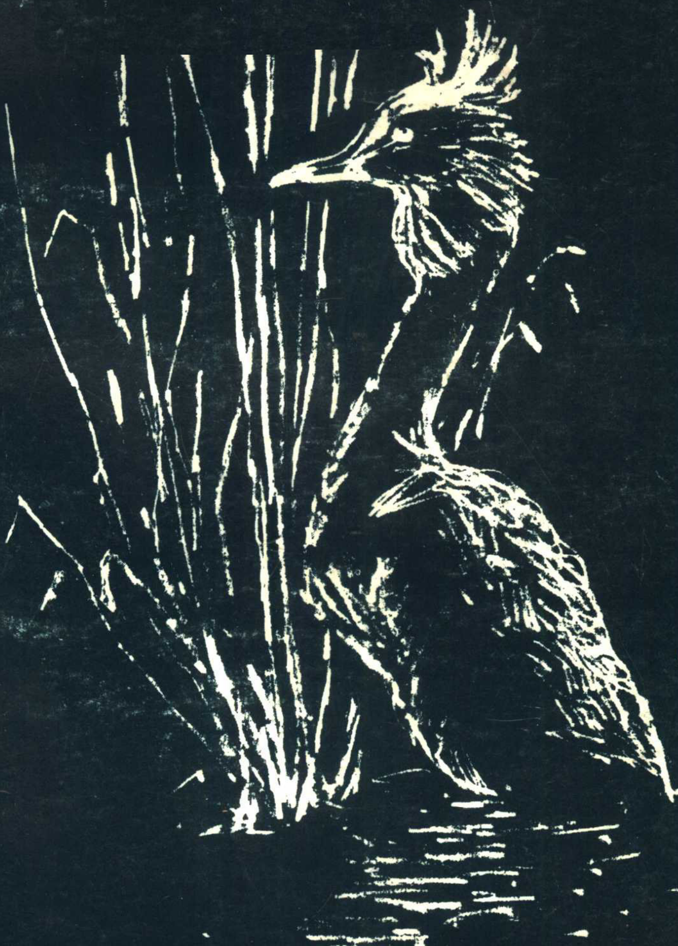
Studies in Biology no. 144

Neo-Darwinism

R. J. Berry



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Neo-Darwinism

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General Preface to the Series

Because it is no longer possible for one textbook to cover the whole field of biology while remaining sufficiently up to date, the Institute of Biology proposed this series so that teachers and students can learn about significant developments. The enthusiastic acceptance of 'Studies in Biology' shows that the books are providing authoritative views of biological topics.

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Readers' comments will be welcomed by the Education Officer of the Institute.

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Preface

Biologists are increasingly taught to approach problems from first principles. This is generally a good thing, but it can lead to difficulties if all the relevant information is not used. For example, when we ask: 'Is evolution true?', the discussion tends to revolve round gaps in evidence. This is the wrong centre for the debate. Evolutionary ideas form a synthesis involving virtually the entire span of biological disciplines. Someone starting from scratch is faced with a jigsaw which took an army of biologists over a century to complete, involving fact and theory, error and arrogance, superstition and success. *Neo-Darwinism* is the picture on the jigsaw box, as it were, charting the progress in our understanding of evolution from Darwin and Wallace's original paper in 1858 to the present. Most biologists tend to be impatient with history; I hope that readers of *Neo-Darwinism* will be able to bear enough of it to recognize that virtually all the criticisms about evolution raised today are repeats of old ones. Knowing the strength and solution of past debates can save time in dealing with the present situation, quite apart from forming a spring-board for the next advances in biology overall.

Professor Arthur Cain of Liverpool University and Mr Ian Lacey of Shrewsbury School read the book in draft, and made various criticisms. Most of them I have incorporated; my thanks are due to them for their comments, and my apologies for sticking to the points where I think I am right and they are wrong.

London, 1982 R.J.B.

