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Excerpt
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1 Investigating plant variation and evolution

The endless variety of different organisms, in their beauty, complexity and diversity, gives to the biological world a special fascination. Some recognition of these different 'kinds' of organisms is a feature of all primitive societies, for the very good reason that humans had to know, and to distinguish, the edible from the poisonous plants, or the harmless from the dangerous animal. There is also a further dimension to the variation pattern. From folk taxonomies, the early product of human societies' need to understand, describe and use the plants and animals around them, the modern scientific biological classifications we use today have been developed. Different 'kinds' of organism are arranged in a hierarchy, each higher group containing one or more members of a lower group. We now distinguish more than a quarter of a million flowering plants, and these are arranged in a hierarchical-nested classification of species in genera, genera in families, families in orders etc.

One of the main issues to be examined in this book concerns the nature of species in this hierarchical system. Anyone familiar with the vegetation of an area, or the plants in a Botanic Garden, has to face a number of questions that have puzzled biologists. Is there any objective way of delimiting species? How can one account for the different degrees of intraspecific variation found in species? Why are certain species clearly distinct, while in other cases we find a galaxy of closely similar species, often difficult to distinguish from each other? Why is it that hybridisation occurs frequently in certain groups of plants and not in others? What is the significance of the hierarchies in classification and what is the origin of these groupings?

Historically, an examination of these questions, as we shall see in Chapter 2, produced a static picture of variation, based on a belief in the fixity of species. The hierarchy of classification reflected the plan of Special Creation. However, since 1859, with the publication of *On the Origin of Species*, all such studies have been made in the light of Darwin's profound generalisation of evolution by natural selection: populations and species vary in time and space and are part of a continuing process of evolution.
The hierarchical classifications of the pre-Darwin era are now reinterpreted in Darwin's' famous metaphor of the Tree of Life, with all organisms having a common origin in the very distant past.

Even though Darwin's theory has not always been accepted, it has had a tremendous impact on all fields of biology. Nowadays, the fact of evolution is sometimes taken for granted by many, in part because of the wealth of evidence assembled by Darwin and other scientists. While there is often an uncritical acceptance of the theory, it is also important to acknowledge that there has also been widespread rejection of the theory of evolution (Chapter 2). Implicit in Darwin's ideas is the assumption that evolution is still taking place. Therefore, in this book we look not only at issues raised by intraspecific variation and patterns of variation, but also the evidence for evolution, particularly experimental evidence for natural selection and other processes in populations, often called 'microevolution'.

Historical evidence reveals how biologists have long been attempting to understand the patterns of variation in organisms (Chapters 2–5). As we shall see, an ever-widening range of techniques has been devised, including morphological studies, hybridisation experiments, cultivation trials and biometrical and cytogenetical investigations. By this means our understanding of evolution at or below the species level has been greatly increased. While these investigations have yielded many insights and provided a framework of concepts and hypotheses, 'historic' techniques had significant limitations. But in the last few years unparalleled advances in our understanding of *all* aspects of plant evolution have been achieved by the use of molecular approaches. As these tools have been developed and refined, we have been provided with the means of critically testing a very wide range of hypotheses. Many recent advances have come through laboratory-based studies. While readily admitting the importance of such experiments and observations, many key insights have come from studying evolution out of doors, whether in the wild, cultivated or weedy habitats. It is increasingly clear that the basic raw material for studies of variation and microevolution exists in every country of the world, not only in 'natural', unspoiled vegetation but also from the study of communities radically altered by human activities. In fact some of the most important insights into microevolution have come from studies of introduced plants, agricultural crops, weeds, and the vegetation of areas subject to pollution. Such studies have revealed how certain species have adapted successfully in agricultural and urban industrial landscapes.

The past few decades have been a period of great excitement and achievement, as molecular, and associated computational, methods have been successfully applied in many areas of plant evolutionary biology. Thus, major insights have been obtained into the underlying basis of variation (Chapter 6); plant breeding systems (Chapter 7); population variability, the effects of chance and gene flow (Chapters 8–11); hybridisation and speciation (Chapters 12–14), threats of species extinction (Chapter 18), and conservation biology (Chapter 20). Often, this fascinating new information could not have been revealed by any other means, and there is huge potential for further insights, as the molecular revolution in biology gathers pace.

