

Chapter 9

Puncturing punctuationalism

The children of Israel, according to the Exodus story, took 40 years to migrate across the Sinai desert to the promised land. That is a distance of some 200 miles. Their average speed was, therefore, approximately 24 yards per day, or 1 yard per hour; say 3 yards per hour if we allow for night stops. However we do the calculation, we are dealing with an absurdly slow average speed, much slower than the proverbially slow snail's pace (an incredible 55 yards per hour is the speed of the world record snail according to the *Guinness Book of Records*). But of course nobody really believes that the average speed was continuously and uniformly maintained. Obviously the Israelites travelled in fits and starts, perhaps camping for long periods in one spot before moving on. Probably many of them had no very clear idea that they were *travelling* in any particularly consistent direction, and they meandered round and round from oasis to oasis as nomadic desert herdsmen are wont to do. Nobody, I repeat, really believes that the average speed was continuously and uniformly maintained.

But now suppose that two eloquent young historians burst upon the scene. Biblical history so far, they tell us, has been dominated by the 'gradualistic' school of thought. 'Gradualist' historians, we are told, literally believe that the Israelites travelled 24 yards per day; they folded their tents every morning, crawled 24 yards in an east-northeasterly direction, and then pitched camp again. The only alternative to 'gradualism', we are told, is the dynamic new 'punctuationalist' school of history. According to the radical young punctuationalists, the Israelites spent most of their time in 'stasis', not moving at all but camped, often for years at a time, in one place. Then they would move on, rather fast, to a new encampment, where they



again stayed for several years. Their progress towards the promised land, instead of being gradual and continuous, was jerky: long periods of stasis punctuated by brief periods of rapid movement. Moreover, their bursts of movement were not always in the direction of the promised land, but were in almost random directions. It is only when we look, with hindsight, at the large scale *macromigrational* pattern, that we can see a trend in the direction of the promised land.

Such is the eloquence of the punctuationalist biblical historians that they become a media sensation. Their portraits adorn the front covers of mass circulation news magazines. No television documentary about biblical history is complete without an interview with at least one leading punctuationalist. People who know nothing else of biblical scholarship remember just the one fact: that in the dark days before the punctuationalists burst upon the scene, everybody else got it wrong. Note that the publicity value of the punctuationalists has nothing to do with the fact that they may be right. It has everything to do with the allegation that earlier authorities were 'gradualist' and wrong. It is because the punctuationalists sell themselves as revolutionaries that they are listened to, not because they are right.

My story about the punctuationalist biblical historians is, of course, not really true. It is a parable about an analogous alleged controversy among students of biological evolution. In some respects it is an unfair parable, but it is not totally unfair and it has enough truth in it to justify its telling at the beginning of this chapter. There is a highly advertised school of thought among evolutionary biologists whose proponents call themselves punctuationalists, and they did invent the term 'gradualist' for their most influential predecessors. They have enjoyed enormous publicity, among a public that knows almost nothing else about evolution, and this is largely because their position has been represented, by secondary reporters more than by themselves, as radically different from the positions of previous evolutionists, especially Charles Darwin. So far, my biblical analogy is a fair one.

The respect in which the analogy is unfair is that in the story of the biblical historians 'the gradualists' were *obviously* non-existent straw men, fabricated by the punctuationalists. In the case of the evolutionary 'gradualists', the fact that they are non-existent straw men is not quite so obvious. It needs to be demonstrated. It is possible to interpret the words of Darwin and many other evolutionists as gradualist in intent, but it then becomes important to realize that the word gradualist can be interpreted in different ways to mean different things. Indeed, I shall develop an interpretation of the word 'gradualist' according to which just about everybody is a gradualist. In the evolutionary case, unlike in

the parable of the Israelites, there is genuine controversy lurking, but that genuine controversy is about little details which are nowhere near important enough to justify all the media hype.

Among evolutionists, the 'punctuationalists' were originally drawn from the ranks of palaeontology. Palaeontology is the study of fossils. It is a very important branch of biology, because evolutionary ancestors all died long ago and fossils provide us with our only direct evidence of the animals and plants of the distant past. If we want to know what our evolutionary ancestors looked like, fossils are our main hope. As soon as people realized what fossils really were - previous schools of thought had held that they were creations of the devil, or that they were the bones of poor sinners drowned in the flood - it became clear that any theory of evolution must have certain expectations about the fossil record. But there has been some discussion of exactly what those expectations are, and this is partly what the punctuationalist argument is about.

We are lucky to have fossils at all. It is a remarkably fortunate fact of geology that bones, shells and other hard parts of animals, before they decay, can occasionally leave an imprint which later acts as a mould, which shapes hardening rock into a permanent memory of the animal. We don't know what proportion of animals are fossilized after their death - I personally would consider it an honour to be fossilized - but it is certainly very small indeed. Nevertheless, however small the proportion fossilized, there are certain things about the fossil record that any evolutionist should expect to be true. We should be very surprised, for example, to find fossil humans appearing in the record before mammals are supposed to have evolved! If a single, well-verified mammal skull were to turn up in 500 million year-old rocks, our whole modern theory of evolution would be utterly destroyed. Incidentally, this is a sufficient answer to the canard, put about by creationists and their journalistic fellow travellers, that the whole theory of evolution is an 'unfalsifiable' tautology. Ironically, it is also the reason why creationists are so keen on the fake human footprints, which were carved during the depression to fool tourists, in the dinosaur beds of Texas.

Anyway, if we arrange our genuine fossils in order, from oldest to youngest, the theory of evolution expects to see some sort of orderly sequence rather than a higgledy-piggledy jumble. More to the point in this chapter, different versions of the theory of evolution, for instance 'gradualism' and 'punctuationalism', might expect to see different kinds of pattern. Such expectations can be tested only if we have some means of *dating* fossils, or at least of knowing the order in which they were

laid down. The problems of dating fossils, and the solutions of these problems, require a brief digression, the first of several for which the reader's indulgence is asked. They are necessary for the explanation of the main theme of the chapter.

We have long known how to arrange fossils in the order in which they were laid down. The method is inherent in the very phrase 'laid down'. More recent fossils are obviously laid down on top of older fossils rather than underneath them, and they therefore lie above them in rock sediments. Occasionally volcanic upheavals can turn a chunk of rock right over and then, of course, the order in which we find fossils as we dig downwards will be exactly reversed; but this is rare enough to be obvious when it occurs. Even though we seldom find a complete historical record as we dig down through the rocks of any one area, a good record can be pieced together from overlapping portions in different areas (actually, although I use the image of 'digging down', palaeontologists seldom literally dig downwards through strata; they are more likely to find fossils exposed by erosion at various depths). Long before they knew how to date fossils in actual millions of years, palaeontologists had worked out a reliable scheme of geological eras, and they knew in great detail which era came before which. Certain kinds of shells are such reliable indicators of the ages of rocks that they are among the main indicators used by oil prospectors in the field. By themselves, however, they can tell us only about the relative ages of rock strata, never their absolute ages.

More recently, advances in physics have given us methods to put absolute dates, in millions of years, on rocks and the fossils that they contain. These methods depend upon the fact that particular radioactive elements decay at precisely known rates. It is as though precision-made miniature stopwatches had been conveniently buried in the rocks. Each stopwatch was started at the moment that it was laid down. All that the palaeontologist has to do is dig it up and read off the time on the dial. Different kinds of radioactive decay-based geological stopwatches run at different rates. The radiocarbon stopwatch buzzes round at a great rate, so fast that, after some thousands of years, its spring is almost wound down and the watch is no longer reliable. It is useful for dating organic material on the archaeological/historical timescale where we are dealing in hundreds or a few thousands of years, but it is no good for the evolutionary timescale where we are dealing in millions of years.

