57. Life and Letters CD I, 81-2.

58. ibid 81.

59. More Letters I, 64-5.

60. See a well publicised diagram of barnacle plates illustrating homology between species, Darwin, C.R. A Monograph on the Sub-class Cirripedia with figures of all the species . . . London, Ray Society, 1854, p 39. Also reprinted in Ghiselin, M.T. The triumph of the Darwinian Method. University of California Press, 1969, p 108.

61. Life and Letters CD I, 347 "he saw the necessity of giving himself such training . . . he did not shirk the labour of obtaining it". However, after Darwin's death Hooker insisted that Huxley's estimate was misguided. Hooker thought that Darwin had taken to monographing that order because he was interested in barnacles rather than training himself. See Hooker to Francis Darwin, Royal Botanic Gardens Kew, outgoing letters volume 3, 133, and Life and Letters JDH II, 298-200 and Life and Letters CD I, 346-7.

62. Ghiselin op cit note 60, pp 103-30, especially p 117.

63. In the Essay of 1844 Darwin made the point that his theory of common descent was, at root, an explanation of the fact that "all the organisms of this world have been produced on a scheme". He continued, "if this scheme can be shown to be the same with that which would result from allied organised beings descending from common stocks, it becomes highly improbable that they have been separately created by individual acts of will of a creator". Essay, p 154. See also

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Darwin MS C 40 e, slip dated July 1847 where he shows a clear understanding of classificatory problems - probably inspired by the barnacle work of this period.

64. To avoid confusion I have omitted the related point that Darwin also began examining the question of 'highness' and 'lowness', a question which was evidently a corollary of his interest in classification theory. See correspondence with Hooker, Darwin MS 114, letters 121-3 and More Letters I, 76-7, and Hooker's replies in Darwin MS 104, p 202. This exchange was brought on by an encounter with Agassiz's work, and led Hooker to propose an "elastic" theory of organisation.

65. Farber, P. L. 'The Type-concept in Zoology during the first half of the nineteenth century'. J. Hist. Biol. 9 (1976) 93-119.

66. Swainson, William op cit note 56, p 245.

67. Plainly a parallel with Lyell's use of statistics for a purely quantitative relationship between the various beds of fossiliferous Tertiary deposits. See my earlier chapter on Statistics in distribution studies, the section on geological statistics.

68. More Letters I, 86-7 where Francis Darwin dated [1855], and Darwin MS 114, letter 148 which I date 11th December 1854.

69. It is, I think, important to remember that for many years extinction was something of a positive force for Darwin. This much is evident in the Notebooks of 1837-9 where theories of transmutation revolve around the idea that it is extinction which renders the relations of organisms into groups called species, genera, families and so on. It has been suggested to me by David Kohn that it was Darwin's unhappy realisation of all the death and destruction which was beneath the serene surface of nature which made him nervously ill every time he thought seriously of it. Certainly, until he came up with a "principle of divergence" in 1857 he had nothing else but extinction to explain the 'gaps' in nature.

70. As in note 68.

71. Darwin MS 114, letter 156. The latter part of the letter is in More Letters I, 82-4.

72. Darwin MS 114, letter 159 and Hooker's reply Darwin MS C 40 i. Bentham did omit the large genera but Hooker thought that it was not proper to include these without including also all anomalous genera to be found in the vegetable kingdom. Hooker - at some times more of a materialist than Darwin - suggested that if one multiplied an anomalous form by 100 then one got a "normal" group. "Anomaly is synonymous with rarity", he wrote. Bentham's list with some further notes by Hooker on the verso is in Darwin MS C 40 i.

73. These lists and notes are in Darwin MS C 40 i. The catalogue of weevils is Schönherr, C. J. Curculionidium disposito methodica cum generum characteribus, descriptionibus atque observationibus variis . . . Leipzig, 1826, republished as Genera et Species (cont)

Curculionidium. Paris, 1833-8.

74. More Letters I, 82-3.

75. That is, a genus with only one species.

76. Origin 429.

77. As in note 68. Darwin is answering Hooker's point as described in note 72.

78. Darwin MS C 40 e, dated 31st July 1844. I might remind the reader that the penguin too has very many individuals, and the platypus, I believe, was once very common. Other oddities such as Stella's Sea cow and the dodo were definitely common at one time, for it was this very abundance which encouraged their destruction (by man) in the first place.

79. ibid unfoliated slip dated November 1854.

80. Hereafter I shall be using the term 'creation' as Darwin used it - to represent speciation. Creation was, to him, the opposite of extinction and synonymous with the more frequently used term "lack of extinction". Thus "lack of extinction" was not neutral but something quite positive.

81. Life and Letters CD II, 60-5, especially p 64 and Calendar of the Letters of C.R.Darwin to Asa Gray. Historical Records Survey, Mass. 1939 (hereafter referred to as Calendar Asa Gray) number 2. Darwin to H.C.Watson 25th August 1855 (?original) and Watson's reply in Darwin MS unmarked box. Darwin also wrote to Henslow on the same topic, see More Letters I, 419.

82. As in Watson's replies Darwin MS unmarked box, and referred to by Darwin in a letter to Hooker, Life and Letters CD I, 354-5, wrongly dated by Francis Darwin as [1847].

83. Gray, Asa Manual of the botany of the northern United States (second edition) New York, 1856. Before this was published Darwin used his interim publication, Gray, Asa 'Statistics of the flora of the northern United States'. Amer. J. Sci. second series (1856) 204-32; ibid 23 (1857) 62-84, 369-403. See More Letters I, 421-2 for Asa Gray's reply to Darwin's of note 81, and for his remarks about close species.

84. Darwin MS 15 (ii), f 22.

85. ibid ff 17-19 are the folios concerned with Darwin's earliest calculations on Gray. f 19 is the source of the quotation.

86. ibid ff 1-16, and Darwin MS 15 (i) f 36.

87. More Letters I, 83.

88. Decandolle, Alphonse Géographie botanique raisonnée. Paris, 1855. Darwin's copy in the Darwin Library, Cambridge University Library.

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89. Darwin MS 114, letter 151 and 155. From a number of notes made by Darwin in the margin of Decandolle's discussion of social plants, Darwin quite evidently thought that they depended "chiefly on other species, except where perhaps conditions very peculiar", p 459, and that "as long as conditions exactly same in relation to physical nature and other species . . . then of course there will be many individuals, and so be social" p 462 Darwin's italics. In all, pp 419-464 bear a number of interesting marginalia relating to Darwin's explanation of sociability.

90. Decandolle op cit note 88, Darwin's copy p 465.

91. ibid pp 465, 466.

92. ibid p 467.

93. ibid p 467.

94. ibid p 476.

95. ibid 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". Decandolle was using severely restricted botanical regions such as France or Holland for his calculations.

96. ibid p 878 tipped in.

97. Darwin's index tipped in, inside back cover volume II. It is useful for Darwinists to remember that these home made indices are a valuable guide to the points which Darwin thought worthy of mention. Many of his books are so indexed, and all are contained in the Cambridge University Library.

98. Boreau, Alexandre Flore du centre de la France . . . Paris, 1840.
Furnrohr, A.E. Flora Ratisbonensis . . . Regensburg, 1839. [volume II of Furnrohr et al. Naturhistorische Topographie von Regensburg]
Miquel, F.A.W. Disquitio geographico-botanica de plantarum regni Batavi distributione . . . Leiden, 1837.

99. Watson, H.C. The London Catalogue of British Plants. London, 1844. Darwin used the fourth edition of 1853.
Gray, Asa Manual as in note 83.
Henslow, J.S. A Catalogue of British Plants. 1835 (second edition). Darwin's copy of this work, bearing his pencil notes, is in the Darwin collection of the American Philosophical Society.
Hooker, J.D. The Botany of the Antarctic voyage of HMS Discovery ships Erebus and Terror . . . 1839-43 part I Flora Antarctica London, 1844-7; and part II Flora Novae Zelandiae. London, 1853-5.
Hooker, J.D. and Thomson, T. Flora Indica . . . Part I [all published] London, 1855.

For the sake of completeness I can add that Darwin also worked on: Babington, C.C. Manual of British Botany . . . London, 1851 (third edition); and Watson, H.C. Cybele Britannica . . . London, 1847-59,

volumes I-III only. Anticipating a later part of this thesis I should mention that these were the only works which Darwin calculated before July 1857, or, at least, the ones which he preserved the workings from. There is a possibility that he glanced at John Lindley's Vegetable Kingdom. London, 1853 (third edition).