Our account will also consider how molecular investigations are providing major advances in our understanding of plant evolution in geological timescales, so-called macroevolution (Chapter 16). Present evidence suggests that the universe is *c.*10–16.5 billion years old, with Earth's geological history beginning of the order of 4.6 billion years ago. Life began to evolve *c.*4 billion years ago (Graur & Li, 2000). A basic question to be considered is whether macroevolution is just microevolution writ large: or whether other processes are involved (Bateman, 1999).

Since the publication of Darwin's *Origin*, evolution of biodiversity has been widely represented as the Tree of Life (Chapter 16). Very considerable progress has recently been made in devising 'phylogenetic trees' and other diagrams to explore evolution on longer timeframes. As we shall see, the study of plant biogeography has also been revolutionised by molecular investigations and advances in computer modelling, and these approaches are providing major new insights into both recent and past evolutionary history (Chapter 17).

This book also examines an issue of great international concern. For decades, there has been growing evidence that more than 10% of the world's flora is endangered by human activities (Briggs, 2009). Guided by our knowledge of pattern and process in microevolutionary change, we consider the effectiveness or otherwise of the historic conservation measures taken to prevent this loss of biodiversity (Chapter 20).

In considering the prospects for successful conservation of biodiversity, the potentially catastrophic scenarios revealed by the projections of future climate change must be seriously considered (IPCC, 2013). Climate change is not the only looming threat to biodiversity. Ecosystems are also endangered by the interactions between climate change and other significant factors: habitat loss, the non-sustainable use of resources, pollution, population growth, invasive species etc. (Chapter 18).

Taxonomists were the first biologists to study plant variation. An important theme of this book, therefore, is the impact that evolutionary investigations have had on the theory and practice of taxonomy, especially studies of phylogenetic relationships (Chapter 16). For instance, there is disagreement about whether/how current plant classifications, based on Linnaean principles, should/

could be modified in the light of the patterns apparent in phylogenetic trees (Ereshefsky, 2001). Also, attempts to find DNA sequences that will allow a unique barcode to be defined for each species are provoking intense debate (Wheeler, 2008).

A major concern is the effect that the present dominance of molecular approaches has had on taxonomy and other traditional fields of research, studies that have made such major contributions to our understanding of plant evolution. Whilst freely acknowledging the progress that has been made through the application of molecular tools and computer modelling, in Chapter 19, I discuss the reports of a number of authorities that studies in taxonomy etc. have recently been under pressure or indeed in decline (see Wheeler, 2008; Stuessy, 2009). Amongst the possible reasons for this decline are issues of funding and the way the subjects are taught. As a consequence of the support given to molecular investigations, are some areas being starved of attention and/or resources? Is a form of Darwinian selection taking place amongst subject areas allied to plant evolution? Some take this view. For instance, Sapp (2003) considers that 'the history of biology is regarded as a contest over what questions are important, what answers are acceptable, what phenomena are interesting, and what techniques are most useful'.

Faced with the evidence of these changes in status and support, how might traditional approaches be revitalised? Will the 'road ahead' for studies of plant evolution remain a 'broad church' with integrated contributions from a wide range of disciplines (Chapter 20), or will the study of evolution increasingly develop into a branch of molecular biology?

2 From Ray to Darwin

In 1660 Robert Sharrock, Fellow of New College, Oxford, wrote a book titled *History of the Propagation and Improvement of Vegetables by the Concurrence of Art and Nature*. He was concerned in its early pages to debate a live issue of the day (Bateson, 1913), namely:

> It is indeed growen to be a great question, whether the transmutation of a species be possible either in the vegetable, Animal or Minerall Kingdome. For the possibility of it in the vegetable; I have heard Mr Bobart and his Son often report it, and proffer to make oath that the Crocus and Gladiolus, as likewise the Leucoium, and Hyacinths by a long standing without replanting have in his garden changed from one kind to the other.