For the evolutionary timescale other kinds of watch, such as the potassium-argon watch, are suitable. The potassium-argon watch is so slow that it would be unsuitable for the archaeological/historical

timescale. That would be like trying to use the hour hand on an ordinary watch to time an athlete sprinting a hundred yards. For timing the megamarathon that is evolution, on the other hand, something like the potassium-argon watch is just what is needed. Other radioactive 'stopwatches', each with its own characteristic rate of slowing down, are the rubidium-strontium, and the uranium-thorium-lead watches. So, this digression has told us that if a palaeontologist is presented with a fossil, he can usually know when the animal lived, on an absolute timescale of millions of years. We got into this discussion of dating and timing in the first place, you will remember, because we were interested in the expectations about the fossil record that various kinds of evolutionary theory – 'punctuonist', 'gradualist', etc. – should have. It is now time to discuss what those various expectations are.

Suppose, first, that nature had been extraordinarily kind to palaeontologists (or perhaps unkind, when you think of the extra work involved), and given them a fossil of every animal that ever lived. If we could indeed look at such a complete fossil record, carefully arranged in chronological order, what should we, as evolutionists, expect to see? Well, if we are 'gradualists', in the sense caricatured in the parable of the Israelites, we should expect something like the following. Chronological sequences of fossils will always exhibit smooth evolutionary trends with fixed rates of change. In other words, if we have three fossils, A, B and C, A being ancestral to B, which is ancestral to C, we should expect B to be proportionately intermediate in form between A and C. For instance, if A had a leg length of 20 inches and C had a leg length of 40 inches, B's legs should be intermediate, their exact length being proportional to the time that elapsed between A's existence and B's.

If we carry the caricature of gradualism to its logical conclusion, just as we calculated the average speed of the Israelites as 24 yards per day, so we can calculate the average rate of lengthening of the legs in the evolutionary line of descent from A to C. If, say, A lived 20 million years earlier than C (to fit this vaguely into reality, the earliest known member of the horse family, *Hyracotherium*, lived about 50 million years ago, and was the size of a terrier), we have an evolutionary growth rate of 20 leg-inches per 20 million years, or one-millionth of an inch per year. Now the caricature of a gradualist is supposed to believe that the legs steadily grew, over the generations, at this very slow rate: say four-millionths of an inch per generation, if we assume a horse-like generation-time of about 4 years. The gradualist is supposed to believe that, through all those millions of generations, individuals

with legs four-millionths of an inch longer than the average had an advantage over individuals with legs of average length. To believe this is like believing that the Israelites travelled 24 yards every day across the desert.

The same is true even of one of the fastest known evolutionary changes, the swelling of the human skull from an *Australopithecus*-like ancestor, with a brain volume of about 500 cubic centimetres (cc), to the modern *Homo sapiens*'s average brain volume of about 1,400 cc. This increase of about 900 cc, nearly a tripling in brain volume, has been accomplished in no more than three million years. By evolutionary standards this is a rapid rate of change: the brain seems to swell like a balloon and indeed, seen from some angles, the modern human skull does rather resemble a bulbous, spherical balloon in comparison to the flatter, sloping-browed skull of *Australopithecus*. But if we count up the number of generations in three million years (say about four per century), the average rate of evolution is less than a hundredth of a cubic centimetre per generation. The caricature of a gradualist is supposed to believe that there was a slow and inexorable change, generation by generation, such that in all generations sons were slightly brainier than their fathers, brainier by 0.01 cc. Presumably the extra hundredth of a cubic centimetre is supposed to provide each succeeding generation with a significant survival advantage compared with the previous generation.

But a hundredth of a cubic centimetre is a tiny quantity in comparison to the range of brain sizes that we find among modern humans. It is an often-quoted fact, for instance, that the writer Anatole France – no fool, and a Nobel prizewinner – had a brain size of less than 1,000 cc, while at the other end of the range, brains of 2,000 cc are not unknown: Oliver Cromwell is frequently cited as an example, though I do not know with what authenticity. The average per-generation increment of 0.01 cc, then, which is supposed by the caricature of a gradualist to give a significant survival advantage, is a mere hundred-thousandth part of the *difference* between the brains of Anatole France and Oliver Cromwell! It is fortunate that the caricature of a gradualist does not really exist.

Well, if this kind of gradualist is a non-existent caricature – a windmill for punctuationalist lances – is there some other kind of gradualist who really exists and who holds tenable beliefs? I shall show that the answer is yes, and that the ranks of gradualists, in this second sense, include all sensible evolutionists, among them, when you look carefully at their beliefs, those that call themselves punctuationalists. But we have to understand why the punctuationalists *thought* that their

views were revolutionary and exciting. The starting point for discussing these matters is the apparent existence of 'gaps' in the fossil record, and it is to these gaps that we now turn.

From Darwin onwards evolutionists have realized that, if we arrange all our available fossils in chronological order, they do *not* form a smooth sequence of scarcely perceptible change. We can, to be sure, discern long-term trends of change – legs get progressively longer, skulls get progressively more bulbous, and so on – but the trends as seen in the fossil record are usually jerky, not smooth. Darwin, and most others following him, have assumed that this is mainly because the fossil record is imperfect. Darwin's view was that a complete fossil record, if only we had one, *would* show gentle rather than jerky change. But since fossilization is such a chancy business, and finding such fossils as there are is scarcely less chancy, it is as though we had a cine film with most of the frames missing. We can, to be sure, see movement of a kind when we project our film of fossils, but it is more jerky than Charlie Chaplin, for even the oldest and scratchiest Charlie Chaplin film hasn't completely lost nine-tenths of its frames.

The American palaeontologists Niles Eldredge and Stephen Jay Gould, when they first proposed their theory of punctuated equilibria in 1972, made what has since been represented as a very different suggestion. They suggested that, actually, the fossil record may not be as imperfect as we thought. Maybe the 'gaps' are a true reflection of what really happened, rather than being the annoying but inevitable consequences of an imperfect fossil record. Maybe, they suggested, evolution really did in some sense go in sudden bursts, punctuating long periods of 'stasis', when no evolutionary change took place in a given lineage.

Before we come to the sort of sudden bursts that they had in mind, there are some conceivable meanings of 'sudden bursts' that they most definitely did not have in mind. These must be cleared out of the way because they have been the subject of serious misunderstandings. Eldredge and Gould certainly would agree that some very important gaps really are due to imperfections in the fossil record. Very big gaps, too. For example the Cambrian strata of rocks, vintage about 600 million years, are the oldest ones in which we find most of the major invertebrate groups. And we find many of them already in an advanced state of evolution, the very first time they appear. It is as though they were just planted there, without any evolutionary history. Needless to say, this appearance of sudden planting has delighted creationists. Evolutionists of all stripes believe, however, that this really does represent a very large gap in the fossil record, a gap that is simply due to

the fact that, for some reason, very few fossils have lasted from periods before about 600 million years ago. One good reason might be that many of these animals had only soft parts to their bodies: no shells or bones to fossilize. If you are a creationist you may think that this is special pleading. My point here is that, when we are talking about gaps of this magnitude, there is no difference whatever in the interpretations of 'punctuationalists' and 'gradualists'. Both schools of thought despise so-called scientific creationists equally, and both agree that the *major* gaps are real, that they are true imperfections in the fossil record. Both schools of thought agree that the only alternative explanation of the sudden appearance of so many complex animal types in the Cambrian era is divine creation, and both would reject this alternative.

There is another conceivable sense in which evolution might be said to go in sudden jerks, but which is also not the sense being proposed by Eldredge and Gould, at least in most of their writings. It is conceivable that some of the apparent 'gaps' in the fossil record really do reflect sudden change in a single generation. It is conceivable that there really never were any intermediates; conceivable that large evolutionary changes took place in a single generation. A son might be born so different from his father that he properly belongs in a different species from his father. He would be a mutant individual, and the mutation would be such a large one that we should refer to it as a macromutation. Theories of evolution that depend upon macromutation are called 'saltation' theories, from *saltus*, the Latin for 'jump'. Since the theory of punctuated equilibria frequently is confused with true saltation, it is important here to discuss saltation, and show why it cannot be a significant factor in evolution.