100. Darwin MS 15 (ii) f 4.

101. Origin 55.

102. As in note 100.

103. As a vague approximation, Darwin's calculations (all on folio sized sheets, versos used) number over ff 330 and are divided into three substantial volumes in the Cambridge University Archives.

104. Yet he proceeded to discuss at some length other botanical calculations; see, for example, Calendar Asa Gray number 2 and Life and Letters CD II, 61-5, where he discussed the proportion which all introduced Compositae bore to the totality of introduced species of Great Britain.

## Notes to Chapter 6

## Charles Darwin's Botanical Arithmetic 1857-1858

1. Life and Letters CD II, 104.
2. ibid 103-4.
3. ibid 104. He was referring to Hooker's Flora Novae Zelandiae. London, 1853-5.
4. ibid 104.
5. See Martin Rudwick's very full account of the case of Glen Roy: Rudwick, M.J.S.'Darwin and Glen Roy: a "Great failure" in scientific method?' Stud. Hist. Phil. Sci. 5 (1974) 99-185.
6. Darwin MS 16 (ii) f 243 verso.
7. ibid as in note 6.
8. ibid f 231A - 238.
9. Lubbock, Sir John William and Drinkwater, J.E. The Laws of Probabilities. London, S.D.U.K., 1844.
10. Darwin MS 16 (ii) f 204B verso.
11. ibid as in note 10.
12. Life and Letters CD II, 105.
13. ibid as in note 12.
14. See for example his instructions, Darwin MS 15 (ii) ff 77-82, 90A, 95, or 16 (i) ff 133A, 136A, 145 verso, 174A, 184A.
15. Life and Letters CD II, 128.
16. Origin 59.
17. Gray, Asa A Manual of the botany of the northern U.S. from New England to Wisconsin and south to Ohio and Pennsylvania inclusive . . Boston, 1848. Darwin used the second edition of this work which was revised to include Virginia, Kentucky and all east of Mississippi etc. New York, 1856.
18. Darwin MS 16 (ii) f 292.
19. Darwin MS 45 f 65.
20. Decandolle, Auguste and Decandolle, Alphonse Prodromus systematis naturalis regni vegetabilis, sive enumeratio contracta . . . Paris, 1824-57. Darwin worked through volumes 2, 10-12, 13(i) and (ii), and 14.

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21. Darwin MS 15 (ii) f 61. See also Darwin MS 114, letter 223 to Hooker 9th February 1858.

22. Darwin MS 16 (ii) f 205.

23. Darwin MS 16 (ii) f 298. The letter only exists in copy at the University Library, Cambridge, though the original remains extant in the Gray Herbarium in Cambridge, Mass., see Darwin MS 156, no foliation, 5th September, 1857. This is the well known letter in which Darwin epitomised his views on evolution and natural selection for Gray's benefit, and which was eventually to be printed in part in Life and Letters II, 120-5. Darwin's question about statistics is, however, omitted in the printed version: see p 112.

24. Life and Letters JDH I, 456.

25. This was something which Darwin had taken into consideration, and he had even got Hooker to confirm the fact for him that variable plants were usually variable over all their range, and that many of them presented exactly the same varieties. See for instance, Darwin MS 114, letter 194 [? really letter 191] of 8th April 1857, and Hooker's reply Darwin MS 104, p 198.

26. Life and Letters JDH I, 457.

27. Darwin MS 104, p 195.

28. Life and Letters JDH I, 456, and apropos of his erring acquaintance (Bentham) p 458.

29. Marginalia H.C.Watson's letter to Darwin 2nd October 1855, Darwin MS unmarked box. Watson had written at length on the problem of splitting and lumping as it related to Darwin's calculations on "close species".

30. Darwin MS 114, letter 217.

31. Life and Letters CD II, 106, given as 21st February [1859] not 1858.

32. Darwin MS 98, ff 146-7.

33. More Letters I, 105 and 106 where Darwin writes "I will make no remarks on your objections, as I do hope you will read my MS which will not cost you much trouble when fairly copied out".

34. More Letters I, 109.

35. Life and Letters JDH I, 458. Hooker here claimed that Darwin had magnified the strength of his objections: "my great desire was to put every possible objection as strongly as I could. I did not feel myself a dissenter or opponent to your views, so much as a non-consenter to them . . ." p 459.

36. More Letters I, 109.

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37. Autobiography, Life and Letters CD I, 84. It is important to note that the "discovery" is usually cited as taking place in 1852, on the slender evidence that Darwin claimed (in 1863) that he first thought of the principle fifteen years after he began working on transmutation. "I believe", he wrote, "it was fifteen years after I began before I saw the meaning and cause of the divergence of the descendents of any one pair". See Life and Letters CD III, 26, letter to George Bentham June 19th [1863]. Sir Gavin De Beer takes Darwin to mean that he thought of divergence in 1852, i.e. fifteen years after he opened his first notebook on the transmutation of species. See De Beer, introduction to the notebooks B.M. (N.H.) Bulletin Historical series 2 (1959)p40. Camille Limoges believes that Darwin could have meant his first doubts about the stability of species, which, according to Limoges, began about 1836 and would give a date for the "discovery" of divergence in 1851.

    I myself do not lay much emphasis on Darwin's remarks for he was, after all, only speaking loosely. However, if scholars are to insist on a term of fifteen years, it is quite possible that Darwin was referring not to his species notebooks or to intangible doubts, but instead to his first written sketch of the theory composed in 1842. If we add fifteen years to this date we get a suggested point of discovery in 1857. As will be made clear this is, in fact, the year that I favour on the basis of entirely unrelated evidence.

38. See Sir Gavin De Beer Evolution by Natural Selection etc. 1959, and his transcripts of the Species notebooks where he points out at every possible opportunity Darwin's cognizance of divergence. See also Sandra Herbert PhD thesis The Logic of Darwin's Discovery Brandeis University, 1968, and Silvan S Schweber, in press.

39. Natural Selection. This contains transcriptions of Darwin's chapters III to XI which is why it is called only the second part of his "Big Book". The remaining manuscripts are thought to be not extant.

40. Autobiography, Life and Letters CD I, 84.

41. Origin 112.

42. Natural Selection 238.

43. ibid 228.

44. ibid 238.

45. Origin folding chart facing p 117 in the section devoted to 'Divergence of Character'; Natural Selection 236-7.

46. Natural Selection 248.

47. Although Darwin did not even then approach entire transparency of meaning: this is one of the most unsatisfactory parts of his argument and one problem which still perplexes modern biologists who

wish to truly understand evolutionary theory. I do not pretend to answer or explain the philosophical difficulties which we now experience, and concentrate instead on what Darwin himself was trying to say.

48. Bowler, P. J. Fossils and Progress. New York, 1976, especially his final chapter Darwinism and Progression pp 117-29, and Ospovat (personal communication) in press.

If Darwin did have notions of a progression from lower to higher forms of life why then did he go to such lengths to link man with the animal world? Progressionism required that man was held to be something above and apart from organic nature, and the 'goal' towards which all kinds of life were striving or gradually approaching. Darwin firmly associated man with his evolutionary predecessors, vide The Descent of Man, London, Murray, 1870 and The Expression of the Emotions. London, Murray, 1872; this was fundamental to selection theory, as pointed out by Sandra Herbert 'The place of Man in the development of Darwin's theory of Transmutation. Part II' J. Hist. Biol. 10 (1977) 155-227, especially pp 198-200.

May he not have recognised that the history of life exhibited a progressive increase in complexity and 'perfection' as indeed it does, but understood this to be due to undirected and fortuitous chance? Once an eye had been 'invented' of course it would remain in circulation, so to speak, until something better turned up, and so there would be a tendency for other organisms to 'advance' to keep pace with the organism with the eyes. This advance could, I believe, be executed under the usual rules of natural selection and does not necessarily require an underlying direction or doctrine of directionality.

49. Natural Selection 252.

50. ibid 252.

51. Origin 112, as quoted some pages back, note 41.

52. Natural Selection 238, as quoted previously note 42.

53. More Letters I, 109 given as 22nd August [1857]. There is a possibility that this was written in 1858 just after Darwin and Hooker had returned to the problem of large genera after the trials and tribulations of the Linnean Society paper (June-July, 1858).

54. Life and Letters CD II, 120. This comes in the famous letter to Gray of 5th September 1857 to which Darwin added an abstract of his views on natural selection. The attribution has suffered from being stated as October in the Linnean Society Journal, and from claims - in the absence of the original sketch - that Darwin might have composed it in 1858 after he had received Wallace's communication in June that year. For these reasons I do not place a great deal of emphasis on this evidence for Darwin's discovery of 'divergence' at a certain time.