The Bobarts were both professional botanists. Sharrock investigated their claim, and found 'diverse bulbs growing as it were on the same stoole, close together, but no bulb half of the one kind, and the other half of the other'. In this age we find it hard to understand a belief in the possibility of transformation of Crocus into Gladiolus. Our reason for disbelief is partly concerned with the nature of evidence; we are not satisfied with the test for the alleged transmutation and would not have been content merely to examine the crowded underground parts. Another reason, however, relates to current ideas of the nature of species. We have a different notion of species from that of the seventeenth century.

Ray and the definition of species

It was the English naturalist John Ray (1628–1705) who was probably the first man to seek a scientific definition of species (Raven, 1950; Oswald & Preston, 2011). In his definition is an implied rejection of the sort of transmutation of species claimed by the Bobarts of Oxford, although in other passages in Ray's work he does not wholly dismiss the possibility of transmutation. For instance, he cites as reliable the case of cauliflower seed supplied by a London dealer, which on germination produced cabbage. Richard Baal, who sold the seed, was tried for fraud and ordered by the court at Westminster to refund the purchase money and pay compensation (De Beer, 1964).

Ray's views on species were published in 1686 in *Historia plantarum*. He wrote (trans. Silk in Beddall, 1957):

> In order that an inventory of plants may be begun and a classification of them correctly established, we must try to discover criteria of some sort for distinguishing what are called 'species'. After a long and considerable investigation, no surer criterion for determining species has occurred to me than distinguishing features that perpetuate themselves in propagation from seed.

He is concerned to define species as groups of plants that breed true within their limits of variation. This definition of species, based as it is partly upon details of the breeding of the plant, was a great advance upon older ideas, which relied entirely upon consideration of the external form.

Ray was also very interested in intraspecific variation. In his letters to various friends (collected by Lankester, 1848), he noted several striking variants of common plants discovered on his journeys around Britain. For example, at Malham in Yorkshire he noticed white-flowered as well as the normal blue-flowered

Jacob's Ladder (*Polemonium caeruleum*), and from other localities he reported white-flowered Foxglove (*Digitalis purpurea*), double-flowered specimens of Water Avens (*Geum rivale*) and white-flowered Red-rattle (*Pedicularis palustris*). Ray also made observations on a prostrate variant of Bloody Cranesbill (*Geranium sanguineum* var. *prostratum*). He wrote to a friend: 'Thousands hereof I found in the Isle [Walney] and have sent roots to Edinburgh, York, London, Oxford, where they keep their distinction.' This report on the constancy of this distinct variant of *Geranium sanguineum* in cultivation is of particular interest, and is referred to again in Chapter 4.

We may learn more of Ray's ideas on the nature of species and intraspecific variation by examining a discourse given to the Royal Society on 17 December 1674 (Gunther, 1928). In this, he expresses his concern that great care should be taken in deciding what constitutes a species and what variation is insufficient for specific distinction. He shows, for instance, that within a species there might occur individuals different from the normal in one or more of the following characters: height, scent, flower colour, multiplicity of leaves, variegation, doubleness of flower, etc. Plants differing by such 'accidents', as Ray calls them, should not be given specific status (Cain, 1996). He records the origin of one notable variant in his own garden: 'I found in my own garden, in yellow-flowered Moth-Mullein (*Verbascum*), the seed whereof sowing itself, gave me some plants with a white flower'. Concerning other variants Ray suggests that they are caused by growing plants under unnatural conditions, for example, a rich or a poor soil, extreme heat, and so on.

He concludes his analysis of specific differences and the problem of intraspecific variation as follows:

> By this way of sowing [rich soil, etc.] may new varieties of flowers and fruits be still produced in infinitum, which affords me another argument to prove them not specifically distinct; the number of species being in nature certain and determinate, as is generally acknowledged by philosophers, and might be proved also by divine authority, God having finished his work of creation, that is, consummated the number of species, in six days.

Ray's views on the origin of specific and intraspecific variation are here laid bare. Given sufficient regard for the variation patterns of a particular group of plants, a botanist should be able to avoid elevating 'accidental' variants to the level of the species (Cain, 1999). Species themselves were, for Ray, all created at the same time, and all therefore of the same age. That new species can come into existence Ray denies, as this is inconsistent with the account of the Creation given in Genesis. This idea is again expressed in a passage written towards the end of his life: 'Plants which differ as species preserve their species for all time, the members of each species having all descended from seed of the same original plant' (Stearn, 1957).