Macromutations – mutations of large effect – undoubtedly occur. What is at issue is not whether they occur but whether they play a role in evolution; whether, in other words, they are incorporated into the gene pool of a species, or whether, on the contrary, they are always eliminated by natural selection. A famous example of a macromutation is 'antennapædia' in fruitflies. In a normal insect the antennae have something in common with the legs, and they develop in the embryo in a similar way. But the differences are striking as well, and the two sorts of limb are used for very different purposes: the legs for walking; the antennae for feeling, smelling and otherwise sensing things. Antennapædic flies are freaks in which the antennae develop just like legs. Or, another way of putting it, they are flies that have no antennae but an extra pair of legs, growing out of the sockets where the antennae ought to be. This is a true mutation in that it results from an

error in the copying of DNA. And it breeds true if antennapædic flies are cossed in the laboratory so that they survive long enough to breed at all. They would not survive long in the wild, as their movements are clumsy and their vital senses are impaired.

So, macromutations do happen. But do they play a role in evolution? People called saltationists believe that macromutations are a means by which major jumps in evolution could take place in a single generation. Richard Goldschmidt, whom we met in Chapter 3, was a true saltationist. If saltationism were true, apparent 'gaps' in the fossil record needn't be gaps at all. For example, a saltationist might believe that the transition from sloping-browed *Australopithecus* to domed-browed *Homo sapiens* took place in a single macromutational step, in a single generation. The difference in form between the two species is probably less than the difference between a normal and an antennapædic fruitfly, and it is theoretically conceivable that the first *Homo sapiens* was a freak child – probably an ostracized and persecuted one – of two normal *Australopithecus* parents.

There are very good reasons for rejecting all such saltationist theories of evolution. One rather boring reason is that if a new species really did arise in a single mutational step, members of the new species might have a hard time finding mates. But I find this reason less telling and interesting than two others which have already been foreshadowed in our discussion of why major jumps across Biomorph Land are to be ruled out. The first of these points was put by the great statistician and biologist R. A. Fisher, whom we met in other connections in previous chapters. Fisher was a stalwart opponent of all forms of saltationism, at a time when saltationism was much more fashionable than it is today, and he used the following analogy. Think, he said, of a microscope which is almost, but not quite perfectly, in focus and otherwise well-adjusted for distinct vision. What are the odds that, if we make some random change to the state of the microscope (corresponding to a mutation), we shall improve the focus and general quality of the image? Fisher said:

It is sufficiently obvious that any large derangement will have a very small probability of improving the adjustment, while in the case of alterations much less than the smallest of those intentionally effected by the maker or the operator, the chance of improvement should be almost exactly one half.

I have already remarked that what Fisher found 'easy to see' could place formidable demands on the mental powers of ordinary scientists, and the same is true of what Fisher thought was 'sufficiently obvious'. Nevertheless, further cogitation almost always shows him to have

been right, and in this case we can prove it to our own satisfaction without too much difficulty. Remember that we are assuming the microscope to be almost in correct focus before we start. Suppose that the lens is slightly lower than it ought to be for perfect focus, say a tenth of an inch too close to the slide. Now if we move it a small amount, say a hundredth of an inch, in a random direction, what are the odds that the focus will improve? Well, if we happen to move it down a hundredth of an inch, the focus will get worse. If we happen to move it up a hundredth of an inch, the focus will get better. Since we are moving it in a random direction, the chance of each of these two eventualities is one half. The smaller the movement of adjustment, in relation to the initial error, the closer will the chance of improvement approach one half. That completes the justification of the second part of Fisher's statement.

But now, suppose we move the microscope tube a large distance – equivalent to a macromutation – also in a random direction; suppose we move it a full inch. Now it doesn't matter which direction we move it in, up or down, we shall still make the focus worse than it was before. If we chance to move it down, it will now be one and one-tenth inches away from its ideal position (and will probably have crunched through the slide). If we chance to move it up, it will now be nine-tenths of an inch away from its ideal position. Before the move, it was only one-tenth of an inch away from its ideal position so, either way, our 'macromutational' big move has been a bad thing. We have done the calculation for a very big move ('macromutation') and a very small move ('micromutation'). We can obviously do the same calculation for a range of intermediate sizes of move, but there is no point in doing so. I think it really will now be sufficiently obvious that the smaller we make the move, the closer we shall approach the extreme case in which the odds of an improvement are one-half; and the larger we make the move, the closer we shall approach the extreme case in which the odds of an improvement are zero.

The reader will have noticed that this argument depends upon the initial assumption that the microscope was already pretty close to being in focus before we even started making random adjustments. If the microscope starts 2 inches out of focus, then a random change of 1 inch has a 50 per cent chance of being an improvement, just as a random change of one-hundredth of an inch has. In this case the 'macromutation' appears to have the advantage that it moves the microscope into focus more quickly. Fisher's argument will, of course, apply here to 'megamutations' of, say, 6 inches movement in a random direction.

Why, then, was Fisher allowed to make his initial assumption that the microscope was nearly in focus at the start? The assumption flows from the role of the microscope in the analogy. The microscope after its random adjustment stands for a mutant animal. The microscope before its random adjustment stands for the normal, unmutated parent of the supposed mutant animal. Since it is a parent, it must have survived long enough to reproduce, and therefore it cannot be all that far from being well-adjusted. By the same token, the microscope before the random jolt cannot be all that far from being in focus, or the animal that it stands for in the analogy couldn't have survived at all. It is only an analogy, and there is no point in arguing over whether 'all that far' means an inch or a tenth of an inch or a thousandth of an inch. The important point is that if we consider mutations of ever-increasing magnitude, there will come a point when, the larger the mutation is, the less likely it is to be beneficial; while if we consider mutations of ever-decreasing magnitude, there will come a point when the chance of a mutation's being beneficial is 50 per cent.

The argument over whether macromutations such as antennapaedia could ever be beneficial (or at least could avoid being harmful), and therefore whether they could give rise to evolutionary change, therefore turns on *how* 'macro' the mutation is that we are considering. The more 'macro' it is, the more likely it is to be deleterious, and the less likely it is to be incorporated in the evolution of a species. As a matter of fact, virtually all the mutations studied in genetics laboratories – which are pretty macro because otherwise geneticists wouldn't notice them – are deleterious to the animals possessing them (ironically I've met people who think that this is an argument *against* Darwinism!). Fisher's microscope argument, then, provides one reason for scepticism about 'saltation' theories of evolution, at least in their extreme form.

The other general reason for not believing in true saltation is also a statistical one, and its force also depends quantitatively on *how* macro is the macromutation we are postulating. In this case it is concerned with the complexity of evolutionary changes. Many, though not all, of the evolutionary changes we are interested in are advances in complexity of design. The extreme example of the eye, discussed in earlier chapters, makes the point clear. Animals with eyes like ours evolved from ancestors with no eyes at all. An extreme saltationist might postulate that the evolution took place in a single mutational step. A parent had no eye at all, just bare skin where the eye might be. He had a freak offspring with a fully developed eye, complete with variable focus lens, iris diaphragm for 'stopping down', retina with millions of

three-colour photoreceptors, all with nerves correctly connected up in the brain to provide him with correct, binocular, stereoscopic colour vision.