Contents

1 Darwin, Darwinism, and Neo-Darwinism

1.1 Closet biology

The word 'biology' means, literally, the study of living things, but we all know how much easier it is to confine ourselves to dead organisms in the comfort of the laboratory or museum. This has meant that the link between the field naturalist working with the formidable complexity of real animals and plants, and the closet biologist necessarily but artificially simplifying the material at his command, is fragile, and too often breaks. (A closet biologist is one who expounds his wisdom from an indoor sanctum, basing himself on an extensive acquaintance with a restricted body of facts.) This broken link is particularly important in understanding the arguments that occur about evolution, for the simple reason that evolution is not a subject in its own right but a synthesis of disciplines as wide as biology itself: anatomy and anthropology; biometrics and biochemistry; ecology and ethology; genetics and geology; physiology and phylogeny; and so on. Few people can adequately cover this span, and, as we shall see, virtually all the criticisms about evolution since Darwin first put forward his ideas have come from genuine misunderstandings. As a matter of history, most have been raised by 'closet biologists', although at times field-workers have contributed to the general confusion (as in the gulf that opened in the 1920s between palaeontologists and other evolutionary biologists).

Five episodes of doubt about Darwinism can be recognized:

1) Objections expressed in Darwin's own time and largely anticipated in the *Origin of Species*.
2) Arguments between the biometricians and Mendelians around the turn of the century.
3) A rift between palaeontologists and geneticists in the 1920s and 1930s, which led to the general consensus usually known as the neo-Darwinian synthesis.
4) A conflict between neutralists and selectionists in the 1960s.
5) A series of independent assaults on neo-Darwinism in the 1980s by an assorted collection of palaeontologists, cladists, philosophers, and creationists.

We shall see the strengths and replies to all these in the following pages. However it is worth noting that the problems in every case have arisen because of confusion about the nature and maintenance of inherited variation. Indeed, this book is mostly about variation, and is really a cautionary parable for specialists, with the moral that they neglect data outside their own expertise at their peril.

1.2 Darwin and Wallace

Although Darwinism and evolution are often used as synonyms, they are not the same thing. Darwin himself acknowledged a galaxy of biologists who had believed before him that species were subject to change: Marchant (1719), Montesquieu (1721), Buffon (1749), Maupertuis (1754), Diderot (1764), Erasmus Darwin (1794), St. Hilaire (1795), Goethe (1795), Lamarck (1801), and Moritzi (1842). Robert Chambers in the *Vestiges of Creation* (first published 1844, tenth edition 1853) had alerted Britain to the idea of evolution maintaining that 'species are not immutable productions . . . (although, animated beings from the simplest and oldest up to the highest and most recent are under the providence of God'. Even Darwin's particular contribution of natural selection was described by Wells in a paper read to the Royal Society of London in 1813 and by Matthew in a book on *Naval Timber and Arboriculture* published in 1831.

Notwithstanding it was Charles Darwin's *The Origin of Species by means of natural selection or the preservation of favoured races in the struggle for life* (first published 1859, sixth and final edition 1872) that started the general acceptance of evolutionary ideas by both the scientific and the general world. The reason for the immediate success of the *Origin* was Darwin's explanations for the distribution of animals and plants, and his convincing interpretation of the significance of vestigial organs. Other lines of evidence, from fossils, anatomical likenesses and so on were fairly well-known to Darwin's contemporaries but were explained away before an acceptable mechanism of evolution was available. For example, the existence of fossils of extinct species was interpreted as either the remains of former creations destroyed by God as He almost destroyed the present world in Noah's flood, or divinely created artefacts, put in the rocks to confuse godless scientists. In the longer term and much more important, it was Darwin's easily-understood *mechanism* of evolution which was his most important contribution. The need for a mechanism before a scientific idea is generally accepted also occurred with continental drift, which was put forward in detail by Wegener in 1915, but not commonly accepted until the nature of tectonic plates was described by geophysicists in the 1960s.

Darwin's doubts about the immutability of species arose from his study of geographical variation in both fossils and living forms during his time as naturalist on board the survey ship *Beagle* (1831–6). For example he wrote in his *Journal* about the Galapagos Islands that 'I never dreamed that islands, about 50 or 60 miles apart, and most of them in sight of each other, formed of precisely the same rocks, placed under a quite similar climate, rising to nearly equal height, would be differently tenanted; but . . . I obtained sufficient materials to establish this most remarkable fact in the distribution of organic beings'. Back in London, Darwin began in July 1837 to make notes on the transmutation of species. In 1838 he read 'for amusement' Malthus's *Essay on the Principle of Population*, and 'being well prepared to appreciate the struggle for existence . . . it at once struck me that under these circumstances favourable variations would tend to be preserved, and unfavourable ones to be destroyed. The result of this would be the formation of new species. Here then I had at last got a theory by which to work'.