Thus, Ray, an ordained minister himself, firmly upholds the doctrine of special creation. Such views were almost universally accepted in the seventeenth century, Protestants being particularly influenced by the works of Milton. However, Ray's views also took account of contemporary philosophical ideas (C. D. Preston, personal communication).

The Great Chain of Being

A very powerful idea underlay the attitudes of philosophers and theologians throughout Classical and Medieval Europe when they attempted to understand the world.

> The ancient *Scala Naturae*, or 'Great Chain of Being', that originated with Aristotle attempted to classify animals in relations to a hierarchical ladder or stair-way of nature, in which matter and living things were arranged according to their structural complexity and function. The ladder of nature was most often depicted graphically as a list of entities arranged vertically, with the most basic elements like air, water,

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> earth and fire at the bottom and man, angels, and God at the top. (Pietsch, 2012)

Significantly, in some representations, humans were not all on the same rung of the ladder: males were on the rung above females (Dawkins, 2009). Lower organisms including plants were at the base of the chain. The relationship between God and Nature was one of the great philosophical questions that underlay the rise of natural science in the sixteenth and seventeenth centuries (see Lovejoy, 1966; Cain, 1996, 1999, 2008). The acceptance by great pioneer biologists, such as Ray, of the natural world as rational and available to observation and experiment marked the beginning of modern science. Pietsch (2012) reviews the wide range of pre-Darwinian representations of the relationships of different organisms, including tree-like structures. The rigid timeless plan of the *Scala Naturae* finally gave way to the evolutionary Tree of Life (Darwin, 1859).

Linnaeus

In our examination of historical aspects of the subject, we must next study Linnaeus (Carl von Linné, 1707–78), the great Swedish systematist, who made extremely important contributions (Goerke, 1989; Koerner, 1999; Blunt, 2004; Harnesk, 2007). He too, in *Critica botanica* (1737), championed the idea of the fixity of species:

> All species reckon the origin of their stock in the first instance from the veritable hand of the Almighty Creator: for the Author of Nature, when He created species, imposed on his Creations an eternal law of reproduction and multiplication within the limits of their proper kinds. He did indeed in many instances allow them the power of sporting in their outward appearance, but never that of passing from one species to another. Hence today there are two kinds of difference between plants: one a true difference, the diversity produced by the all-wise hand of the Almighty, but the other, variation in the outside shell, the work of Nature in a sportive mood. Let a garden be sown with a thousand different seeds, let to these be given the incessant care of the Gardener in producing abnormal forms, and in a few years it will contain six thousand varieties, which the common herd of Botanists calls species. And so I distinguish the species of the Almighty Creator which are true from the abnormal varieties of the Gardener: the former I reckon of the highest importance because of their Author, the latter I reject because of their authors. The former persist and have persisted from the beginning of the world, the latter, being monstrosities, can boast of but a brief life. (trans. Hort, 1938)

The approaches of both Ray and Linnaeus were typological; they upheld the Greek philosophical view that beneath natural intraspecific variation there existed a fixed, unchangeable type of each species. It was the job of botanists to see these 'elemental species': 'natural variation' was in a sense an illusion.

We see also in the passage quoted above that Linnaeus had a very similar attitude to intraspecific variation to that of Ray. Stearn (1957), in an interesting analysis of the origin of Linnaeus' views, draws attention to his love for gardening and his experience as personal physician and superintendent of gardens to George Clifford, a banker and director of the Dutch East India Company. During this period of his life, Linnaeus, working on his great illustrated book on the plants in Clifford's gardens – the *Hortus Cliffortianus* – lived at Hartekamp, near Haarlem, in the centre of the Dutch bulb-growing area. Here thousands of varieties of Tulips and Hyacinths were grown. At this time, Linnaeus wrote the *Critica botanica*, and no doubt his personal observations at the time prompted the following outburst: 'Such monstrosities, variegated, multiplied, double, proliferous, gigantic, wax fat and charm the eye of the beholder with protean variety so long as gardeners perform daily sacrifice to their idol: if they are neglected these elusive ghosts glide away and are gone.'