In the biomorph model we assumed that this kind of multi-dimensional improvement could not occur. To recapitulate on why that was a reasonable assumption, to make an eye from nothing you need not just one improvement but a large number of improvements. Any one of these improvements is pretty improbable by itself, but not so improbable as to be impossible. The greater the number of simultaneous improvements we consider, the more improbable is their simultaneous occurrence. The coincidence of their simultaneous occurrence is equivalent to leaping a large distance across Biomorph Land, and happening to land on one particular, pre-designated spot. If we choose to consider a sufficiently large number of improvements, their joint occurrence becomes so improbable as to be, to all intents and purposes, impossible. The argument has already been sufficiently made, but it may be helpful to draw a distinction between two kinds of hypothetical macromutation, both of which *appear* to be ruled out by the complexity argument but only one of which, in fact, *is* ruled out by the complexity argument. I label them, for reasons that will become clear, Boeing 747 macromutations and Stretched DC8 macromutations.

Boeing 747 macromutations are the ones that really are ruled out by the complexity argument just given. They get their name from the astronomer Sir Fred Hoyle's memorable misunderstanding of the theory of natural selection. He compared natural selection, in its alleged improbability, to a hurricane blowing through a junkyard and chancing to assemble a Boeing 747. As we saw in Chapter 1, this is an entirely false analogy to apply to natural selection, but it is a very good analogy for the idea of certain kinds of macromutation giving rise to evolutionary change. Indeed, Hoyle's fundamental error was that he, in effect, thought (without realizing it) that the theory of natural selection *did* depend upon macromutation. The idea of a single macromutation's giving rise to a fully functioning eye with the properties listed above, where there was only bare skin before, is, indeed, just about as improbable as a hurricane assembling a Boeing 747. This is why I refer to this kind of hypothetical macromutation as a Boeing 747 macromutation.

Stretched DC8 macromutations are mutations that, although they may be large in the magnitude of their effects, turn out not to be large in terms of their complexity. The Stretched DC8 is an airliner that was made by modifying an earlier airliner, the DC8. It is like a DC8, but

with an elongated fuselage. It was an improvement at least from one point of view, in that it could carry more passengers than the original DC8. The stretching is a large increase in length, and in that sense is analogous to a macromutation. More interestingly, the increase in length is, at first sight, a complex one. To elongate the fuselage of an airliner, it is not enough just to insert an extra length of cabin tube. You also have to elongate countless ducts, cables, air tubes and electric wires. You have to put in lots more seats, ashtrays, reading lights, 12-channel music selectors and fresh-air nozzles. At first sight there seems to be much more complexity in a Stretched DC8 than there is in an ordinary DC8, but is there really? The answer is no, at least to the extent that the 'new' things in the stretched plane are just 'more of the same'. The biomorphs of Chapter 3 frequently show macromutations of the Stretched DC8 variety.

What has this to do with mutations in real animals? The answer is that some real mutations cause large changes that are very like the change from DC8 to Stretched DC8, and some of these, although in a sense 'macro' mutations, have definitely been incorporated in evolution. Snakes, for instance, all have many more vertebrae than their ancestors. We could be sure of this even if we didn't have any fossils, because snakes have many more vertebrae than their surviving relatives. Moreover, different species of snakes have different numbers of vertebrae, which means that vertebral number must have changed in evolution since their common ancestor, and quite often at that.

Now, to change the number of vertebrae in an animal, you need to do more than just shove in an extra bone. Each vertebra has, associated with it, a set of nerves, a set of blood vessels, a set of muscles etc., just as each row of seats in an airliner has a set of cushions, a set of head rests, a set of headphone sockets, a set of reading-lights with their associated cables etc. The middle part of the body of a snake, like the middle part of the body of an airliner, is composed of a number of segments, many of which are exactly like each other, however complex they all individually may be. Therefore, in order to add new segments, all that has to be done is a simple process of duplication. Since there already exists genetic machinery for making one snake segment - genetic machinery of great complexity, which took many generations of step-by-step, gradual evolution to build up - new identical segments may easily be added by a single mutational step. If we think of genes as 'instructions to a developing embryo', a gene for inserting extra segments may read, simply, 'more of the same here'. I imagine that the instructions for building the first Stretched DC8 were somewhat similar.

We can be sure that, in the evolution of snakes, numbers of vertebrae changed in whole numbers rather than in fractions. We cannot imagine a snake with 26.3 vertebrae. It either had 26 or 27, and it is obvious that there must have been cases when an offspring snake had at least one whole vertebra more than its parents did. This means that it had a whole extra set of nerves, blood vessels, muscle blocks, etc. In a sense, then, this snake was a *macro*-mutant, but only in the weak 'Stretched DC8' sense. It is easy to believe that individual snakes with half a dozen more vertebrae than their parents could have arisen in a single mutational step. The 'complexity argument' against saltatory evolution does not apply to Stretched DC8 macromutations because, if we look in detail at the nature of the change involved, they are in a real sense not true macromutations at all. They are only macromutations if we look, naively, at the finished product, the adult. If we look at the *processes* of embryonic development they turn out to be micromutations, in the sense that only a small change in the embryonic *instructions* had a large apparent effect in the adult. The same goes for antennapaedia in fruitflies and the many other so-called 'homeotic mutations'.

This concludes my digression on macromutation and saltatory evolution. It was necessary, because the theory of punctuated equilibria is frequently confused with saltatory evolution. But it was a digression, because the theory of punctuated equilibria is the main topic of this chapter, and that theory in truth has no connection with macromutation and true saltation.

The 'gaps' that Eldredge and Gould and the other 'punctuationalists' are talking about, then, have nothing to do with true saltation, and they are much much smaller gaps than the ones that excite creationists. Moreover, Eldredge and Gould originally introduced their theory, *not* as radically and revolutionarily antipathetic to ordinary, 'conventional' Darwinism – which is how it later came to be sold – but as something that *followed* from long-accepted conventional Darwinism, properly understood. To gain this proper understanding, I'm afraid we need another digression, this time into the question of how new species originate, the process known as 'speciation'.

Darwin's answer to the question of the origin of species was, in a general sense, that species were descended from other species. Moreover, the family tree of life is a branching one, which means that more than one modern species can be traced back to one ancestral one. For instance, lions and tigers are now members of different species, but they have both sprung from a single ancestral species, probably not very long ago. This ancestral species may have been the same as one of

the two modern species, or it may have been a third modern species; or maybe it is now extinct. Similarly, humans and chimps now clearly belong to different species, but their ancestors of a few million years ago belonged to one single species. Speciation is the process by which a single species becomes two species, one of which may be the same as the original single one.

The reason speciation is thought to be a difficult problem is this. All the members of the single would-be ancestral species are capable of interbreeding with one another: indeed, to many people, this is what is meant by the phrase 'single species'. Therefore, every time a new daughter species begins to be 'budded off', the budding off is in danger of being frustrated by interbreeding. We can imagine the would-be ancestors of the lions and the would-be ancestors of the tigers failing to split apart because they keep interbreeding with one another and therefore staying similar to one another. Don't, incidentally, read too much into my use of words like 'frustrated', as though the ancestral lions and tigers, in some sense, 'wanted' to separate from each other. It is simply that, as a matter of fact, species obviously *have* diverged from one another in evolution, and at first sight the fact of interbreeding makes it hard for us to see how this divergence came about.

It seems almost certain that the principal correct answer to this problem is the obvious one. There will be no problem of interbreeding if the ancestral lions and the ancestral tigers happen to be in different parts of the world, where they can't interbreed with each other. Of course, they didn't go to different continents in order to allow themselves to diverge from one another: they didn't think of themselves as ancestral lions or ancestral tigers! But, given that the single ancestral species spread to different continents anyway, say Africa and Asia, the ones that happened to be in Africa could no longer interbreed with the ones that happened to be in Asia because they never met them. If there was any tendency for the animals on the two continents to evolve in different directions, either under the influence of natural selection or under the influence of chance, interbreeding no longer constituted a barrier to their diverging and eventually becoming two distinct species.