55. Darwin MS C 40 e, unfoliated slip.

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56. ibid, unfoliated slip here given in its entirety:

"Sept. 23 1856. The advantage in each group becoming as different as possible may be compared to the fact that by division of labour most people can be supported in each country - not only do the individuals of each group strive one against the other, but each group itself with all its members, some more numerous, some less, are struggling against all other groups, as indeed follows from each individual struggling."

57. Darwin MS C 40 c, unfoliated slip.

58. In the beginning of 1857 Darwin was so fascinated with the division of labour, and the amount of life which a given area could support, that he started a "weed garden". In this he marked and identified each seedling which came up in a cleared patch of ground (meadow-land); he told Hooker on 21st March that he had started by clearing the ground, and on 12th April reported that he had counted 52 seed-lings. See Darwin MS 114, letters 192b, 192.

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# The Charles Darwin – Joseph Hooker correspondence: an analysis of manuscript resources and their use in biography

By JANET BROWNE

Department of History of Science,
Imperial College,
London S.W.7

The Charles Darwin (1809–1882) – Joseph Hooker (1817–1911) correspondence spans the most tumultuous and eventful years of the nineteenth century, when natural history forced itself into scientific and public affairs through the debate over evolution and natural selection. Yet, ironically, the letters between these two eminent protagonists for selection reflect only a small part of the debate. From 1843 to Darwin's death in 1882 they spontaneously confined discussion to purely scientific matters in which botanical questions and problems of plant distribution predominated. The point is made not to denigrate botany nor to criticise the quality of the correspondence, but rather to stress the importance of plant studies to the history of natural selection and evolution theory.

The correspondence totals some 1300 items: about 800 letters from Darwin to Hooker, and about 500 the other way. Not as large as many manuscript collections, this is certainly the largest body of Darwin letters to one individual that also remains intact with its replies. It makes up for what it lacks in volume by sheer intellectual weight: singly, and as a collection, the letters make significant contributions to Darwinian and Hookerian studies.

But why use the manuscripts – the autograph letters – when there is such a wealth of published sources? A dip into the *Life and Letters of Charles Darwin*[1] could lead through a library of comparable works: *More Letters of Charles Darwin;*[2] *Emma Darwin: A Century of Family Letters;* the *Lives and Letters* of Sir Joseph Hooker, Charles Lyell, Thomas Henry Huxley, A. R. Wallace, Asa Gray, and perhaps on to those of Richard Owen, R. I. Murchison, A. Sedgwick, L. Agassiz, Edward Forbes, and so on.[3] These are all universally regarded as authoritative sources for nineteenth century naturalists.

Yet a re-evaluation of the *Life and Letters* type of biography is essential. When the manuscripts are extant it is important and necessary to compare them with the printed works: the latter not only contain errors of transcription and dating, but they also suffer from questionable methods of composition. The authors were high Victorians and invariably closely connected with their subjects through family, personal, or intellectual ties. The mere fact of living one generation removed from the great man gave biographers the necessary detachment whilst ensuring that they had to rely heavily on friends and relatives for information. The end-product consequently offers a selection of hazy recollection, polemic and evasion, anecdote and family tradition, disguised under an air of 'tell it like it was'.

Because the genre explicitly includes letters the books tend to be treated as primary sources. Here they will be examined as historical documents within their own significant context, and the *Lives and Letters* of Darwin and Hooker will be compared with the manuscript collections of their letters, not to characterise the one as 'bad' evidence against the

'good' but to show how a complementary study can significantly aid our interpretations of biography, and perhaps alter the received widsom about these two eminent naturalists. Such an approach is commonplace among critics of literature and hence the study of biography is well advanced,[4] but few attempts have been made to place scientific biography in this tradition and apparently none for the *Life and Letters* group. Dr. Outram's work on the biographies of Cuvier is, however, a noteworthy exception.[5]

What is known of biographers and biography in the nineteenth century? The basic information in *Lives and Letters* was often presented so that the subject was moulded to fit the ideals and conventions of his memorialist, and so that myth and dogma were perpetuated. More important however, is the fact that the great man frequently cast himself in a particular role, or roles, during his lifetime and a famous figure could thus create his own biography. In the scientific world Huxley and Murchison[6] immediately spring to mind. A dutiful biographer would do nothing to dispel or modify such images and, indeed, *Lives and Letters* as a literary style were not designed to cope with informed assessments of scientific achievement. They were purely a vehicle for the revelation of the 'inner man' and an exemplary character study: hence biographers relied on the subject's own estimate of his scientific worth and were uncritically laudatory.

Most people dismiss such 'Victorian' memorials for their lack of artistic quality and their over-solid pragmatic approach, but it is useful to remember that it is this prosaic element that encourages us to use them as sources for history. Over the nineteenth century the number of commemorative volumes increased exponentially and were rapidly standardised into the two volume, crown octavo sets that are so familiar today. The desire to read of the famous ensured a stable market for the publisher and, by mid-century, it was expected (though not always endorsed) that death was followed by a resurrection in print. Carlyle,[7] with his belief that history was the lives of great men, did more to encourage the genre than perhaps even Boswell, and towards the end of the century *Lives* were being produced, and read, in enormous quantities. Uniform sets such as the *Men of Letters* and *Men of Science* series attempted to fill the gap left by personal memorabilia for some serious evaluation of 'lives and works' but even these were couched in eulogistic terms. Typical of the era and symptomatic of the popularity and saleability of biography was, of course, Leslie Stephen's tribute to his nation, the *Dictionary of National Biography.*

The universal justification was its didactic worth and elevating message, and much of the limited discussion over the aims of biography was dominated by the question of ethics. Since Boswell had revealed Dr. Johnson 'warts and all' public opinion had swung fiercely towards reticence, moral evaluation and enlightenment in its reading matter.[8] The Evangelical movement, although it could hardly have caused this development, nevertheless fostered and furthered such an approach to the extent that even biographers with little or no sympathy for religious enthusiasm adopted the style. The second generation pushed it to the excesses that we now characterize as 'Victorian' and which, at the end of the century, provoked such violent rebuttals as Gosse's *Father and Son* and Strachey's *Eminent Victorians.*

Exemplary biographies depended for their merit not on the writer but on the moral quality of their subject. The biographer was modestly supposed to be only the compiler and organiser of documents that displayed in their proper order virtues and suitably stigmatised vices. The power to make or break a hero must have indirectly encouraged the author to waive his own judgement (or at least to say so) and present the evidence so that the reader could draw his own conclusions; by allowing the great man to tell his own story the contem-

porary goal of objectivity was assured. The use of letters went hand-in-hand with this 'documentary' ideal and the quasi-scientific desire to let facts speak for themselves, increasingly bearing the burden of the book as impartiality, reticence and sensibility became the norm. As there already was in existence a strong alternative tradition of epistolary novels and collected letters of literary figures, late Victorians must have felt that adding letters to a *Life* in some way increased its adherence to the truth. Although it is difficult to imagine what a biographer could produce without correspondence as his raw material, authors in the last third of the nineteenth century relied solely on the published letter – in its entirety – to fill up the pages of their books. And fill them up they did: not only were vast numbers of letters written, but almost as many were preserved, so that biographers suffered under an *embarras de richesses.*

With this in mind it is easy to dismiss Francis Darwin's (1848–1925) *Life and Letters* and *More Letters* of his father Charles as typical of the genre. Credit must, however, be given to Francis for realising that the best way to portray his father was through his large and varied correspondence. During a secluded life Darwin's main contact with the outside world was via the written word and that was how many of his colleagues came to know and respond to him. As he lived through letters, so letters reflect his life – more accurately perhaps than Hooker's. Both the *Life and Letters* and *More Letters* of Charles Darwin were widely acclaimed when first published in 1887 and 1903 respectively, and remain highly praised not just for the mass of information they contain but for genuine literary merit and charm. Over and above its expected sales the *Life and Letters* proved to be a best-seller and, about one month after publication, John Murray could boast that he had disposed of 4000 copies, and the following week that he was printing the sixth thousand.[9] However the success of Francis Darwin's collections of Darwin's letters should not obscure the case that they contain many editorial errors; errors which might appear to be trivial but which hide valuable historical information.