Other observations of Linnaeus in the *Critica botanica* show his familiarity with variation in wild plants and his experimental approach to problems. For instance, he studied flower colour, noting that purple flowers tend to fade after a few days, turning to a bluish colour; but '. . . sprinkle these fading flowers with any acid, and you will recover the pristine red hue'. Concerning aquatic plants he notes: 'Many plants which are purely aquatic put forth under water only multifid leaves with capillary segments, but above the surface of the water later produce broad and relatively entire leaves. Further, if these are planted carefully in a shady garden, they lose almost all these capillary leaves, and are furnished only with the upper ones, which are more entire.' As an example Linnaeus gives *Ranunculus aquaticus folio rotundo et capillaceo*, the aquatic species of *Ranunculus* to which we refer later.

Linnaeus was particularly interested in cultivation and its effect upon plants:

> *Martagon sylvaticum* is hairy all over, but loses its hairiness under cultivation. Hence plants kept a long while in dry positions become narrow-leaved as *Sphondylium, Persicaria* . . . Hence broad-leaved plants, when grown for a long while in spongy, fertile, rich soil have been known to produce curly leaves, and have been distinguished as varieties . . . the following have been distinguished as '*crispum*': *Lactuca, Sphondylium, Matricaria*, etc.

The early botanical work of Linnaeus is extremely important in the history of ideas about species and variation. He championed firmly the reality, constancy and sharp delimitation of species. He was also concerned to refute the Ancient Greek idea of transmutation of species, which was still widely believed in his day. In *Critica botanica* he wrote:

> No sensible person nowadays believes in the opinion of the Ancients, who were convinced that plants 'degenerate' in barren soil, for instance, that in barren soil Wheat is transformed into Barley, Barley into Oats, etc. He who considers the marvellous structure of plants, who has seen flowers and fruits produced with such skill and in such diversity, and who has given more credence to experiments of his own, verified by his own eyes, than to credulous authority, will think otherwise.

Linnaeus is immortalised for botanists by his great work *Species plantarum* (1753), in which are described in a concise and methodical fashion all the approximately 5,900 species of plants then known. In classifying these species, Linnaeus grouped species into genera and genera into classes on the basis of the number and arrangement of their stamens. These groups were then subdivided into orders on the number of pistils. This classification, which Linnaeus acknowledged as artificial, was to be a preliminary to a more natural classification – of which he only produced a fragment – based on overall resemblance. Linnaeus' classification of the plant kingdom did not yield a 'Chain of Being' but a hierarchical classification that he likened to the pattern of countries on a map (Jonsell, 1978; Bowler, 1989a, b).

However, Linnaeus' concept of the species seems to have been subject to change as his experience grew. In early works, and most explicitly in the theoretical *Philosophia botanica* (1751, now available in a new translation by Freer, 2003), he stresses the clear distinction between *species*, which were constituted as such by the Creator from the beginning, and mere *varieties*, which may be induced by changed environmental conditions, or raised by the art of gardeners. Nevertheless, not infrequently in *Species plantarum*, there are comments which show that Linnaeus did not always find specific distinctions clear: for example, under *Rosa indica* we find that 'the species of *Rosa* are with difficulty to be distinguished, with even greater difficulty to be defined; nature seems to me to have blended several or by way of sport to have formed several from one' (Stearn, 1957). It is even true that Linnaeus speculates, in a few cases, on the possible evolutionary derivation of one species from another in the pages of *Species plantarum*. Thus, under *Beta vulgaris*, we find, after a list of seven agricultural crop varieties, the fascinating statement: 'Probably born of *B. maritima* in a foreign country'. *B. maritima*, the Wild Beet (now called *B. vulgaris* ssp. *maritima*), is given separate treatment as a distinct species! This and several other cases are interestingly discussed by Greene (1909), who points out that there is good evidence to support the view that the dogmatic 'special creation' statements of *Philosophia botanica* and similar writings of Linnaeus did not, even in his earlier days, represent Linnaeus' real views, but were diplomatic writings to satisfy the 'orthodox ecclesiastics who, in his day, ruled the destinies of all seats of learning in Sweden'.