Darwin wrote down his ideas for the first time in 1842, whilst on a brief visit to his in-laws (Josiah Wedgwood II, the potter) and his parents (in Shrewsbury). He expanded his 1842 sketch in 1844, and this latter version formed the basis of his first public pronouncement on the subject in 1858.

Darwin's original intention was to write a definitive book on evolution. However in the spring of 1858 he was sent by Alfred Russel Wallace an essay 'On the tendency of varieties to depart indefinitely from the original type', written by Wallace whilst recovering from fever in the Moluccas. Darwin felt that this should be published, but on the urging of his friends Charles Lyell (author of the *Principles of Geology*, which Darwin had read on the *Beagle*, and which had first alerted him to the reality of long-continued gradual geological change) and J. D. Hooker (son of the effective founder of Kew Botanic Gardens, and instigator of the study of plant geography), he allowed a revised version of his 1844 essay to be forwarded with it to the Linnean Society.

Darwin's and Wallace's papers were read at a Linnean Society meeting on 1st July 1858, and published in the Society's *Journal* on the 20th August. They attracted little attention; the President of the Society declared in his report for 1858 that 'The year which has passed . . . has not been marked by any of those striking discoveries which revolutionise the department of science on which they bear . . . A Bacon or a Newton, an Oersted or a Wheatstone, a Davy or a Daguerre, is an occasional phenomenon, whose existence and career seem to be specially appointed by Providence, for the purpose of effecting some great important change in the condition or pursuits of man'. Controversy only broke out after the publication of the *Origin of Species* in the following year, and more vehemently after the confrontation between T. H. Huxley and 'Soapy Sam' Wilberforce, Bishop of Oxford (inadequately briefed by Richard Owen, first director of the Natural History Museum in South Kensington) at the British Association meeting in Oxford on 30th June 1860.

1.2.1 Darwin's paper to the Linnean Society

Since we are concerned in this book with the vicissitudes of the ideas which became public at the Linnean Society in 1858, it is worth recalling the actual words used. Darwin wrote 'All nature is at war, one organism with another, or with external nature. Seeing the contented face of nature, this may at first well be doubted: but reflection will inevitably prove it to be true. The war, however, is not constant, but recurrent in a slight degree at short periods, and more severely at occasional more distant periods; and hence its effects are easily overlooked . . . But the amount of food for each species must, *on an average*, be constant, whereas the increase of all organisms tends to be geometrical, and in a vast majority of cases at an enormous ratio . . . In the majority of cases it is most difficult to imagine where the check falls – though generally, no doubt, on the seeds, eggs, and young. Lighten any check in the least degree, and the geometrical powers of increase in every organism will almost instantly increase the average number of the favoured species. Nature may be compared to a surface on which rest ten thousand sharp wedges touching each other and driven inwards by incessant blows. Fully to realize these views much reflection is requisite'.

'But let the external conditions of a country alter . . . can it be doubted from the struggle each individual has to obtain subsistence, that any minute variation in structure, habits, or instincts, adapting that individual better to the new conditions, would tell upon its vigour and health? In the struggle it would have a better *chance* of surviving; and those of its offspring which inherited the variation, be it ever so slight, would also have a better chance. Yearly more are bred than can survive; the smallest grain in the balance, in the long run, must tell on which death shall fall, and which shall survive. Let this work of selection on the one hand, and death on the other, go on for a thousand generations, who will pretend to affirm that it would have no effect, when we remember what, in a few years, Bakewell effected in cattle, and Western in sheep, by this identical principle of selection?'

1.2.2 Wallace's paper to the Linnean Society

Wallace's views were remarkably similar: 'The life of wild animals is a struggle for existence. The full exertion of all their faculties and all their energies is required to preserve their own existence and provide for that of their infant offspring . . . Even the least prolific of animals would increase rapidly if unchecked, whereas it is evident that the animal population of the globe must be stationary, or perhaps, through the influence of man, decreasing. So long as a country remains physically unchanged, the numbers of its animal population cannot materially increase'.

'Most or perhaps all the variations from the typical form of a species must have some definite effect, however slight, on the habits or capacities of the individuals. Even a change of colour might, by rendering them more or less distinguishable, affect their safety; a greater or less development of hair might modify their habits . . . Now, let some alteration of physical conditions occur in the district – a long period of drought, a destruction of vegetation by locusts, the irruption of some new carnivorous animal seeking 'pastures new' – any change in fact tending to render existence more difficult to the species in question, and tasking its utmost powers to avoid complete extermination; it is evident that, of all the individuals composing the species, those forming the least numerous and most feebly organised variety would suffer first, and, were the pressure severe, must soon become extinct . . . The superior variety would alone remain, and on a return to favourable circumstances would rapidly increase in numbers and occupy the place of the extinct species and variety . . . This new, improved, and populous race might itself, in course of time, give rise to new varieties, exhibiting several diverging modifications of form, any of which, tending to increase the facilities for preserving existence, must, by the same general law, in their turn become predominant. Here, then, we have *progression and continued divergence* deduced from the general laws which regulate the existence of animals in a state of nature, and from the undisputed fact that varieties do frequently occur . . .'

'The hypothesis of Lamarck – that progressive changes in species have been produced by the attempts of animals to increase the development of their own organs, and thus modify their structure and habits – has been repeatedly and easily refuted by all writers on the subject of varieties and species, and it seems to have been considered that when this was done the whole question has been finally settled; but the view here developed renders such an hypothesis quite unnecessary, by showing that similar results must be produced by the action of principles constantly at work in nature . . . (For example) the giraffe did not acquire its long neck by desiring to reach the foliage of the more lofty shrubs, and constantly stretching its neck for the purpose, but because any varieties which occurred among its antetypes with a longer neck than usual at once secured a fresh range of pasture over the same ground as their shorter-necked companions, and on the first scarcity of food were thereby enabled to outlive them.'

'We believe we have now shown that there is a tendency in nature to the continued progression of certain classes of *varieties* further and further from the original type – a progression to which there appears no reason to assign any definite limits . . . This progression, by minute steps, in various directions, but always checked and balanced by the necessary conditions, subject to which alone existence can be preserved, may, it is believed, be followed out so as to agree with all the phenomena presented by organised beings, their extinction and succession in past ages, and all the extraordinary modifications of form, instinct, and habits which they exhibit.'

1.2.3 The essence of evolutionary mechanism

Both these papers clearly contain the three facts and two conclusions which are commonly taken as the simple summary of Darwinism evolution: the potential of all species to increase greatly in numbers, coupled with an approximate constancy of numbers, implies that there is a *struggle for existence*; and when variation is added to this, it is clear that *natural selection* must operate.

It was the ease with which these propositions could be understood that helped the *fact* of evolution to be generally accepted. In fact Darwin devoted more than half of the *Origin* to different lines of evidence that evolution has occurred: he has two chapters on the fossil record, two on geographical distributions, and one each on morphological likenesses (including comparative embryology, the interpretation of vestigial organs, and the meaning of classification), behaviour, and domestication. He devoted later books specifically to the origin of man and sexual selection, domestication, and adaptations in plants for pollination, insect-eating, and climbing. All these were parts of the book Darwin had originally intended to write before being forced into print by Wallace.

1.3 First series of objections: Darwin's own answers

In Chapters 6 and 7 of the *Origin* Darwin deals with 'difficulties' and 'miscellaneous objections' to his theory. His main points concern the nature of species and questions about the efficacy of selection. In a later chapter, he discusses the imperfections of the fossil record. Darwin knew that the maintenance of variation was a key weakness in his theory. The causes of variation are repeatedly referred to in the book and in later editions of the *Origin*, he tended to accept that some Lamarckian explanation might be necessary (*i.e.* that the heredity of an individual might be affected by an environmental modification of its phenotype. No claim of Lamarckian inheritance by Kammerer, Lysenko, Steele, and many others over the years, has ever been substantiated). The problem was not resolved until the physical basis of heredity was discovered following the embryological conclusions of Weissman (1883) and the re-discovery of Mendel's work in 1900. These are dealt with in sections 1.4 and 1.5. The position in palaeontology is reviewed in sections 6.5 and 7.2.

The issues faced by Darwin in the *Origin* are still raised today, and it is therefore relevant to begin with them.

1.3.1 Species transitions

If one species may evolve into another, why are not forms linking two species found? R. A. Fisher has argued that the reason Darwin had to discuss this was the hangover from Lamarckian speculation that existed when he was writing. Lamarck had suggested that evolutionary change arises from the use or disuse of organs and traits, so that transmutation arises from a varying response in an existing group. It would follow from this that there are no firm limits to any species, nor is a 'natural' classification realistically possible since the evolving unit is the individual.

Darwin rejected this idea of species from his personal study of species in nature, and assumed a definition close to the modern one, that a species is an effectively isolated population or group of populations. He recognized that:

(i) Closely-related forms are likely to compete for the same resources, leading to the less-favoured one(s) becoming extinct. This has been shown repeatedly by experiment (perhaps most exhaustively in the flour-beetle *Tribolium*), with the important qualification that different varieties (or species) can survive together only where a heterogeneous environment allows different varieties to occupy different niches. However the point at issue here is that one form will normally become extinct if a selectively advantageous form competes with it.

(ii) In a large area, different species replace each other geographically. In most cases these species seemed to have evolved in isolation and then expanded their ranges to come into contact. Geological changes (separating and recombining tracts of land) play a part here, but at the level of present species the most important factor has been the Pleistocene, when previously widely-distributed forms were isolated in a number of warmer or wetter refuges for relatively long periods, and changed sufficiently to remain distinct when the climate improved and they were able to re-occupy their former territory. Well-worked examples of this process are the Palaearctic ring of *Larus* gull species, and the *Heliconius* butterflies (and their mimics) in the Amazon basin. It is interesting that Darwin recognized the dynamic influence of historical events in forming new species, in contrast to the implicit assumption of both his contemporaries and many recent biologists that environments are stable and largely homogeneous.

(iii) Transitional forms will almost certainly be less common than either the ancestral or descendent form, and hence liable to be overlooked or to become extinct. As collecting and the description of variation has progressed, it has been recognized that some species previously collected only from widely separated areas may be in fact be connected by intermediate forms. We now recognize *clines* of change in particular traits, and also that a species may be polytypic, *i.e.* contain several geographically distinguishable forms which interbreed to a limited extent. Linnaeus confused matters by giving the name 'variety' indiscriminately to geographical races, domesticated races, non-genetic variants, and inherited 'sports'. The idea of a polytypic species radically altered the Linnean concept of a species: the older idea is of a species characterized by a gap separating it from other groups, while a polytypic species is defined by actual or potential genetic continuity between allopatric populations. This does not, however, affect Darwin's point that forms in the process of change are likely to be uncommon. As we shall see, the discovery of active speciation (for example, *Drosophila* flies in Hawaii and cichlid fishes in Lake Victoria: section 6.2.2); the rarity of transitional forms; and the study of hybrid zones (section 5.2) is throwing a great deal of light on the nature and integrity of species.

1.3.2 The effectiveness of natural selection

The most persistent criticism of Darwinism has always been that natural selection is merely a negative instrument removing inefficiency, but incapable of producing novelty or the seemingly perfect adaptation of such features as the eye of a mammal or bird, or the pattern of a butterfly's wing:

1) *Cases of special difficulty* Darwin recognized three situations:

(*a*) An organ (such as the wing of a bat) may be so specialized for its functions as to bear little resemblance to the prototype (the forelimb of an insectivore) from which it must be presumed to have arisen. The difficulty is envisaging a series of organisms with organs of intermediate grades connecting these widely-separated extremes.

(*b*) An organ of extreme perfection (such as the eye in the higher vertebrates) may show such perfect and detailed adaptation that by comparison with the obstacles which the design of such an apparatus would present to human ingenuity, the mind is staggered by the effort of conceiving it as the product of so undirected a process as trial and error.

(*c*) Some organs of seemingly trifling importance (such as the 'fly-whisk' tail of the giraffe) are yet so clearly adapted to the function they perform that they cannot be regarded as accidental. In these cases it may be asked how such a trifling function can ever have been a matter of life and death to the organism, and so have determined its survival in the struggle for existence.

The first of these classes of objection applies to all evolution, whilst the second and third are difficulties more of imagination than of reason. It is impossible to deal with them in detail; R. A. Fisher has commented that 'the cogency and wealth of illustration with which Darwin was able to deal with these cases was, perhaps, the largest factor in persuading biologists of the truth of his views'. Here we can only note that:

(*i*) *Function as well as structure evolves.* For example, there are organisms which have no image-forming eyes, but light-sensitive cells. Any inherited variants which allowed detection of the direction of light, its size, movement, etc., could be of potential advantage, and subject to natural selection. The eye as we know it would be built up by the accumulation of many small steps, each of which could be adaptive. The result is efficiency in a particular environment, not perfection: one could envisage the human eye being 'improved' by functioning better in poor light or under water, or failing to deteriorate with age; these attributes have never been 'necessary' for human survival.