For my own work on the development of plant geography it has been important to know precisely when Darwin familiarised himself with Edward Forbes' (1815–1854) famous paper published in the first memoir of the Geological Survey, 1846: *On the connexion between the distribution of the existing fauna and flora of the British Isles, and the geological changes which have affected their area.*[10] This is conventionally regarded as the first formal merger between geology and botanicozoological distribution: in other words, Forbes here proposed a series of invading floras and faunas moving over the British Isles as and when land movements permitted. Darwin too had been working on similar ideas and it might reasonably be expected that he would have expressed immediate interest in Forbes' theory.

However, in Darwin's correspondence with Hooker such a discussion occurs only before the event – in 1845 – and some ten years later in 1855 and 1856. The comments form the basis of an interesting psychological study of Darwin and his reaction to being 'forestalled' by Forbes, which adds a significant factor to Darwin's rejection of continental extensions as an explanation for distribution. In his *Autobiography;* in the long manuscript version of his book *Natural selection;* in *On the origin of species* and in letters to Hooker[11] Darwin insisted that Forbes had anticipated his own theory on the origins of alpine and arctic geographical distribution patterns. But if the two published presentations are compared there are fundamental differences which Darwin would have noticed had he fully examined Forbes' account. The comments arising in Darwin's correspondence of 1845 are based only on verbal and informal written communications about Forbes' theory as put forward to the British Association of that year, whereas those arising at the later time of 1855 are clearly based on

a recent reading or re-reading of his formal and fullest statement to the Geological Survey of 1846. The major piece of evidence in favour of Darwin reading Forbes' long article on publication is a letter from him to Hooker, published in *More Letters of Charles Darwin,* and dated '1845 or 1846'.[12] The editor, Francis Darwin, stated that "Sir Joseph Hooker's letters to Mr. Darwin seem to fix the date as 1845, while the reference to Forbes' paper indicates 1846".[13]

Going through the preceding letters to Hooker in the autograph collection it becomes clear that Darwin senior was not referring to this, 1846, paper, nor even to the similarly worded notice of 1845, but instead to a completely different report on the fauna of the Aegean seas.[14] So there is no evidence that Darwin did read Forbes on publication and, although this does not prove that he did *not* read it, a source of confusion has been eliminated. The question would not have arisen had not Francis Darwin introduced a spurious connection between the letter and this particular paper. The letter itself can now be dated to the summer of 1845.[15]

Not only dates can be recovered from studying the manuscripts in conjunction with the published works. A simple mistake introduced unwittingly into Darwin's *Life and Letters* by Joseph Hooker, has led to scholarly ignorance of a long and interesting, unpublished, letter. It deserves attention as the first to be sent from Hooker to Darwin, and because it invalidates the published 'first' letter.[16] In his reminiscences for the *Life and Letters of Charles Darwin* Hooker stated that he received his first letter from Darwin in December 1843. Francis Darwin printed the text of the letter using Hooker's account as the 'lead-in', although he dated the letter itself with only the year. By the time that Hooker's *Life and Letters* was published in 1918 this date – December 1843 – was an unquestioned part of the Darwin legend. Hooker's biographer, his godson Leonard Huxley (1860–1933), would however have done well to question it, for his concentration on December caused him to overlook Hooker's first reply dated November of the same year. Leonard Huxley compounded the error by publishing another letter (actually the second reply) in Hooker's *Life* and calling that the first response to Darwin.[17] So the first Darwin to Hooker letter is printed in Darwin's *Life* with a date that has only illusory exactitude, and the mistake in Hooker's reminiscences led to the publication of another letter – the supposed reply – in Hooker's own *Life* thirty years later. The genuine reply according to Leonard Huxley could not exist, nor does it exist for historians today unless they have consulted the manuscript collection.[18]

Leonard Huxley was drawn into error by not questioning the accuracy of Francis Darwin's editorial work and through ignorance that the date had, in the first instance, been derived from Hooker. This case, and that which preceded it, are salutory examples of the benefits of using manuscript material. But consultation of autograph letters is always essential if dates and readings are to possess any real authority. Unfortunately, the *Life and Letters* treatment can contain more fundamental and far-reaching faults than these. However, before presenting a critique of *Life and Letters* it is both logical and useful to digress to its counterpart and to stress the intrinsic value of original resources, and, in particular, the Darwin – Hooker correspondence. It is a measure of the quality of this collection that, despite exhaustive examination by Darwinists, it can and does provide such fresh and stimulating source material.

The letters written before the *Origin of Species,* 1859, can be seen as a dialectic between botany and geology, which seems to have been Hooker's and Darwin's own characterisation of their positions. Hooker over some twenty years called Darwin a geologist in the face of ample contradictory evidence for Darwin as a zoologist, botanist, entomologist, or any of the

'ists' pertaining to nature study. Darwin, on the other hand, always referred to 'you Botanists' when writing to Hooker. Equally, they describe themselves in similar terms. Taking up such positions was not strictly necessary, as both men were competent over an enormous range of contemporary science, and it perhaps reflected a desire to polarise issues and to reduce mutual problems to their simplest terms by asking 'What would a non-botanist or non-geologist say to this?' Consciously or unconsciously Darwin projected a certain image of himself as a geologist and no doubt Hooker reciprocated. Writing in August 1856 Hooker told Darwin that:

> "The difference between us lies in this: that you are more of a geologist than botanist & feel the real weight of the geological objections – I am no geologist at all & enjoy the aforesaid freedom of motion . . ."[19]

In reply Darwin stated that Hooker's geological letters were of more value to him than even Lyell's, and implied that the advantage lay in Hooker standing outside geology. This was an attribute that Hooker correspondingly recognised in Darwin, as he wrote to John Tyndall:

> "Darwin is the only one of them [geologists] I know who has any accurate conception of the right or wrong of a botanical problem . . . "[20]

The correspondence presents an opportunity to see not only what Darwin and Hooker did, and what they thought that they were doing, but also helps us to recover their self-images. The historical necessity for such a recovery can hardly be over-stated nor can its corollary, the several shades of truth behind self-perception and projection, be ignored.

Immediately related to these questions is the utilisation that each man made of his colleague's scientific knowledge. Darwin deliberately took botanical concepts from Hooker and introduced them into his geology, whilst Hooker followed up several geological problems during the course of his studies that are essentially derived from Darwin. If this exchange had been less self-conscious nothing more could have been drawn from the fact but, from their obvious awareness of their 'roles' considerable historical weight can be laid on it. Darwin, in particular, extracted methods, concepts, and techniques from allied and subsidiary disciplines, firstly to provide a wide range of evidence for his theories, and secondly, to see if these additions and cross-fertilisations offered anything to his methodology. In botany he found a new and exciting field opening out in front of him from which he could pick and choose information and interpretations like flowers.

These general relations between the sciences – botany and geology – and their physical expression in the correspondence between Hooker and Darwin take definite direction if the history of the development of biogeography is superimposed. Biogeography is, after all, the merging of geology with botany and zoology to form a science of plant and animal distribution in time and space. Reducing it to dangerously simple terms, biogeography was the child of geology. But it did not spring fully formed from Zeus' head: it required shaping and continuing inter-penetration of the various factors involved, in the manner suggested by Darwin's and Hooker's correspondence. Naturalists who were familiar with spatial distribution such as Hooker, Brown, H. C. Watson, Gray, Bentham and De Candolle, had to co-ordinate with geologists and palaeontologists such as Darwin, Edward Forbes, Murchison and Agassiz, who knew about fossil distribution in time, before biogeography became a discipline in its own right. Contrary to expectation, Darwin's work, which gave such continuity and unity to the natural world, did not effect this fusion. Biogeography was already established, admittedly in diffuse form, before Darwin imposed evolution theory and thereby gave it direction. The prevailing methodology of this nascent science dictated that concepts from one discipline

should be transposed to others. The Darwin-Hooker correspondence presents an actual example of a conscious attempt at cross-fertilisation through Darwin's use of botanical statistics under Hooker's guidance.

In close collaboration with Hooker through the 1850s Darwin tabulated some dozen floras and one or two monographs from the animal kingdom to show the relative proportions of certain taxa in large and small groups.[21] Statistics were, to naturalists, more of a study of proportions than anything else, and closely resembled population surveys and actuarial tables. In botany the proportions were worked out of species to their families or genera; the major taxonomic groups to the whole flora; or the proportion of endemic forms to commoners, first in absolute terms and then converted to decimals or expressed as numerators of 1000. Augustin De Candolle was the first to popularise such arithmetical analysis and it had been rapidly integrated into the botanist's repertoire, and rather more slowly, via Lyell, into geology. Lyell had made the study of proportions an original and productive technique for estimating the relative ages of strata by the comparison of extant to extinct species.[22] Yet Darwin could not make the intellectual leap from statistical geology to statistical botany. He needed the active intervention of Hooker. Hooker reinforced Darwin's high opinion of botanical methodology and convinced him that he could profitably use a technique that can hardly have been unfamiliar to him within the geological context.

The results of Darwin's calculations demonstrated that more varieties were produced in numerically large species which also occupied a wide area. Using various methods he showed that these were also the varieties most likely to turn into species ('incipient species') and that the advantages which had made the parent successful would equally contribute to the success of the offspring. He became preoccupied with large and dominant species, spread over wide ranges, with many individuals, and which belonged to similarly potent genera. Darwin affirmed that these were the source of most new species. This idea of 'winner takes all' is very different from his first attempts at explaining the origin of species in which he relied heavily on geographical isolation.[23] Now, with widespread and dominant species in his theory he had to find some mechanism other than isolation.

He did this by inventing a 'principle of divergence' that was to be used in tandem with natural selection.

(Darwin's thinking can be followed this far through his correspondence: indirectly the same correspondence throws new light on his published works and in particular offers an explanation for the series of revisions and amendments in his long, unpublished manuscript from which *On the origin of species* was abstracted.[24] The sequence of composition and interpolation that has been brought out by Stauffer in his editorial notes to this manuscript can, for the first eight chapters, be attributed to Darwin's discovery of the principle of divergence.)

Darwin's explanation of divergence is confusing and his use of it appears to be methodologically unsound, but he was emphatic about its importance, arguing that it was crucial to the action of selection. The principle expressed the tendency for natural selection to favour the most different variety out of any continuum, and that this extreme form was most likely to occupy a different niche, or place, in nature. A continuous selection for difference in the one direction would eventually make the variety a species in its own right. Darwin's use of divergence is therefore closely linked with arguments about the evolutionary potential of widespread and dominant species. His letters to Hooker show the botanist to be his mentor for the latter, and by implication an important factor in the discovery of the former.

It is customary when tracing historical influences at this point to insert a caveat and state that once exerted the influence loses status because it is absorbed and transformed by the recipient. However, in the case of botanical statistics it is curious to see Hooker not only providing the basic information, but also regulating the result – with Hooker's continuing guidance and criticism Darwin had substantially modified and improved his theories about the kind of species that contributed most to evolution. Over and above this achievement Darwin had virtually simultaneously uncovered a conceptual gap and, happily, thought of something – divergence – to fill it.

When Darwin in his *Autobiography* retrospectively analysed the difference between his first essay on species and the *Origin* of 1859 he stated that the earlier works lacked only one thing: his principle of divergence. Substantiating evidence comes from the fact that he felt it necessary, when under great personal distress, to add a description of divergence to his submission to the Linnean Society in July 1858. This took the form of a copy of a letter to Asa Gray (1810–1888), the American botanist, dated 5 September 1857.[25] Much has been made of Darwin's effortless abstraction of his theory for Gray in September, compared with his excuse that it was 'really impossible' to do so for A. R. Wallace some few months beforehand.[26] But in May 1857 it surely was impossible for Darwin to precis his work for he had not thought of divergence; by September he had. The principle possessed such heuristic power that, once discovered, he could reduce a mass of interrelated propositions and probabilities to manageable proportions, and even welcome an opportunity to present an abstract.

Study of the autograph letters has thus revealed noteworthy ideas and problems that deserve further attention: the roles in which Hooker and Darwin cast themselves; their attempts to effect a cross-fertilisation between the various sciences; Darwin's faith in this principle as exemplified by his use of botanical statistics; the part that botanical statistics played in the sophistication of evolution and natural selection theories, and the subsequent discovery of a remarkable conceptual aid in divergence. None of these could have come from an examination of the appropriate *Lives and Letters.*

To return to the more general historiographic problems concerned with *Lives and Letters,* it can be seen that the extant manuscript collections provide important clues to the writing of official biographies.

After Darwin's death in April 1882 Hooker offered the Darwin autograph letters to his eldest son William and they were gratefully accepted.[27] But the letters were not permanently handed over until 1889[28] although they were actively used by the Darwin family during the intervening years for the compilation of the *Life and Letters.* Even after publication they returned at least once to Hooker for his advice on the sequel volumes of *More Letters.* Francis Darwin had, at first, no intention of drawing up a life of his father, especially since the role of biographer had immediately been assumed by others. Darwin had died on April 19th and within three days proposals were made to publish some kind of extended scientific memoir. Romanes (1848–1894), the sub-editor of *Nature,* wrote simultaneously to both Hooker and Huxley asking for a notice, and after some initial confusion Hooker gladly relinquished the task to Huxley.[29] He did however suggest that a longer article might follow under his own direction and in early May outlined his plans to Francis Darwin – the article was to assess Darwin's place in the honorium of science and to include a selection of his letters to Hooker. But by the 6th May Romanes who, no doubt, wanted a more tangible part in the creation of Darwin's memorial, had proposed to Hooker that the article should become a book with several contributors, himself among them. It is interest-

ing to see that Romanes conducted his enquiries through Hooker and received answers from the Darwin family along the same channel: apart from a sensitivity towards the bereaved, Romanes probably thought that the intervention of Hooker would materially aid his cause. His proposal, meeting with Hooker's approval, was forwarded to Francis Darwin. At this point Francis stepped in and quashed everything: "It seems to me to be always a mistake", he wrote,

> "that anything like a biography of anyone should be written immediately after his death . . . the fact that a good part of the work would fall into other hands does cause us some apprehension. I know and fully appreciated Romanes' regard for my father but I have but small confidence either in his tact or literary taste, and I think he is especially likely to go wrong when writing under the influence of strong recent feeling."[30]

Romanes compromised and brought out a five part memoir in *Nature* through May and June 1882 in which each section was by 'other hands'.[31] Francis Darwin lost no time in inserting his own notice in *Nature*,[32] and later the newspapers and the *Athenaeum*, asking for gifts of or copies of his father's letters to be kept for an official biography.[33] He told Hooker that he hoped this would deter others yet that he was not prepared to write it himself.

However, in September 1882 Francis was pushed into declaring himself an author through an unfortunate incident with the German naturalist Haeckel. Haeckel had contravened the family's instructions by publishing one of Darwin's rare letters relating to Christianity and his lack of faith in the established Church.[34] The 'Haeckel business' caused them a certain amount of distress and a great deal of displeasure so that Francis was virtually obliged by the norms of the day to produce a *Life*, as an official commemoration.

It is instructive to compare this apparent unwillingness with the easy path to literary production that Leonard Huxley enjoyed. As T. H. Huxley's son he ascended to the role of his biographer through the determined intervention of his mother Henrietta with Macmillan. A potential scientific biographer, Michael Foster, was pushed aside in favour of Leonard, who was, according to Henrietta, "too retiring . . . too modest to take the initiative".[35] In August 1895 Leonard Huxley told Macmillan:

> "At my mother's particular wish I propose to write a Life of my father. Prof. Michael Foster and Ray Lankester have offered to help me in all the technical scientific part . . . "[36]

After the success of the *Life and Letters of T. H. Huxley*, 1900, Leonard Huxley proceeded to edit a selection of educational writings by his wife's uncle, Matthew Arnold,[37] before acquiring the commission from Lady Hyacinthe Hooker to write the *Life and Letters* of Sir Joseph.

The general conclusions to be drawn from only two examples indicate that the choice of biographer was firmly under the control of the family and that, wherever possible, a member of that family should take on the work. By this emphasis on the personal rather than on scientific qualifications the contents of the ensuing biography were almost pre-determined and any evaluation of the great man's contributions to science would certainly be derivative. Although there is no reason to believe that filial feeling was incompatible with a knowledge of contemporary science and its problems, it seems to be the case that *Lives and Letters* were thought to be inappropriate places for an examination and analysis of science. Henrietta Huxley persuaded Michael Foster and Ray Lankester to give way to Leonard Huxley yet maintained their interests by allowing them to contribute to the scientific parts.[38] Similarly, Hyacinthe Hooker bypassed Hooker's son-in-law Thiselton-Dyer, who as Assistant-Director of Kew Gardens was well qualified to undertake a botanical biography, to give Leonard

Huxley the work. Even Francis Darwin's botanical interests and scientific background, which gave him a unique sympathy with his father's aims and methods, appear not to have been the decisive element in his taking up the task of a biography. It is fortunate though that Francis Darwin was so familiar with plant studies, as it is this background knowledge that adds substantially to the charm and authenticity of his *Life and Letters* and *More Letters*. But generally speaking the science in the *Life and Letter* genre is either derivative, actually contributed by some-one else, or, in the rare case of a scientific author, attenuated. Proof sheets were circulated amongst the subject's friends for comments and advice was solicited. Whole chapters, such as Huxley's on the reception of the *Origin of species*,[39] or Hooker's reminiscences of Darwin, were included in the various biographies. And, as will be seen, accounts and characterisations of events and personalities become stereotyped into the mould given them by the biographer or even by the great man himself during his lifetime.