If he was orthodox on these matters in the main works that established his academic and scientific reputations, Linnaeus allowed himself much more freedom in several of the 186 dissertations which his research students, following the medieval rules of disputation, had to defend in Latin. It is clear from these writings that Linnaeus came to believe less rigidly in the fixity of species. For instance, in 1742 a student brought to him, from near Uppsala, an unusual specimen of Toadflax (*Linaria vulgaris*). The flower was not of the usual structure but had five uniform petals and five spurs. Experiments showed that the plant bred true and Linnaeus called it *Peloria* (Fig. 2.1). After close study Linnaeus decided that *Peloria* was a new species, which had arisen from *L. vulgaris* (Linnaeus, 1744).

He also considered that certain other species might have arisen as a result of hybridisation (see Linnaeus (1749–90; Eriksson, 1983). In *Plantae hybridae* (1751), records are given of 100 plants that might be regarded as hybrids. In *Somnus plantarum* (1755) we read: 'The flowers of some species are impregnated by the farina (pollen) of different genera, and species, inasmuch that hybridous or mongrel plants are frequently produced, which if not admitted as new species, are at least permanent varieties.' Later, in the summer of 1757, Linnaeus made what might be considered to be the first scientifically produced interspecific hybrid, between the Goatsbeards

Fig. 2.1. *Linaria vulgaris* (a) and its *Peloria* variant (b). ((Illustrations by Sowerby in Boswell Syme, 1866.)

Tragopogon pratensis (yellow flowers) and *T. porrifolius* (violet flowers). Ownbey (1950), who studied *Tragopogon* species introduced in America, gives the following details of Linnaeus' experiment. After removing the pollen from the flower-heads of *T. pratensis* early in the morning, Linnaeus sprinkled the stigmas with pollen of *T. porrifolius* at about 8 a.m. The flower-heads were marked, the seed eventually harvested and subsequently planted. The first-generation hybrid plants flowered in 1759, producing purple flowers yellow at the base. Seed of the cross, together with an account of the experiment and its bearings upon the problems of the sexuality of plants, formed the basis for a contribution to a competition arranged by the Imperial Academy of Sciences at St Petersburg. Linnaeus was awarded the prize in September 1760. It is of great historical interest that the seed sent by Linnaeus was planted in the Botanic Garden in St Petersburg, where the progeny flowered in 1761. Here it was examined by the great hybridist Kölreuter, who concluded that 'the hybrid Goatsbeard . . . is not a hybrid plant in the real sense, but at most only a half hybrid, *and indeed in different degrees*'. It is also interesting that the second generation progeny produced by the inter-crossings of Linnaeus' hybrid plants clearly showed segregation of different types, a very early record of genetic segregation which we discuss in Chapter 4.

We see how Linnaeus came to believe that, as in the case of *Peloria*, certain species had arisen from others in the course of time, and also that new species could arise by hybridisation. There is, however, contemporary evidence against Linnaeus' views (Glass, 1959). Adanson, an eighteenth-century French botanist whose originality has only recently been appreciated, tested *Peloria* more fully than Linnaeus. He found that *Peloria* specimens supplied by Linnaeus to the Paris Jardin des Plantes were not stable, producing flowering stems with both 'peloric' and normal flowers. Germination of seed of these plants often gave normal progeny as well as 'peloric'. Adanson concluded that the plant was a monstrosity, not a new species. He came to similar conclusions in two other cases, after experiments with an entire-leaved strawberry (*Fragaria*) discovered by the horticulturalists Duchesnes and son at Versailles in 1766, and the famous laciniate plant of *Mercurialis annua* discovered by Marchant in 1715. There was also evidence against the origin of new species by hybridisation. Kölreuter made a large number of crosses in Tobacco (*Nicotiana*) and other genera. True-breeding new species were not produced by hybridisation; indeed the hybrids were often almost completely sterile, and even when they were fertile there was great variation in the progeny.