I have spoken of different continents to make it clear, but the principle of geographical separation as a barrier to interbreeding can apply to animals on different sides of a desert, a mountain range, a river, or even a motorway. It can also apply to animals separated by no barrier other than sheer distance. Shrews in Spain cannot interbreed with shrews in Mongolia, and they can diverge, evolutionarily speaking, from shrews in Mongolia, even if there is an unbroken chain

of interbreeding shrews connecting Spain to Mongolia. Nevertheless the idea of geographical separation as the key to speciation is clearer if we think in terms of an actual physical barrier, such as the sea or a mountain range. Chains of islands, indeed, are probably fertile nurseries for new species.

Here, then, is our orthodox neo-Darwinian picture of how a typical species is 'born', by divergence from an ancestral species. We start with the ancestral species, a large population of rather uniform, mutually interbreeding animals, spread over a large land mass. They could be any sort of animal, but let's carry on thinking of shrews. The landmass is cut in two by a mountain range. This is hostile country and the shrews are unlikely to cross it, but it is not quite impossible and very occasionally one or two do end up in the lowlands on the other side. Here they can flourish, and they give rise to an outlying population of the species, effectively cut off from the main population. Now the two populations breed and breed separately, mixing their genes on each side of the mountains but not across the mountains. As time goes by, any changes in the genetic composition of one population are spread by breeding throughout that population but *not* across to the other population. Some of these changes may be brought about by natural selection, which may be different on the two sides of the mountain range: we should hardly expect weather conditions, and predators and parasites, to be exactly the same on the two sides. Some of the changes may be due to chance alone. Whatever the genetic changes are due to, breeding tends to spread them *within* each of the two populations, but *not between* the two populations. So the two populations diverge genetically: they become progressively more unlike each other.

They become so unlike each other that, after a while, naturalists would see them as belonging to different 'races'. After a longer time, they will have diverged so far that we should classify them as different species. Now imagine that the climate warms up so that travel through the mountain passes becomes easier and some of the new species start trickling back to their ancestral homelands. When they meet the descendants of their long-lost cousins, it turns out that they have diverged so far in their genetic makeup that they can no longer successfully interbreed with them. If they do hybridize with them the resulting offspring are sickly, or sterile like mules. So natural selection penalizes any predilection, on the part of individuals on either side, towards hybridizing with the other species or even race. Natural selection thereby finishes off the process of 'reproductive isolation' that began with the chance intervention of a mountain range. 'Speciation' is complete. We now have two species where previously

there was one, and the two species can coexist in the same area without interbreeding with one another.

Actually, the likelihood is that the two species would not coexist for very long. This is not because they would interbreed but because they would compete. It is a widely accepted principle of ecology that two species with the same way of life will not coexist for long in one place, because they will compete and one or other will be driven extinct. Of course our two populations of shrews might no longer have the same way of life; for instance, the new species, during its period of evolution on the other side of the mountains, might have come to specialize on a different kind of insect prey. But if there is significant competition between the two species, most ecologists would expect one or other species to go extinct in the area of overlap. If it happened to be the original, ancestral species that was driven extinct, we should say that it had been replaced by the new, immigrant species.

The theory of speciation resulting from initial geographical separation has long been a cornerstone of mainstream, orthodox neo-Darwinism, and it is still accepted on all sides as the main process by which new species come into existence (some people think there are others as well). Its incorporation into modern Darwinism was largely due to the influence of the distinguished zoologist Ernst Mayr. What the 'punctuationalists' did, when they first proposed their theory, was to ask themselves: Given that, like most neo-Darwinians, we accept the orthodox theory that speciation starts with geographical isolation, what should we expect to see in the fossil record?

Recall the hypothetical population of shrews, with a new species diverging on the far side of a mountain range, then eventually returning to the ancestral homelands and, quite possibly, driving the ancestral species extinct. Suppose that these shrews had left fossils; suppose even that the fossil record was *perfect*, with no gaps due to the unfortunate omission of key stages. What should we expect these fossils to show us? A smooth transition from ancestral species to daughter species? Certainly not, at least if we are digging in the main landmass where the original ancestral shrews lived, and to which the new species returned. Think of the history of what actually happened in the main landmass. There were the ancestral shrews, living and breeding happily away, with no particular reason to change. Admittedly their cousins the other side of the mountains were busy evolving, but their fossils are all on the other side of the mountain so we don't find them in the main landmass where we are digging. Then, suddenly (suddenly by geological standards, that is), the new species returns, competes with the main species and, perhaps, replaces the

main species. Suddenly the fossils that we find as we move up through the strata of the main landmass change. Previously they were all of the ancestral species. Now, abruptly and without visible transitions, fossils of the new species appear, and fossils of the old species disappear.

The 'gaps', far from being annoying imperfections or awkward embarrassments, turn out to be exactly what we should positively expect, if we take seriously our orthodox neo-Darwinian theory of speciation. The reason the 'transition' from ancestral species to descendant species appears to be abrupt and jerky is simply that, when we look at a series of fossils from any one place, we are probably not looking at an *evolutionary* event at all: we are looking at a *migrational* event, the arrival of a new species from another geographical area. Certainly there were evolutionary events, and one species really did evolve, probably gradually, from another. But in order to see the evolutionary transition documented in the fossils we should have to dig elsewhere – in this case on the other side of the mountains.

The point that Eldredge and Gould were making, then, could have been modestly presented as a helpful rescuing of Darwin and his successors from what had seemed to them an awkward difficulty. Indeed that is, at least in part, how it was presented – initially. Darwinians had always been bothered by the apparent gappiness of the fossil record, and had seemed forced to resort to special pleading about imperfect evidence. Darwin himself had written:

The geological record is extremely imperfect and this fact will to a large extent explain why we do not find interminable varieties, connecting together all the extinct and existing forms of life by the finest graduated steps. He who rejects these views on the nature of the geological record, will rightly reject my whole theory.

Eldredge and Gould could have made this their main message: Don't worry Darwin, even if the fossil record were perfect you shouldn't expect to see a finely graduated progression if you only dig in one place, for the simple reason that most of the evolutionary change took place somewhere else! They could have gone further and said:

Darwin, when you said that the fossil record was imperfect, you were understating it. Not only is it imperfect, there are good reasons for expecting it to be *particularly* imperfect just when it gets interesting, just when evolutionary change is taking place; this is partly because evolution usually occurred in a different place from where we find most of our fossils, and it is partly because, even if we are fortunate enough to dig in one of the small outlying areas where most evolutionary change went on, that

evolutionary change (though still gradual) occupies such a short time that we should need an extra *rich* fossil record in order to track it:

But no, instead they chose, especially in their later writings in which they were eagerly followed by journalists, to sell their ideas as being radically *opposed* to Darwin's and opposed to the neo-Darwinian synthesis. They did this by emphasizing the 'gradualism' of the Darwinian view of evolution as opposed to the sudden, jerky, sporadic 'punctationism' of their own. They even, especially Gould, saw analogies between themselves and the old schools of 'catastrophism' and 'saltationism'. Saltationism we have already discussed. Catastrophism was an eighteenth- and nineteenth-century attempt to reconcile some form of creationism with the uncomfortable facts of the fossil record. Catastrophists believed that the apparent progression of the fossil record really reflected a series of discrete creations, each one terminated by a catastrophic mass extinction. The latest of these catastrophes was Noah's flood.

Comparisons between modern punctationism on the one hand, and catastrophism or saltationism on the other, have a purely poetic force. They are, if I may coin a paradox, deeply superficial. They sound impressive in an artsy, literary way, but they do nothing to aid serious understanding, and they can give spurious aid and comfort to modern creationists in their disturbingly successful fight to subvert American education and textbook publishing. The fact is that, in the fullest and most serious sense, Eldredge and Gould are really just as gradualist as Darwin or any of his followers. It is just that they would compress all the gradual change into brief bursts, rather than having it go on all the time; and they emphasize that most of the gradual change goes on in geographical areas away from the areas where most fossils are dug up.