In his notice in *Nature* Francis Darwin had called for gifts or copies of his father's letters, and during the five years that he worked on the *Life and Letters* and the subsequent years on *More Letters* he had transcribed for him the larger part of Darwin's correspondence. He wrote to Huxley:

> "Will you whenever you have time (there is no sort of hurry) look out any letters of my father's to you that I might see and make copies of. Of course your wishes or slightest feeling about what should & should not be published shall be law . . . "[40]

But, although Francis Darwin was later to receive editorial aid and major contributions from Huxley, he never relied on him to the extent that he relied on Hooker for advice at every stage, nor did he send Huxley copies of letters – as he did to Hooker – for comments. Apart from Francis Darwin, Hooker was the only one of Charles Darwin's friends to use the material at all stages of composition: the original manuscripts; the transcripts; and eventually the proof sheets. It appears that during the first few years after Darwin's death in 1882 Francis Darwin kept all the original Darwin to Hooker letters, effecting some preliminary sorting and dating, and having transcripts made. In July 1885 he wrote to Hooker hinting that he might like to add comments to the proof enclosed:

> "I wonder if you would read over this chapter and give me any suggestions that occur to you – I feel as if it were scrappy – & has a poor sort of feel about it from the arrangement I think. You will see that Fitton, Boot (or Bootl) Lonsdale etc are only casually mentioned so that the briefest note would do . . . "[41]

On hearing that Hooker was, in fact, drawing up considerable notes about Charles Darwin, Francis offered to return the original letters:

> "I am extremely glad that you are making notes about my father – shall I send the earlier of the two vol[umes] now? or do you not at all care for it till August."[42]

Hooker used the earlier manuscript letters to write up the reminiscences that are featured in the introductory chapters of the *Life and Letters*.[43] If he had not already done so (i.e. before sending the originals to Francis in the first instance) this was probably the time that Hooker added the many dates to the earlier part of the collection, which, by being printed in the *Life and Letters*, and subsequently used again for *More Letters*, are of great historical significance. Even checking against an original does not necessarily verify a date when dealing with Darwin letters.

In addition to his enthusiastic proof reading Hooker tossed out ideas and information at an astonishing rate for Francis Darwin to incorporate at will: whilst proof reading Chapter IX Hooker suggested:

> "Is it worth a passing allusion to his having taken into his service a sailor from the Beagle, or was this before he went to Down. I thought I remembered one. Passibly [sic] an allusion to Parslow may be lugged in – he was so integral a part of the family and known to all visitors as such."[44]

This point was repeated verbatim by Francis Darwin in the *Life and Letters,*[45] as were many others. With few exceptions all Hooker's contributions were incorporated into the published work: he had not only corrected the text of the letters, but also added notes about chronology, events and personalities, and reminiscences to the editorial sections that linked items. Francis Darwin obviously valued these additions and therefore called again on Hooker to help with the composition of *More Letters.*

For *More Letters* he sent Hooker the originals of his own letters to Darwin (which Hooker was delighted to find preserved) and copies of all Darwin's letters in reply. Hooker made a number of pencil corrections to both copies and originals which Francis Darwin acknowledged gratefully, and, no doubt, it was this continuing interest of Hooker's that encouraged Francis to send him the proof 'slips' of the two geographical distribution chapters. Again, Hooker made corrections and footnotes that appear in print.

The transcribed correspondence seems to have led as active a life as the genuine letters, and it deserves a brief digression. There are two sets of copies in addition to the real letters at the University Library, Cambridge (Darwin to Hooker; Hooker to Darwin – this last is now incomplete),[46] and a further shorter set of Darwin to Hooker copies at the Royal Botanic Gardens Kew. These were made at Francis Darwin's request in 1889 to acknowledge Hooker's gift of the originals.[47] The copyist was H. W. Rutherford (?–1924) a member of the Cambridge Library staff and collaborator with Francis Darwin on the catalogue of Charles Darwin's books left to the Botany School there. Francis Darwin made a particular effort to help Rutherford, financially and otherwise, and employed him in his spare time for many years in copying Darwin's papers.[48] Rutherford received 3d. per page of transcript, apparently 1d. over the usual rate, as explained by Lady Hooker to her friend and anxious authoress, Marianne North:

> "Mr. Fr. Darwin paid for copying his father's letters; this I find was 3d. per page or copy (i.e. *side* of paper) . . . but this seems a large sum and I did not tell the Miss Nobles what Mr. Darwin had paid his copyists; and I find that a *usual* charge is 2d. a page for copy."[49]

The general historiographical point to this analysis of the composition of one particular *Life and Letters* is that such processes should always be taken into account. Most of the ground work was conducted from copies of letters, often by someone other than the author, and the proof sheets were hawked around for notes and emendments, because strong feelings of nepotism and regard for suitability often meant that the authors were not scientifically capable. In Hooker, Francis Darwin had a fairly reliable associate, but the potential for abuse in such situations was enormous. Equally, the autograph letters have a history that by itself should invite caution about the biographies: from original to transcript, from transcript to proof, there were many opportunities for error. Added to this there are problems concerned with unacknowledged contributions. Hooker's all-pervasive influence over the published Darwin collections leaves room for serious distortion, a distortion which is magnified by the fact that his role in constructing the Darwin story is largely anonymous.

This last point is one that deserves, and even demands, expansion. Hooker's contributions were, through modesty or strategy, mostly concealed in the Darwin biographies. Because passages and notes were not published as his opinions, the reader is invited to believe them as the simple truth. Hence a tentative thought can turn into dogma and tradition which is nur-

tured by continuing use of various *Lives and Letters* as primary historical sources. The stereotyped account of the famous Oxford meeting of the British Association in 1860 is an excellent example of this 'invitation to believe', and well illustrates the conjoined power of anonymity and the official biography.

The event hardly needs more than a reminder that the meeting provided a platform for statements about evolution, and that Thomas Henry Huxley exchanged insults with the Bishop of Oxford, Samuel Wilberforce (1805–1873). The main points of the debate are entrenched in Victorian scientific 'mythology'. Even the most recent and scholarly of papers on this meeting typifies a whole series of reconstructions by accrediting Leonard Huxley in the *Life and Letters* of his father, with the most complete body of information available to historians,[50] and follows the popular account. Yet what is this history based on? Contemporaries were agreed that they could not remember Huxley's or the Bishop's exact words, and even Hooker, as one of Huxley's closest friends and an active participant in the debate, could not remember such a crucial point as which of Huxley's female relatives Wilberforce had besmirched.[51] Huxley left no account of his own except for a letter to Dyster[52] and another to Francis Darwin at a later date.[53] Not only was there contemporaneous disagreement as to Huxley's words, there was also some controversy over which of the 'combatants' had triumphed: Balfour Stewart (1828–1887) wrote on the 4th July 1860 that he thought that "the Bishop had the best of it".[54] There was even contemporaneous distortion, lucidly ridiculed by Monckton Milnes in the House of Commons, and chronicled by Grant Duff in his *Notes from a Diary, 1851–1872:*[55]

> "The British Association is meeting this year at Oxford, and there has been a great scene between the Bishop of Oxford and Huxley, of which Monckton Milnes has brought to the House of Commons a comic version. According to him, Huxley asserted "that the blood of guinea pigs crystallises in rhombohedrons". Thereupon the Bishop sprang to his feet and declared that "such notions led directly to Atheism!" "[56]

There is in the literature far more to the story than that which is transmitted through Leonard Huxley's biography. But historians continue to use the published accounts in the *Lives and Letters* of Darwin, Huxley, and Hooker, and their reconstructions therefore conform to the evidence which is selectively put forward for an 'official' version. As published, the story is a composite one ultimately based on the 'eyewitness' account in the *Life and Letters of Charles Darwin.* And this was written by Hooker some twenty-five years after the event.

Hooker had volunteered a sketch of the Oxford meeting merely to add colour to what he supposed to be Francis Darwin's account:

> "Have you any account of the Oxford meeting? if not, I will, if you like, see what I can do towards vivifying it (and vivisecting the Bishop) for you. I had utterly forgotten that letter of mine, and am amused to find that it recalls the scene so clearly. I am perhaps not a fair judge of Huxley's contribution . . . "[57]

Francis Darwin seized the opportunity to write to Huxley and asked him for his own recollections:

> "I wish I had some account of the celebrated Oxford meeting. It is a thousand pities that my father destroyed his letters [,] there seems to have been one from you – and I think from Hooker – I should be glad of any account of it even if slightly Tichbornian."[58]

but had to be satisfied with his promise to read the proof sheets. Hooker, on the other hand provided a mass of entertaining material that was eventually published as the 'eyewitness' account. At the time of submission Hooker was careful to point out that "it is impossible

to be sure of what one heard, or of impressions formed, after nearly 30 years of active life",[59] and asked that Huxley should vet it:

> "Here is my screed. I do not like it altogether, but can do no better. I should like Huxley to see it if you put it in print. Pray Anglicise it where necessary. Huxley may not like the bit about himself: if so it must come out. I have been driven wild formulating it from memory"[60]

It is at present impossible to say if Huxley did edit Hooker's account, but he certainly saw the page proofs which contained Francis Darwin's presentation, and thus, by implication, approved this account.[61] The *Life and Letters of Charles Darwin* therefore contains as 'official' a version as could be devised.

Five years after the *Life and Letters,* in 1892, Francis Darwin printed a one volume abbreviated *Life* of his father[62] and for this added to Hooker's story some minor details from other sources and two important contributions: one from the Rev. W. H. Freemantle; and the other from Huxley himself.[63] The latter is the famous letter in which he remembered crying 'The Lord has delivered him into my hands'. It is sufficient to point out that Huxley had had thirty-one years to remember this point, and five years to decide what, if anything, he desired to add to the record.

When Leonard Huxley came to prepare a separate rendering of the meeting to honour his late father he naturally used the Francis Darwin one volume *Life* as his source material. In 1898 – three years after Huxley had died – Francis Darwin replied to Leonard's query:

> "The eyewitness was Hooker – I suppose he told me not to publish his name tho' I can't imagine why. I am pretty certain it was written for the *Life* i.e. in the 80s. It is most curious how different accounts vary. You will see your father's account of "The Lord has delivered" etc in the one volume version of the *Life* "Charles Darwin, his life told etc" 1892 p.240 . . Your father's letter to me is by a misprint dated 1861 instead 1891."[64]

In the event Leonard Huxley paraphrased Francis Darwin's second, more complete, description for his *Life and Letters of T. H. Huxley,* 1900, to which he added some embellishments from other sources.[65] Then, even though the 'eyewitness' account had gone through three biographies picking up extra details in each one, Leonard Huxley revamped it for a fourth time for the *Life and Letters of Sir Joseph Hooker* 1918.[66] This biography, published in the same year as Lytton Strachey's *Eminent Victorians,* represents everything that is typical of the *Life and Letters* genre, and Leonard Huxley's conservative use of evidence aptly came full circle when Hooker's account passed through three biographies only to return to his own. By repeating and reaffirming the same story the younger Darwin and Huxley, abetted by Hooker in his old age and endorsed by Huxley before his death, had forged a legend that remains in the same conventional format today. The source material without Hooker's 'vivifying and vivisecting' recollections, and without the four biographies, is inadequate and anecdotal at worst, and unexplored at best. Surely it is fruitless to continue to reconstruct the Oxford meeting when the evidence cannot, at the moment, provide the answers, and the history of the transmission of even that evidence is ignored.

In drawing a general conclusion it is only necessary to state that in these instances, and possibly many others, manuscripts and autograph letters are much more than a simple alternative to the published version; such material transcends the 'facts' and legends that are passed on to modern historians through the medium of *Lives and Letters.* No-one would, however, deny the value of these biographies and it is unrealistic (not to mention unnecessary) to demand that all research should be conducted from archival resources. But *Lives and Letters* should be acknowledged as historical documents in their own right, with all their

concomittant problems, and be considered as limited sources for the history of Victorian science.

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NOTES

[1] DARWIN, F. 1887. *The life and letters of Charles Darwin including an autobiographical chapter edited by his son.* London, Murray.

[2] DARWIN, F. and SEWARD, A. C. 1903. *More letters of Charles Darwin. A record of his work in a series of hitherto unpublished letters.* London, Murray.

[3] LITCHFIELD, H. 1904 and 1915. *Emma Darwin: a century of family letters 1792–1896.* London, privately printed and Murray.
HUXLEY, L. 1918. *Life and letters of Sir Joseph Dalton Hooker based on materials collected and arranged by Lady Hooker.* London, Murray.
HUXLEY, L. 1900. *Life and letters of Thomas Henry Huxley.* London, Macmillan.
LYELL, K. M. 1881. *Life, letters and journals of Sir Charles Lyell.* London, Murray.

[4] The most useful works on biography and its trends that I have found are:
REED, J. W. 1966. *English biography in the early nineteenth century 1801–1838.* Yale University Press.
ATTICK, R. D. 1966. *Lives and letters. A history of literary biography in England and America.* New York.
CLIFFORD, J. L. 1970. *From puzzles to portraits, problems of a literary biographer.* North Carolina.
GARRATY, J. A. 1957. *The nature of biography.* New York.
NICOLSON, H. 1968. *The development of English biography.* Oxford.
I am grateful to David Ross, Fulbright scholar at Imperial College, London (now at Northwestern University, Illinois) for his advice and enthusiasm about this section, and for his more general criticisms of the paper as a whole.

[5] OUTRAM, D. 1976. Cuvier and scientific biography. *Hist. Sci.* 14, 24: 107–142. Dr. Outram makes the point that biography was probably the most important medium for the diffusion of the history of the life sciences in the nineteenth century.

[6] Murchison had told Geike that he would leave him suitable financial incentives for the preparation of a biography long before his death. It is easy to suppose that Geike immediately began collecting material whilst Murchison was still alive. I am grateful to John Thackray of the Institute of Geological Sciences for this information.

[7] ANNAN, N. 1952. Historians reconsidered: Carlyle. *History Today* 2: 659–665.

[8] CLIFFORD, J. L. 1962. *Biography as an art. Selected criticism 1560–1960.* London & Oxford.

[9] *Life and letters C.D.* appeared in the review columns on 19 November 1887. Dr. Richard Freeman has kindly suggested to me a publication date in late October or early November, to catch the Christmas market. Joseph Hooker wrote to Francis Darwin on 19 and 26 December 1887 with the information about Murray: Royal Botanic Gardens Kew, J. D. H. outgoing letters, vol. 3, 164–165.

[10] *Memoirs of the Geological Survey of Great Britain* I: 336–403.

[11] *Autobiography* as printed in *Life and letters C.D.* I, 88.
STAUFFER, R. C. (ed.) 1975. *Charles Darwin's Natural Selection being the second part of his big species book written from 1856–1858.* London, Cambridge University Press. p. 535.
DARWIN, C. R. 1859. *On the origin of species by means of natural selection or the preservation of favoured races in the struggle for life.* London, Murray, p.366.
Darwin to Hooker, 29 June 1845, Cambridge University Library Darwin MS 104, 35, also printed in *More Letters C.D.* I, 408–409: "Forbes is doing apparently very good work about the introduction and distribution of plants. He has forestalled me in what I had hoped would have been an interesting discussion . ."

[12] *More Letters C.D.* I, 51 and also C.U.L. Darwin MS 114, 37.

[13] There are two other related letters which Francis Darwin could not date precisely: *More Letters C.D.* I, 411, which I can date to January 1846; *Life and Letters C.D.* II, 38, which can be dated to September 1845.

[14] FORBES, E. 1844. Report on the Mollusca and Radiata of the Aegean Sea, and on their distribution as bearing on geology. *Rep. Br. Ass. Advmt Sci.* 1843: 130–194. Darwin was probably referring to Forbes' 'time-notions' of pp.173–174.

[15] The history of Darwin's and Forbes' equally elegant theories to account for arctic and alpine distribution, and Darwin's extension of the idea to encompass worldwide distribution patterns, deserve more space than a footnote and I intend to develop them elsewhere.

[16] Since this paper was read the first Hooker to Darwin letter has been published in ALLAN, Mea. 1977. *Darwin and his flowers.* London, Faber and Faber, p.135, but with no comments about its significance. See BROWNE, E. J. 1977. Review of *Darwin and his flowers. Journal Museums Assoc.* 77(2): 81.

[17] *Life and letters J.D.H.* I, 436.