(*ii*) *The usefulness (or 'adaptive value') of a character can be tested by experiment.* Victorian biologists wasted a vast amount of effort speculating about the function or value of particular organs; there is a similar tendency in the 1980s to pontificate about the significance of particular behaviour patterns (section 7.1). Apparently trivial traits may be shown to be highly important: it has only been recently shown that flies may seriously disturb a tropical herbivore, and an efficient 'fly-whisk' may add notably to fitness. Conversely other traits (even the horns of the Irish elk) may be incidental results of selection for other traits associated with growth.

The persistence of these criticisms has come from ignorance, often resulting from lack of research, rather than defects in the underlying ideas.

2) *The origin of novelty*

How can natural selection which functions to filter out deleterious variants lead to completely new developments? Is not natural selection limited to modifying existing adaptations? The answer is no, as consideration of three facts reveals (see also section 6.3):

(*a*) *All* traits are subject to variation.

(*b*) In evolution, novelty is introduced by a change in the environment: animals and plants invaded land because of an available habitat, not because it seemed a good idea. Some characters will be *pre-adapted* to the new environment.

(*c*) Even a very small selective advantage can lead to genetical change (Chapter 4).

In the *Origin*, Darwin quoted Agassiz's work on echinoderms, showing how modification of spines may lead to the development of an apparently new and important trait, tube feet. Many similar examples are known. One of the major biological recognitions of the 1960s was the enormous amount of variation present in virtually every population (Chapter 3), which means that a species can respond rapidly and precisely to new environmental stresses: bacteria can digest oil, aphids detoxify artificial poisons, and plants grow when introduced to the Antarctic Continent. There is no reason for disbelieving that any reasonable novelties cannot occur in evolutionary time. Indeed even apparent *dis*-advantage (such as sterile castes of insects) can evolve in appropriate conditions (section 5.4); natural selection is a mechanism for producing *a priori* improbable contingencies (see below). (This fact, incidentally answers claims that there has not been enough time for evolution to have taken place since the earth became habitable. The commonly used analogy that a monkey randomly typing will produce the works of Shakespeare, but only if he has astronomical time is irrelevant, since selection can rapidly and ruthlessly change the frequency of apparently random variation.)

3) *The strength of natural selection*
The power of natural selection to produce adaptation could only be illustrated by anecdote until quantitative methods of estimating fitness differences, rates and conditions of gene frequency change, and similar parameters became available. These were developed by R. A. Fisher, J. B. S. Haldane and Sewall Wright during the 1920s, and demonstrated the ability of selection differentials of less than 1% to bring about evolutionary change. The force of their theoretical arguments has been greatly strengthened with the discovery that selection pressures in nature commonly reach 10% or 20% (Table 4) (see also section 4.1).

Without condoning speculation by protagonists and opponents alike about the possible course of evolution, it can nevertheless be affirmed that answers given by Darwin to his critics in successive editions of the *Origin* have been repeatedly proved right by subsequent research.

1.4 Second series of objections: biometricians and Mendelians

Darwin had no doubt that inherited variations were extremely common. He had been convinced of this by his observation of varieties in nature, but more especially by his contacts with practical animal breeders and horticulturists. On the other hand, he knew nothing about the mechanism of inheritance. He accepted the conclusions of the botanists Kölreuter (1733–1806) and Gärtner (1771–1850) who crossed vast numbers of plant varieties. Their common finding was that the characteristics of both parents blended in the offspring, which tended to be intermediate between the parents. This meant that if a new variant arose, it would have only half its expression in its offspring, one quarter in the grand-children (because it would almost certainly have to cross with the non-variant form), and so on. New variation would have to arise at a high rate if it was going to persist long enough to be operated on by selection.

In *The Variation of Plants and Animals under Domestication* (1868), Darwin put forward his 'provisional hypothesis of pangenesis' in an attempt to account for this. He suggested that each part of an organism produces 'free and minute atoms of their contents, that is gemmules' which pass to the reproductive organs and are thence passed to the next generation. 'Direct and indirect' influences of the 'conditions of life' (as suggested by Lamarck) could in this way become part of the hereditary constitution of the organism; as he wrestled with the problem, Darwin found himself more and more adopting Lamarckian ideas.

Meanwhile Darwin's cousin, Francis Galton, had been carrying out his own investigations into heredity. In 1869, he published *Hereditary Genius*, presenting the pedigrees of numerous distinguished families, and argued from these that talent must be inherited. This was followed in 1889 by *Natural Inheritance* which summarized data on size, disease, temperament, etc. into a general 'law of

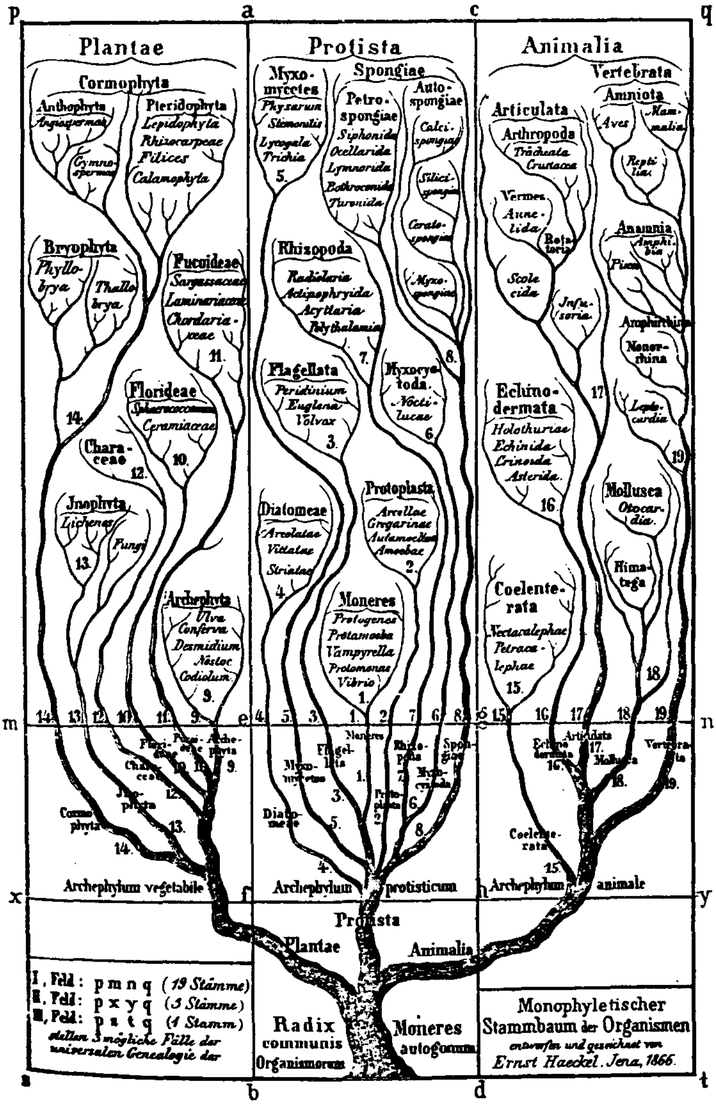

Fig. 1–1 The first phylogenetic tree, drawn up by Ernst Haeckel in 1866.

ancestral heredity', based on the share of inherited constitution an individual transmits to his descendants ($1/2$ to his children, $1/4$ to grandchildren, $1/8$ to great-grandchildren). This was a simple quantitative corollary of the currently-accepted ideas of blending inheritance; but it enabled Galton to develop statistical ideas of correlation and regression, which have remained central to biometrical analysis and quantitative inheritance ever since.

Galton's ideas were seized on by a mathematician, Karl Pearson, and by W. R. Weldon, who was Professor of Zoology at University College London and then Oxford. Weldon realized the importance of Galton's work for evolution, since the frequency of deviations from the type could be measured and associations measured. He believed that 'the questions raised by the Darwinian hypothesis are purely statistical, and the statistical method is the only one at present obvious by which that hypothesis can be experimentally checked', and co-operated with Pearson in seeking methods to test and extend Galton's law. They persuaded the Royal Society of London to establish in 1894 an Evolution Committee 'for the purpose of conducting statistical enquiries into the variability of organisms', and this committee sponsored work on the death-rates of crabs in Plymouth Sound, and measurements of herring and of ox-eyed daisies.

In 1897 the Evolution Committee was joined by William Bateson, a Cambridge zoologist and first director of the John Innes Institute (1910–1926). Bateson was convinced of the importance of discontinuity in evolution, and dubious about the early work of the Committee. He criticized Weldon for measuring crabs at different stages of moult. He rapidly brought about a change in the approach of the Committee, and in 1900 Pearson and Weldon resigned.