So, it is not really the *gradualism* of Darwin that the punctationists oppose: gradualism means that each generation is only slightly different from the previous generation; you would have to be a saltationist to oppose that, and Eldredge and Gould are not saltationists. Rather, it turns out to be Darwin's alleged belief in the constancy of rates of evolution that they and the other punctationists object to. They object to it because they think that evolution (still undeniably gradualistic evolution) occurs rapidly during relatively brief bursts of activity (speciation events, which provide a kind of crisis atmosphere in which the alleged normal resistance to evolutionary change is broken); and that evolution occurs very slowly or not at all during long intervening periods of stasis. When we say 'relatively' brief we mean, of course, brief relative to the geological timescale in general.

Even the evolutionary jerks of the punctuationalists, though they may be instantaneous by geological standards, still have a duration that is measured in tens or hundreds of thousands of years.

A thought of the famous American evolutionist G. Ledyard Stebbins is illuminating at this point. He isn't specifically concerned with jerky evolution, but is just seeking to dramatize the speed with which evolutionary change can happen, when seen against the timescale of available geological time. He imagines a species of animal, of about the size of a mouse. He then supposes that natural selection starts to favour an increase in body size, but only very slightly. Perhaps larger males enjoy a slight advantage in the competition for females. At any time, males of average size are slightly less successful than males that are a tiny bit bigger than average. Stebbins put an exact figure on the mathematical advantage enjoyed by larger individuals in his hypothetical example. He set it at a value so very very tiny that it wouldn't be measurable by human observers. And the rate of evolutionary change that it brings about is consequently so slow that it wouldn't be noticed during an ordinary human lifetime. As far as the scientist studying evolution on the ground is concerned, then, these animals are not evolving at all. Nevertheless they are evolving, very slowly at a rate given by Stebbins's mathematical assumption, and even at this slow rate, they would eventually reach the size of elephants. How long would this take? Obviously a long time by human standards, but human standards aren't relevant. We are talking about geological time. Stebbins calculates that at his assumed very slow rate of evolution, it would take about 12,000 generations for the animals to evolve from an average weight of 40 grams (mouse size) to an average weight of over 6,000,000 grams (elephant size). Assuming a generation-time of 5 years, which is longer than that of a mouse but shorter than that of an elephant, 12,000 generations would occupy about 60,000 years. 60,000 years is too short to be measured by ordinary geological methods of dating the fossil record. As Stebbins says, 'The origin of a new kind of animal in 100,000 years or less is regarded by paleontologists as "sudden" or "instantaneous".'

The punctuationalists aren't talking about jumps in evolution, they are talking about episodes of relatively rapid evolution. And even these episodes don't have to be rapid by human standards, in order to appear instantaneous by geological standards. Whatever we may think of the theory of punctuated equilibria itself, it is all too easy to confuse gradualism (the belief, held by modern punctuationalists as well as Darwin, that there are no sudden leaps between one generation and the next) with 'constant evolutionary speedism' (opposed by punctuationalists

and allegedly, though not actually, held by Darwin). They are not the same thing at all. The proper way to characterize the beliefs of punctuationalists is: 'gradualistic, but with long periods of "stasis" (evolutionary stagnation) punctuating brief episodes of rapid gradual change'. The emphasis is then thrown onto the long periods of stasis as being the previously overlooked phenomenon that really needs explaining. It is the emphasis on stasis that is the punctuationalists' real contribution, not their claimed opposition to gradualism, for they are truly as gradualist as anybody else.

Even the emphasis on stasis can be found, in less-exaggerated form, in Mayr's theory of speciation. He believed that, of the two geographically separated races, the original large ancestral population is less likely to change than the new, 'daughter' population (on the other side of the mountains in the case of our shrew example). This is not just because the daughter population is the one that has moved to new pastures, where conditions are likely to be different and natural selection pressures changed. It is also because there are some theoretical reasons (which Mayr emphasized but whose importance can be disputed) for thinking that large, breeding populations have an inherent tendency to resist evolutionary change. A suitable analogy is the inertia of a large heavy object; it is hard to shift. Small, outlying populations, by virtue of being small, are inherently more likely, so the theory goes, to change, to evolve. Therefore, although I spoke of the two populations or races of shrews as diverging from each other, Mayr would prefer to see the original, ancestral population as relatively static, and the new population as diverging from it. The branch of the evolutionary tree does not fork into two equal twigs: rather, there is a main stem with a side twig sprouting from it.

The proponents of punctuated equilibrium took this suggestion of Mayr, and exaggerated it into a strong belief that 'stasis', or lack of evolutionary change, is the norm for a species. They believe that there are genetic forces in large populations that actively resist evolutionary change. Evolutionary change, for them, is a rare event, coinciding with speciation. It coincides with speciation in the sense that, in their view, the conditions under which new species are formed - geographical separation of small, isolated subpopulations - are the very conditions under which the forces that normally resist evolutionary change are relaxed or overthrown. Speciation is a time of upheaval, or revolution. And it is during these times of upheaval that evolutionary change is concentrated. For most of the history of a lineage it stagnates.

It isn't true that Darwin believed that evolution proceeded at a constant rate. He certainly didn't believe it in the ludicrously extreme

sense that I satirized in my parable of the children of Israel, and I don't think he really believed it in any important sense. Quotation of the following...well-known passage from the fourth edition (and later editions) of *The Origin of Species* annoys Gould because he thinks it is unrepresentative of Darwin's general thought:

Many species once formed never undergo any further change. . . . ; and the periods, during which species have undergone modification, though long as measured by years, have probably been short in comparison with the periods during which they retain the same form.

Gould wants to shrug off this sentence and others like it, saying:

You cannot do history by selective quotation and search for qualifying footnotes. General tenor and historical impact are the proper criteria. Did his contemporaries or descendants ever read Darwin as a saltationist?

Gould is right, of course, about general tenor and historical impact, but the final sentence of this quotation from him is a highly revealing *faux pas*. *Of course*, nobody has ever read Darwin as a saltationist and, of course, Darwin was consistently hostile to saltationism, but the whole point is that saltationism is not the issue when we are discussing punctuated equilibrium. As I have stressed, the theory of punctuated equilibrium, by Eldredge and Gould's own account, is not a saltationist theory. The jumps that it postulates are not real, single-generation jumps. They are spread out over large numbers of generations over periods of, by Gould's own estimation, perhaps tens of thousands of years. The theory of punctuated equilibrium is a gradualist theory, albeit it emphasizes long periods of stasis intervening between *relatively* short bursts of gradualistic evolution. Gould has misled himself by his own rhetorical emphasis on the purely poetic or literary resemblance between punctationism, on the one hand, and true saltationism on the other.

I think it would clarify matters if, at this point, I summarized a range of possible points of view about rates of evolution. Out on a limb we have true saltationism, which I have already discussed sufficiently. True saltationists don't exist among modern biologists. Everyone that is not a saltationist is a gradualist, and this includes Eldredge and Gould, however they may choose to describe themselves. Within gradualism, we may distinguish various beliefs about rates of (gradual) evolution. Some of these beliefs, as we have seen, bear a purely superficial ('literary' or 'poetic') resemblance to true, anti-gradualist saltationism, which is why they are sometimes confused with it.

At another extreme we have the sort of 'constant speedism' that I

caricatured in the Exodus parable with which I began this chapter. An extreme constant speedist believes that evolution is plodding along steadily and inexorably all the time, whether or not there is any branching or speciation going on. He believes that quantity of evolutionary change is strictly proportional to time elapsed. Ironically, a form of constant speedism has recently become highly favoured among modern molecular geneticists. A good case can be made for believing that evolutionary change at the level of protein molecules really does plod along at a constant rate exactly like the hypothetical children of Israel; and this *even if* externally visible characteristics like arms and legs are evolving in a highly punctuated manner. We have already met this topic in Chapter 5, and I shall mention it again in the next chapter. But as far as adaptive evolution of large-scale structures and behaviour patterns are concerned, just about all evolutionists would reject constant speedism, and Darwin certainly would have rejected it. Everyone that is not a constant speedist is a variable speedist.

Within variable speedism we may distinguish two kinds of belief, labelled, 'discrete variable speedism' and 'continuously variable speedism'. An extreme 'discretist' not only believes that evolution varies in speed. He thinks that the speed flips abruptly from one discrete level to another, like a car's gearbox. He might believe, for instance, that evolution has only two speeds: very fast and stop (I cannot help being reminded here of the humiliation of my first school report, written by the Matron about my performance as a seven-year-old in folding clothes, taking cold baths, and other daily routines of boarding-school life: 'Dawkins has only three speeds: slow, very slow, and stop'). 'Stopped' evolution is the 'stasis' that is thought by punctationists to characterize large populations. Top-gear evolution is the evolution that goes on during speciation, in small isolated populations round the edge of large, evolutionarily static populations. According to this view, evolution is always in one or other of the two gears, never in between. Eldredge and Gould tend in the direction of discretism, and in this respect they are genuinely radical. They may be called 'discrete variable speedists'. Incidentally, there is no *particular* reason why a discrete variable speedist should necessarily emphasize speciation as the time of high-gear evolution. In practice, however, most of them do.

'Continuously variable speedists', on the other hand, believe that evolutionary rates fluctuate continuously from very fast to very slow and stop, with all intermediates. They see no particular reason to emphasize certain speeds more than others. In particular, stasis, to

them, is just an extreme case of ultra-slow evolution. To a punctuationalist, there is something very special about stasis. Stasis, to him, is not just evolution that is so slow as to have a rate of zero: stasis is not just passive lack of evolution because there is no driving force in favour of change. Rather, stasis represents a positive *resistance* to evolutionary change. It is almost as though species are thought to take active steps *not* to evolve, *in spite of* driving forces in favour of evolution.

More biologists agree that stasis is a real phenomenon than agree about its causes. Take, as an extreme example, the coelacanth *Latimeria*. The coelacanths were a large group of 'fish' (actually, although they are called fish they are more closely related to us than they are to trout and herrings) that flourished more than 250 million years ago and apparently died out at about the same time as the dinosaurs. I say 'apparently' died out because in 1938, much to the zoological world's astonishment, a weird fish, a yard and a half long and with unusual leg-like fins, appeared in the catch of a deep-sea fishing boat off the South African coast. Though almost destroyed before its priceless worth was recognized, its decaying remains were fortunately brought to the attention of a qualified South African zoologist just in time. Scarcely able to believe his eyes, he identified it as a living coelacanth, and named it *Latimeria*. Since then, a few other specimens have been fished up in the same area, and the species has now been properly studied and described. It is a 'living fossil', in the sense that it has changed hardly at all since the time of its fossil ancestors, hundreds of millions of years ago.

So, we have stasis. What are we to make of it? How do we explain it? Some of us would say that the lineage leading to *Latimeria* stood still because natural selection did not move it. In a sense it had no 'need' to evolve because these animals had found a successful way of life deep in the sea where conditions did not change much. Perhaps they never participated in any arms races. Their cousins that emerged onto the land did evolve because natural selection, under a variety of hostile conditions including arms races, forced them to. Other biologists, including some of those that call themselves punctuationalists, might say that the lineage leading to modern *Latimeria* actively resisted change, *in spite of* what natural selection pressures there might have been. Who is right? In the particular case of *Latimeria* it is hard to know, but there is one way in which, in principle, we might go about finding out.

Let us, to be fair, stop thinking in terms of *Latimeria* in particular. It is a striking example but a very extreme one, and it is not one on which

the punctuationalists particularly want to rely. Their belief is that less extreme, and shorter-term, examples of stasis are commonplace; are, indeed, the norm, because species have genetic mechanisms that actively resist change, even if there are forces of natural selection urging change. Now here is the very simple experiment which, in principle at least, we can do to test this hypothesis. We can take wild populations and impose our own forces of selection upon them. According to the hypothesis that species actively resist change, we should find that, if we try to breed for some quality, the species should dig in its heels, so to speak, and refuse to budge, at least for a while. If we take cattle and attempt to breed selectively for high milk yield, for instance, we should fail. The genetic mechanisms of the species should mobilize their anti-evolution forces and fight off the pressure to change. If we try to make chickens evolve higher egg-laying rates we should fail. If bullfighters, in pursuit of their contemptible 'sport', try to increase the courage of their bulls by selective breeding, they should fail. These failures should only be temporary, of course. Eventually, like a dam bursting under pressure, the alleged anti-evolution forces will be overcome, and the lineage can then move rapidly to a new equilibrium. But we should experience at least some resistance when we first initiate a new program of selective breeding.

The fact is, of course, that we do not fail when we try to shape evolution by selectively breeding animals and plants in captivity, nor do we experience a period of initial difficulty. Animal and plant species are usually immediately amenable to selective breeding, and breeders detect no evidence of any intrinsic, anti-evolution forces. If anything, selective breeders experience difficulty *after* a number of generations of successful selective breeding. This is because after some generations of selective breeding the available genetic variation runs out, and we have to wait for new mutations. It is conceivable that coelacanths stopped evolving because they stopped mutating – perhaps because they were protected from cosmic rays at the bottom of the sea! – but nobody, as far as I know has seriously suggested this, and in any case this is not what punctuationalists mean when they talk of species having built-in resistance to evolutionary change.

They mean something more like the point I was making in Chapter 7 about 'cooperating' genes: the idea that groups of genes are so well adapted to each other that they resist invasion by new mutant genes which are not members of the club. This is quite a sophisticated idea, and it can be made to sound plausible. Indeed, it was one of the theoretical props of Mayr's inertia idea, already referred to. Nevertheless, the fact that, whenever we try selective breeding, we

encounter no initial resistance to it, suggests to me that, if lineages go for many generations in the wild without changing, this is not because they resist change but because there is no natural selection pressure in favour of changing. They don't change because individuals that stay the same survive better than individuals that change.

Punctuationalists, then, are really just as gradualist as Darwin or any other Darwinian; they just insert long periods of stasis between spurts of gradual evolution. As I said, the one respect in which punctuationalists do differ from other schools of Darwinism is in their strong emphasis on stasis as something positive: as an active resistance to evolutionary change rather than as, simply, absence of evolutionary change. And this is the one respect in which they are quite probably wrong. It remains for me to clear up the mystery of why they *thought* they were so far from Darwin and neo-Darwinism.

The answer lies in a confusion of two meanings of the word 'gradual', coupled with the confusion, which I have been at pains to dispel here but which lies at the back of many peoples' minds, between punctuationalism and saltationism. Darwin was a passionate anti-saltationist, and this led him to stress, over and over again, the extreme gradualness of the evolutionary changes that he was proposing. The reason is that saltation, to him, meant what I have called Boeing 747 macromutation. It meant the sudden calling into existence, like Pallas Athene from the head of Zeus, of brand-new complex organs at a single stroke of the genetic wand. It meant fully formed, complex working eyes springing up from bare skin, in a single generation. The reason it meant these things to Darwin is that that is exactly what it meant to some of his most influential opponents, and they really believed in it as a major factor in evolution.