[18] Hooker to Darwin, C.U.L. Darwin MS 100, I, dated 28 November 1843. This naturally means that the preceding Darwin to Hooker letter was written pre- 28 November.

[19] Hooker to Darwin 4 August 1856, C.U.L. Darwin MS 100, 100.

[20] Hooker to John Tyndall n.d. [? 1860s], Imperial College Archives, Huxley papers H.P.8, 313.

[21] A selection of titles includes the following:
WATSON, H. C. (various editions after 1844). *London catalogue of British plants.*
HENSLOW, J. S. 1835. *A catalogue of British plants arranged according to the natural system.* Cambridge.
LEDEBOUR, C. F. 1842–1853. *Flora Rossica.* Stuttgart.
DE CANDOLLE, Augustin; DE CANDOLLE, Alphonse (and others). 1824–1857. *Prodromus systematis naturalis Regnii vegetabilis.* Paris. Darwin worked through many but not all of the 17 volumes.
GRAY, A. 1856. *Manual of the botany of the Northern United States.* New York, second edition.
1840 BOREAU, A. 1854. *Flore du Centre de la France.* Paris.
GRISEBACH, A. R. H. 1843–1844. *Spicilegium Florae Rumelicae et Bithynicae.* Braunsweig.
WOLLASTON, T. V. 1854. *Insecta Maderensia.* London.
WESTWOOD, J. O. 1839–1840? *An introduction to the modern classification of insects.* London.
GOULD, J. 1848. *Birds of Australia.* London.
The mass of notes and tables relating to these calculations can be found in C.U.L. Darwin MS 15(ii); 16(i) and (ii). Darwin used the results in Chapter II of the *Origin of Species.*

[22] LYELL, C. 1830–1833. *Principles of geology.* London. Lyell used this technique to illustrate his subdivisions of the Tertiary. See also RUDWICK, M. J. 1972. *The meaning of fossils.* London. and RUDWICK, M. J. 1977. *Charles Lyell's dream of a statistical palaeontology.* 20th Annual Address to the Palaeontological Association (to be published).

[23] DE BEER, G. 1958. *Evolution by natural selection.* Cambridge University Press in which he reprints the Darwin *Sketch* of 1842 and the *Essay* of 1844.

[24] *Charles Darwin's Natural Selection* (see note 11).

[25] Reprinted in DE BEER, G. 1958. *Evolution by natural selection* pp.264–267.

26 BEDDALL, B. G. 1968. Wallace, Darwin and the theory of natural selection. *J. Hist. Biol.* **1:** 261–323.

27 Hooker to Francis Darwin, Kew, J.D.H. outgoing letters 3, 12.

28 Emma Darwin to Hooker, Kew, J.D.H. incoming letters 6, 1.

29 Imperial College HP 2, 240. Huxley's obituary appeared in *Nature* (1882) **25:** 597.

30 Francis Darwin to Hooker, Kew, J.D.H. incoming letters 6, 13.

31 *Nature* (1882) **26:** 49–51, 73–75, 97–100, 145–147, 169–171, with contributions from Romanes on zoology and psychology, Geike on geology, and Thiselton-Dyer on botany.

32 June 1st 1882. *Nature* (1882) **26:** 104.

33 Many of the letters which these notices inspired are in C.U.L. Darwin MS 112.

34 I have not been able to trace this article further than what seems to be an edited translation: HAECKEL, E. H. P. A. 1882. On Darwin, Goethe, and Lamarck. *Nature* **26:** 533–541. This was not only published at the right time (28 Sept) but is overtly concerned with Goethe's, Lamarck's and Darwin's 'religion of nature'. However the Darwin letter is not printed although there are suggestive ellipses on p.540 column two.

35 Henrietta Huxley to Macmillan. British Museum Macmillan Archives, 55211, vol CDXXVI, 55.

36 Leonard Huxley to Macmillan. *Ibid* f.143.

37 HUXLEY, L. 1912. *Thoughts on education chosen from the writings of Matthew Arnold.* London, Macmillan. Leonard Huxley later produced *Jane Welsh Carlyle: letters to her family 1839–1863.* London (1924) and *Elizabeth Barratt Browning: letters to her sister 1846–1859.* London (1929).

38 FOSTER, M. and LANKESTER, R. 1898–1903. *The scientific memoirs of T. H. Huxley.* London, was to be their 'consolation prize'.

39 HUXLEY, T. H. 1887. On the reception of the *Origin of Species. Life and letters C.D. II,* 179–204.

40 Francis Darwin to T. H. Huxley, Imperial College HP 13, 12.

41 Francis Darwin to Hooker, Kew, J.D.H. incoming letters 6, 20.

42 Francis Darwin to Hooker, *ibid* 6, 27. This letter is also valuable as evidence that the early Darwin to Hooker letters had, by this date (1885), been bound into the two volumes now at Cambridge. It is possible that Dawson Turner, Hooker's favourite grandfather, bibliophile and noted collector, could have had the first volume of Darwin's letters (1843–1858) bound up, especially as he had already done so for Darwin's letters to Henslow (now at Kew), but this leaves one guessing as to the origin of the second, matching binding on Darwin's letters to Hooker (1859–1866), which must have been bound after Dawson Turner's death in 1858. For notes on Dawson Turner's extraordinary collection of autographs and his distinctive bindings see MUNBY, A. N. L. 1962. *The cult of the autograph letter.* London. pp.46, 58–59. I am grateful to Sydney Smith of St. Catherine's College, Cambridge, for directing my attention to Dawson Turner as the binder and for his knowledge of, and enthusiasm for, such problems.

43 *Life and letters C.D.* II, 19–27.

44 Hooker to Francis Darwin 26 Feb 1886, Kew, J.D.H. outgoing letters 3, 137.

45 *Life and letters C.D.* I, 318 footnote.

46 Leonard Huxley was later to use these same transcripts for his *Life* of Hooker.

47 Emma Darwin to Hooker, Kew, J.D.H. incoming letters 6, 1.

48 I particularly want to thank Mr. Peter Gautrey of the Cambridge University Library for his help and interest in biographical details of H. W. Rutherford, and for his timely production of a signed photograph of the C.U.L. staff of that period.

49 I am grateful to Miss Brenda Moon for this reference which she cited in her paper on Miss Marianne North, at this same Easter Meeting, 1977, and to Mr. Roger North for his permission to quote from his collection of Miss North's manuscripts.

50 BLINDERMAN, C. S. 1971. The Great Bone Case. *Perspect. Biol. Med.* **14:** 370–393, and again in FOSKETT, D. J. 1953. Wilberforce and Huxley on evolution. *Nature* **172:** 920.

51 Hooker to Francis Darwin, Kew, J.D.H. outgoing letters 3, 155, recollecting that the Bishop spoke of Huxley's *mother.* He later retracted and followed the general opinion that it was Huxley's *grandmother.* The larger the generation gap the less indelicate the Bishop's insult.

52 Imperial College HP 15, 117–8, and printed in BLINDERMAN, C. S. 1954. The Oxford Debate and after, *Notes & Queries o.s.* **202:** *n.s.* **4**: 126–128, and again in FOSKETT, D. J. as in note 50.

53 In DARWIN, F. 1892. *Charles Darwin: his life told in an autobiographical chapter and in a selected series of his published letters.* London, Murray. p.240.

54 Balfour Stewart to J. D. Forbes, St. Andrews University Archives, J. D. Forbes papers, incoming letters f.133.

55 GRANT-DUFF, M. E. 1897. *Notes from a Diary 1851–1872.* London, Murray. First two volumes only. I am grateful to David Roos for these two references.

56 *Ibid* I, 139.

57 Hooker to Francis Darwin, Kew, J.D.H. outgoing letters 3, 150.

58 Francis Darwin to T. H. Huxley, Imperial College HP 13, 45.

59 Hooker to Francis Darwin, Kew, J.D.H. outgoing letters 3, 153.

60 Hooker to Francis Darwin, *ibid* 6, 151.

61 Francis Darwin to T. H. Huxley, Imperial College HP 13, 47: "I send you the account of the B. Assoc at Oxford. It begins at p.320 of what I send. The printers have set it up in sheets (against my orders) but it shall be altered to any extent you wish". The account is in *Life and letters C.D.* II, 320.

62 As in note 51.

63 *Ibid* pp. 236–240.

64 Francis Darwin to Leonard Huxley, Imperial College HP 13, 80.

65 *Life and letters T.H.H.* I, 179.

66 *Life and letters J.D.H.* I, 521.