Meanwhile the search for a better understanding of the genetical process led in 1910 to the rediscovery of Gregor Mendel's work originally published in Brno, Czechoslovakia in 1866 by the botanist de Vries in Holland, von Tschermak in Austria, and Correns in Germany. Mendel's main conclusions (the regular segregation and independent assortment of inherited traits) were soon confirmed in animals by Bateson and Punnett in Cambridge and Cuénot in Paris.

The application of Mendelian ideas had two important consequences for evolutionary ideas: they indicated that inherited factors did not blend, but persisted unchanged through the generations, thus removing the chronic problem of variation loss; and they appeared to show that inherited variation was discontinuous. In reaction the biometricians (*i.e.* Pearson and Weldon) regarded Mendelism as a threat. The six years following the rediscovery of Mendelism (until the death of Weldon in 1906) witnessed increasingly bitter confrontations between the Mendelians and biometricians over 'homotyposis' (Pearson's attempt to weld together heredity and differentiation), mutation theory, the meaning of genetical dominance, etc.

The physical basis of heredity was not generally accepted until the work of T. H. Morgan and his colleagues on sex determination, linkage, and mutation in *Drosophila melanogaster* linked breeding results with cytological knowledge (summarized in *The Mechanism of Mendelian Heredity*, published in 1915). However, Mendel's 'laws' (Mendel himself did not state any laws, but his conclusions are most easily summarized in this way) were everywhere being confirmed, and the Mendelians increasingly gained the upper hand. The biometric-Mendelian controversy degenerated into personal conflict, and ended when Weldon died of pneumonia at the age of 46. but the split between the supporters of continuous and discontinuous evolution continued to grow, and was only resolved in the 1930s (section 1.5).

1.5 Third series of objections: palaeontologists and geneticists

In the early 1900s, the importance of natural selection in evolutionary change was believed to be of little importance; the emphasis was increasingly laid on the origin of variation rather than its maintenance. Huxley and Bateson believed that continuous variations were too small to generate significant selection pressures; Galton believed that the selection of continuous variations soon reached a limit because of the counteracting effect of regression. A Danish botanist, Wilhelm Johannsen, showed (1903) that selection for weight within pure (i.e. self-fertilized) lines of beans had no effect, and concluded from this that continuous variation was not inherited and therefore unimportant in evolution. (The significance of the fact that different lines produced beans of different mean weight was not realized at the time, although it is an aspect of Johannsen's work which is almost always quoted nowadays.)

The mutation theory of Hugo de Vries (one of Mendel's re-discoverers) was particularly influential at this time. De Vries worked with the evening primrose, *Oenothera lamarckiana* and observed frequent mutations in his stocks. He argued that evolution depended on such, and that species originated by 'jumps' or saltations rather than the accumulation of small differences as suggested by Darwin (see section 7.2). We now know that de Vries's *Oenothera* mutations were mostly due to chromosomal rearrangements, together with the segregation of recessive traits, and are not mutations in the modern sense. Notwithstanding, a generation of biologists grew up convinced that evolution was 'driven' by mutation, with natural selection taking a minor role.

Meanwhile palaeontologists were building up an increasingly confident picture of evolutionary changes in fossil strata. It seemed clear that much change was continuous and progressive; evolutionary 'jumps' did not exist when the record was continuous over long periods. The mutations being studied by laboratory geneticists appeared to have nothing in common with real evolution. Darwin's own emphasis on gradual evolution was continued by the palaeontologists, *via* the biometricians.

During the 1920s the gap between palaeontologists and geneticists widened. As knowledge of mutations *sensu stricto* increased, it seemed that they almost invariably produced deleterious traits which were inherited as recessives, whereas adaptively useful traits were virtually always dominant. It is no wonder that this period led to a widespread disenchantment with classical Darwinism, and the propounding of a variety of other theories of evolutionary mechanisms: Berg's *Nomogenesis*, Willis's *Age and Area*, Smuts's *Holism*, Driesch's entelechy, and others. None of these was satisfactory, and all depended upon an almost mystical inner urge (or *élan vital*) to progress. It is unfortunate that three standard and still-read histories of biology (by Nordenskiöld, Rádl, and Singer) were written during this time, and the idea that evolutionary theory is an illogical mess has been perpetuated.

1.5.1 Fisher's theory of the evolution of dominance

At the height of the Mendelian-biometrician controversy, a British mathe-