The Duke of Argyll, for instance, accepted the evidence that evolution had happened, but he wanted to smuggle divine creation in by the back door. He wasn't alone. Instead of a single, once and for all creation in the Garden of Eden, many Victorians thought that the deity had intervened repeatedly, at crucial points in evolution. Complex organs like eyes, instead of evolving from simpler ones by slow degrees as Darwin had it, were thought to have sprung into existence in a single instant. Such people rightly perceived that such instant 'evolution', if it occurred, would imply supernatural intervention: that is what they believed in. The reasons are the statistical ones I have discussed in connection with hurricanes and Boeing 747s. 747 saltationism is, indeed, just a watered-down form of creationism. Putting it the other way around, divine creation is the ultimate in saltation. It is the ultimate leap from inanimate clay to fully formed

man. Darwin perceived this too. He wrote in a letter to Sir Charles Lyell, the leading geologist of his day:

If I were convinced that I required such additions to the theory of natural selection, I would reject it as rubbish. . . . I would give nothing for the theory of Natural selection, if it requires miraculous additions at any one stage of descent.

This is no petty matter. In Darwin's view, the whole *point* of the theory of evolution by natural selection was that it provided a *non* - miraculous account of the existence of complex adaptations. For what it is worth, it is also the whole point of this book. For Darwin, any evolution that had to be helped over the jumps by God was not evolution at all. It made a nonsense of the central point of evolution. In the light of this, it is easy to see why Darwin constantly reiterated the *gradualness* of evolution. It is easy to see why he wrote that sentence quoted in Chapter 4:

If it could be demonstrated that any complex organ existed, which could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down.

There is another way of looking at the fundamental importance of gradualness for Darwin. His contemporaries, like many people still today, had a hard time believing that the human body and other such complex entities could conceivably have come into being through evolutionary means. If you think of the single-celled *Amoeba* as our remote ancestor - as, until quite recently, it was fashionable to do - many people found it hard in their minds to bridge the gap between *Amoeba* and man. They found it inconceivable that from such simple beginnings something so complex could emerge. Darwin appealed to the idea of a gradual series of small steps as a means of overcoming this kind of incredulity. You may find it hard to imagine an *Amoeba* turning into a man, the argument runs; but you do not find it hard to imagine an *Amoeba* turning into a slightly different kind of *Amoeba*. From this it is not hard to imagine it turning into a slightly different kind of slightly different kind of . . . , and so on. As we saw in Chapter 3, this argument overcomes our incredulity only if we stress that there was an extremely large number of steps along the way, and only if each step is very tiny. Darwin was constantly battling against this source of incredulity, and he constantly made use of the same weapon: the emphasis on gradual, almost imperceptible change, spread out over countless generations.

Incidentally, it is worth quoting J. B. S. Haldane's characteristic piece of lateral thinking in combating the same source of incredulity. Something like the transition from *Amoeba* to man, he pointed out, goes on in every mother's womb in a mere nine months. Development is admittedly a very

different process from evolution but, nevertheless, anyone sceptical of the very *possibility* of a transition from single cell to man has only to contemplate his own foetal beginnings to have his doubts allayed. I hope I shall not be thought a pedant if I stress, by the way, that the choice of *Arnoeba* for the title of honorary ancestor is simply following a whimsical tradition. A bacterium would be a better choice, but even bacteria, as we know them, are modern organisms.

To resume the argument, Darwin laid great stress on the gradualness of evolution because of what he was arguing *against*: the misconceptions about evolution that were prevalent in the nineteenth century. The *meaning* of 'gradual', in the context of those times, was 'opposite of saltation'. Eldredge and Gould, in the context of the late twentieth century, use 'gradual' in a very different sense. They in effect, though not explicitly, use it to mean 'at a constant speed', and they oppose to it their own notion of 'punctuation'. They criticize gradualism in this sense of 'constant speedism'. No doubt they are right to do so: in its extreme form it is as absurd as my Exodus parable.

But to couple this justifiable criticism with a criticism of Darwin is simply to confuse two quite separate meanings of the word 'gradual'. In the sense in which Eldredge and Gould are opposed to gradualism, there is no particular reason to doubt that Darwin would have agreed with them. In the sense of the word in which Darwin was a passionate gradualist, Eldredge and Gould are also gradualists. The theory of punctuated equilibrium is a minor gloss on Darwinism, one which Darwin himself might well have approved if the issue had been discussed in his time. As a minor gloss, it does not deserve a particularly large measure of publicity. The reason it has in fact received such publicity, and why I have felt obliged to devote a whole chapter of this book to it, is simply that the theory has been sold — oversold by some journalists — as if it were radically opposed to the views of Darwin and his successors. Why has this happened?

There are people in the world who desperately want not to have to believe in Darwinism. They seem to fall into three main classes. First, there are those who, for religious reasons, want evolution itself to be untrue. Second, there are those who have no reason to deny that evolution has happened but who, often for political or ideological reasons, find Darwin's theory of its *mechanism* distasteful. Of these, some find the idea of natural selection unacceptably harsh and ruthless; others confuse natural selection with randomness, and hence 'meaninglessness', which offends their dignity; yet others confuse Darwinism with Social Darwinism, which has racist and other disagreeable overtones. Third, there are people, including many working

in what they call (often as a singular noun) 'the media', who just like seeing applegarts upset, perhaps because it makes good journalistic copy; and Darwinism has become sufficiently established and respectable to be a tempting applegart.

Whatever the motive, the consequence is that if a reputable scholar breathes so much as a hint of criticism of some detail of current Darwinian theory, the fact is eagerly seized on and blown up out of all proportion. So strong is this eagerness, it is as though there were a powerful amplifier, with a finely tuned microphone selectively listening out for anything that sounds the tiniest bit like opposition to Darwinism. This is most unfortunate, for serious argument and criticism is a vitally important part of any science, and it would be tragic if scholars felt the need to muzzle themselves because of the microphones. Needless to say the amplifier, though powerful, is not hi-fi: there is plenty of distortion! A scientist who cautiously whispers some slight misgiving about a current nuance of Darwinism is liable to hear his distorted and barely recognizable words booming and echoing out through the eagerly waiting loudspeakers.

Eldredge and Gould don't whisper, they shout, with eloquence and power! What they shout is often pretty subtle, but the message that gets across is that something is wrong with Darwinism. Hallelujah, 'the scientists' said it themselves! The editor of *Biblical Creation* has written:

it is undeniable that the credibility of our religious and scientific position has been greatly strengthened by the recent lapse in neo-Darwinian morale. And this is something we must exploit to the full.

Eldredge and Gould have both been doughty champions in the fight against redneck creationism. They have shouted their complaints at the misuse of their own words, only to find that, for *this* part of their message, the microphones suddenly went dead on them. I can sympathize, for I have had a similar experience with a different set of microphones, in this case politically rather than religiously tuned.

What needs to be said now, loud and clear, is the truth: that the theory of punctuated equilibrium lies firmly within the neo-Darwinian synthesis. It always did. It will take time to undo the damage wrought by the overblown rhetoric, but it will be undone. The theory of punctuated equilibrium will come to be seen in proportion, as an interesting but minor wrinkle on the surface of neo-Darwinian theory. It certainly provides no basis for any 'lapse in neo-Darwinian morale', and no basis whatever for Gould to claim that (the synthetic theory [another name for neo-Darwinism]) 'is effectively dead'. It is as if the discovery that the Earth is not a perfect

sphere but a slightly flattened spheroid were given banner treatment under the headline:

COPERNICUS WRONG. FLAT EARTH THEORY VINDICATED.

But, to be fair, Gould's remark was aimed not so much at the alleged 'gradualism' of the Darwinian synthesis as at another of its claims. This is the claim, which Eldredge and Gould dispute, that all evolution, even on the grandest geological timescale, is an extrapolation of events that take place within populations or species. They believe that there is a higher form of selection which they call 'species selection'. I am deferring this topic to the next chapter. The next chapter is also the place to deal with another school of biologists who, on equally flimsy grounds, have in some cases been passed off as anti-Darwinian, the so-called 'transformed cladists'. These belong within the general field of taxonomy, the science of classification.