Returning to the writings of Linnaeus, we find that in later life he also gave further thought to the origins of the patterns of variation in plant groups. He speculated on the Creation as follows (*Fundamenta fructificationis*, 1762–3, trans., quoted from Ramsbottom, 1938):

> We imagine that the Creator at the actual time of creation made only one single species for each natural order of plants, this species being different in habit and fructification from all the rest. That he made these mutually fertile, whence out of their progeny, fructification having been somewhat changed, Genera of natural classes have arisen as many in number as the different parents, and since this is not carried further, we regard this also as having been done by His Omnipotent hand directly in the beginning; thus all Genera were primeval and constituted a single Species. That as many Genera having arisen as there were individuals in the beginning, these plants in course of time became fertilised by others of different sort and thus arose Species until so many were produced as now exist . . . these Species were sometimes fertilised out of congeners, that is other Species of the same Genus, whence have arisen Varieties.

Linnaeus ascribes here almost an evolutionary origin to present-day species, genera having been formed at the Creation, species-formation being a more recent process (see Erikkson, 1983; Linroth, 1983). This most important change in Linnaeus' views relates to his hybridisation studies. He appears to have been convinced in later life that species can arise by hybridisation, and moved away from the idea of a fixed number of species all created at the same moment in time. Linnaeus' early views on the fixity of species received wide circulation in Europe in his main works, *Critica botanica, Systema naturae* and *Species plantarum*, while his more mature views, presented in the dissertations, did not have such a wide readership. So it is not surprising that even today he is often credited with rigid views on the question.

Buffon and Lamarck

In the mid-eighteenth century zoologists, too, were considering special creation. Linnaeus' contemporary, the French zoologist Buffon (1707–88), had also started his career with orthodox beliefs: 'We see him, the Creator, dictating his simple but beautiful laws and impressing upon each species its immutable characters.' Later, in 1761, however, he speculated on the mutability of species: 'How many species, being perfected or degenerated by the great changes in land and sea, . . . by the prolonged influences of climate, contrary or favourable, *are no longer what they formerly were*?' (Osborn, 1894).

The speculative ideas of Buffon and others remained untested by experiment; the majority of botanists and zoologists, engaged as they were in the late eighteenth century on the naming and classification of the world's flora and fauna, believed in the fixity of species. This belief was indeed so firmly held by naturalists that Cuvier (1769–1832), who had studied many fossil animals, accounted for extinct species by postulating a series of great natural catastrophes, which wiped out certain intermediate species. Cuvier believed that there had been only one Creation, and that after each disaster the Earth was repopulated by the offspring of the survivors. The last catastrophe was the Great Flood recorded in Genesis.

The doctrine of fixity of species was not without its critics in the nineteenth century (see Corsi, 1988; Ruse, 2013). Lamarck (1744–1829), in his *Philosophie zoologique* (1809), attacked the belief that all species were of the same age, created at the beginning of time in a special act of Creation. He believed, much as Ray and Linnaeus did, that species could be changed by growth in different environments, but he also believed that modifications in plant structure brought about by environmental change were inherited (Elliot, 1914):

> In plants, . . . great changes of environment . . . lead to great differences in the development of their parts . . . and these acquired modifications are preserved by reproduction among the individuals in question, and finally give rise to a race quite distinct from that in which the individuals have been continuously in an environment favourable to their development . . . Suppose, for instance, that a seed of one of the meadow grasses . . . is transported to an elevated place on a dry, barren and stony plot much exposed to the winds, and is there left to germinate; if the plant can live in such a place, it will always be badly nourished, and if the individuals reproduced from it continue to exist in this bad environment, there will result a race fundamentally different from that which lives in the meadows and from which it originated.

Thus Lamarck believed that a normally tall plant, dwarfed by growth at high altitude, would produce dwarf offspring. His belief in such an inheritance of acquired characters, which closely parallels the writings of Erasmus Darwin (1731–1802), formed the basis of his evolutionary speculation: one species evolved into another as hereditary changes arose in a plant under the impact of environmental variation. Lamarck, who suffered ill-health at the end of his life and was totally blind for the last 10 years, did not make any experimental investigations in search of evidence for his hypothesis (Jordanova, 1984). He did, however, cite a number of possible cases of apparent change of species brought about by environmental agency. For example: