Charles Darwin has had more impact on biological sciences, and society generally, than any other 19th century biologist but his ‘modus operandi’ as a scientist is poorly known, and often seriously misunderstood. Three important aspects of his reasoning – his hypothetico-deductive approach, his search for mechanisms to explain past events, and his insistence on continuity between humans and a common ancestor with apes – are discussed here. His autobiography and letters show that he worked explicitly in the hypothetico-deductive model, and included statements that theories were essential even to know what data to collect; to hold theories only as hypotheses; and the necessity to search for data that contradict a cherished theory. He built upon the very mechanistic geological tradition of James Hutton and Charles Lyell, and thus brought into historical biology the search for mechanisms that could be studied in the present in order to explain events in the past. His prediction of continuity, including in mental powers, between humans and a common ancestor with apes is only now coming to fruition. It is important to evolutionists, especially in teaching or interacting with the public, that Darwin’s mode of working is better known.

The work of Charles Darwin is intensely interesting for scientists concerned with innovative science and/or understanding the testability of evolutionary theories. These are important scientific questions but also help in both education and involving the public in discussion of the implications of evolution. In many areas of science, major theories have been followed by many subsidiary developments and improvements, but in evolution there was little major development in theory from 1859, when the *Origin of Species* (Darwin 1859) was published, until the new synthesis in the 1930s onwards (Mayr & Provine 1980; Bowler 1983). Consequently it is natural to ask: Was there something about Charles Darwin’s thinking/reasoning/knowledge that led him to be so innovative in his thinking about evolutionary biology?

Perhaps the apparent complexity of Darwin’s overall theory (Penny 2009a) is one reason why, qualitatively, his thinking was not surpassed until the 1930s. In that publication I analyse the theory into 20 (simple and testable) components, but we have also found it useful (Riddiford & Penny 1984) to consider three major aspects:

- The microevolutionary processes that can be studied in the present (Figure 1, Part A, summarised as ‘natural selection’);
- Macroevolution in referring to Darwin’s theory of descent with modification (Figure 1, Part B); and
- The Darwinian hypothesis (Part C) that the processes of microevolution are sufficient to fully account for macro-evolution.

There are other ways to analyse Darwin’s theory; Mayr (1985) considered it as five theories. What is important is that the overall theory and its implications appear complex [sic], even if the individual ideas are both relatively simple and testable. The second aspect in the figure, that evolution has occurred and continues to occur, was accepted by most biologists within a decade of the publication of the *Origin of Species* (Hull et al. 1978). However, the many sub-processes of microevolution were not accepted as a necessary part of the mechanism until the ‘new Synthesis’ of evolution and population genetics (Mayr

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**Figure 1. Three main components of Darwin’s theory. They are mutually supporting in that, for example, the theory of descent is supported by the existence of a mechanism that could lead to species modification and divergence; but the theory of descent also leads to a search for mechanisms that would result in descent with modification. Hypothesis 3 is the one still being debated (based on Riddiford & Penny 1984).**

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& Provine 1980). However, there have still been doubts, especially in relation to the origin of humans, that the processes of microevolution were sufficient for macroevolution.

It is important that the conclusions about the Darwinian reasoning be presented in a way relevant to scientists, and it will help them interpreting evolution to others. The three main themes considered here are Darwin’s explicit use of hypotheses for testing (conjectures and falsification, or hypothetico-deductive reasoning); his geological background leading him to search for mechanisms acting in the present that could explain events in the distant past; and his prediction of continuity (including mental powers) between humans and a common ancestor with apes. Taken together, it is hoped that the analysis presented here (and based on Penny 2009b) will help scientists in their own work and in presenting evolution to others.

Hypothetico-deductive reasoning

There has often been an assumption that Darwin simply collected data, and almost ‘stumbled’ across his theory. Nothing could be further from reality, but the conclusion is often based on a well known quote in his autobiography (Darwin 1969) taken out of context. The whole statement is given below, but the part in bold is usually quoted. It is perhaps best to read the part in bold first, and then to go back and read the whole extract.

It was evident that facts such as these, as well as many others, could be explained on the supposition that species gradually became modified; and the subject haunted me. But it was equally evident to me that neither the action of the surrounding conditions, nor the will of the organisms (especially in the case of plants), could account … I had always been much struck by such adaptations, and until these could be explained it seemed to me almost useless to endeavour to prove by indirect evidence that species had been modified.

After my return to England it appeared to me that … by collecting all facts which bore in any way on the variation of animals and plants under domestication and [in] nature, some light might perhaps be thrown on the whole subject.

My first note-book was opened in July 1837. I worked on true Baconian principles, and without any theory collected facts on a wholesale scale, more especially with respect to domesticated productions, by printed enquiries, by conversation with skilful breeders and gardeners, and by extensive reading (p. 118–119, emphasis added).

Thus the full quotation gives a very different picture from just the portion in bold. It is clear that the hypothesis that species gradually became modified (evolution) was ‘haunting’ Darwin. The extract shows six main points.

- concluded that continued and gradual evolution of species was possible (and likely),
- rejected Plato’s concept of an ‘unchangeable essence’ for species,
- started searching for a mechanism to explain adaptations,
- rejected the direct ‘action of the environment’ as a potential mechanism,
- rejected the ‘will of the organism’ as a potential mechanism, and
- focused on variation within species and on artificial selection for mechanisms.

Thus he had already identified the question, rejected two potential mechanisms, and was focusing on both natural variation and plant and animal breeding for ideas about mechanisms. He had already rejected the nemesis of many (but certainly not all) earlier biologists – namely, that each species had an unchangeable ‘form’ or ‘essence’ – a philosophical concept from Plato and Aristotle that appears to have entered biology by the early 18th century. If ‘species’ really did have an ‘unchangeable essence’, then any continued change (virtually by definition) was impossible. Thus the full quotation is very informative about Darwin’s thinking at the time of starting his Notebooks, and certainly shows a far more sophisticated reasoning than just ‘collecting factlets’.

Indeed, on the very next page of his autobiography, after further reading, we find the opening quotation from his autobiography: Here, then, I had at last got a theory by which to work (p. 120). That statement is worth reading again: ‘I had at last got a theory by which to work’. Darwin was certainly not suggesting in the earlier extract that ‘collecting facts’ was sufficient for a scientist; rather he was bemoaning that ‘not having a theory by which to work’ he was reduced to collecting facts (as well as reading widely). However, even in his reading he had narrowed down the area (natural variation, and artificial selection) where he was looking for information.

The hypothetico-deductive method is now often associated with Karl Popper from the mid 20th century (e.g. Popper 1972). However, as mentioned above, the ingredients of good science were actively discussed 100 years earlier, including William Whewell’s advocacy of using different lines of evidence to support a theory, his ‘consilience of induction’. The conclusion that Darwin worked in a hypothetic-deductive mode is similar to that of Ayala (2009), though our interpretation of the main extract differs slightly.

The extent of Darwin’s commitment to predictions and testing is discussed elsewhere (Penny 2009b), but a couple of quotations from his autobiography (Darwin 1969) help reinforce the conclusion. For example: I had, also, during many years, followed a golden rule, namely, that whenever a published fact, a new observation or thought came across me, which was opposed to my general results, to make a memorandum of it without fail and at once; for I had found by experience that such facts and thoughts were far more apt to escape from the memory than favourable ones. Owing to this habit, very few objections were raised against my views which I had not at least noticed and attempted to answer (p. 123). A similar quotation is: I have steadily endeavoured to keep my mind free, so as to give up any hypothesis, however much beloved (and I cannot resist forming one on every subject), as soon as facts are shown to be opposed to it. (p. 141).

Darwin’s autobiography was mostly written nearly 20 years after the Origin of Species was published. However, it was not just Darwin being ‘wise after the event’; writings from earlier periods show similar statements. The following are from 1856 to 1857. To one correspondent he wrote: My determination to put difficulties, as far as I can see them, on both sides is a great aid to candour: because I console myself, when finding some great difficulty, in endeavouring to put it as forcibly as I
can (p. 80–81). Another letter includes both falsifiability and testing aspects of theories: You say most truly about multiple creations & my notions; if any one case could be proved I should be smashed: but as I am writing my Book, I try to take as much pains as possible to give the strongest cases opposed to me, ... (p. 178). Later again: It is my intention to give fully all the facts in favour of the eternal immutability of species & I have taken as much pains to collect them, as I possibly could do (p. 236). (All extracts are from Burkhardt & Smith 1990.)

The Origin of Species itself has the powerful statement: 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. (Darwin 1859, p. 189). ‘My theory would absolutely break down’ is another example of how he considered his theory to be falsifiable – and therefore scientific. It is worth noting here that there is nothing in the above statement that assumes equal rates of change, just ‘numerous successive slight modifications’ – there is certainly no ‘phyletic gradualism’ in that statement.

Thus it is clear that Darwin was consciously aware of the importance of theories, and the testing of theories, even while he was still developing his theory of evolution by natural selection. Not only did Darwin consciously work in a hypothetico-deductive model but he also sought evidence that could potentially falsify his hypotheses. From the modern viewpoint it is difficult to imagine any scientist in the 19th century being more ‘Popperian’, although that approach has a long history in science – there is nothing to limit it to the 20th century.

Geology and mechanisms for explaining the past

The next question is the source of Charles Darwin’s very mechanistic approach to historical biology – his searching for mechanisms that might explain past biology. We saw in the earlier extract that, even by the time he started his notebooks, he was looking toward domestication and to plant and animal breeders for ideas on the processes that might be involved. In the 1830s there was already a healthy debate within geology (Rudwick 2008) on the extent that past geological events could be explained by mechanisms that can be studied in the present. The largest single influence on developing Darwin’s search for mechanisms was Charles Lyell (1797–1875) and his Principles of Geology (Lyell 1830–33), and during the voyage of the Beagle he had the opportunity of evaluating Lyell’s approach. Lyell’s subtitle in the first edition (An attempt to explain the former changes of the earth’s surface, by reference to causes now in operation) puts his mechanistic approach right into the front page of his work. Lyell himself followed another earlier Scottish geologist, James Hutton (1726–1797); both advocated studying mechanisms that could potentially explain geological events that had occurred in the past – they were mechanistic rather than descriptive.

For several years after the voyage of the Beagle (1831–35) Darwin primarily considered himself a geologist (Herbert 2005), rather than a biologist. The following six points support this:

- His letters during the voyage of the Beagle show confidence on geological subjects, but show concern about the inadequacy of his biological collecting (Sulloway 1985).
- Some of his geological letters had already been published before his return from the voyage (Barrett 1977).
- On his return from the voyage he joined the Geological Society of London (rather than the Linnean or Zoological Societies) and was an active participant in this Society. He presented papers, published in its journal, was elected to its Council, and became its Foreign Secretary.
- Darwin’s early papers were almost exclusively on geology (see Barrett 1977; Penny 2009b).
- Soon after the return of the Beagle he became a close associate of the leading geologist, Charles Lyell, and was a frequent visitor to his London home.

Indeed, Darwin published little on biological topics until the 1850s (though he was working on subjects such as barnacles, fertilisation of orchids, pigeon breeding, climbing plants, different forms of flowers in the same species, and earthworms). However, the outline of his evolutionary theory, with its search for mechanisms that would lead to change, was developed in 1838, and he wrote extensive ‘Abstracts’ in 1842 and 1844.

To the young Darwin, being a geologist was not as restricting as we might think today, given our higher specialisation within science. Lyell’s Principles of Geology was in three volumes, and the second was mainly on biological factors that might help understanding of, for example, the reduced rate of erosion resulting from the presence of plant cover. Lyell’s second volume considered the stability of species and, until recently, had probably the most detailed account in English of Lamarck’s evolutionary theory (which Lyell certainly rejected). The rest of the volume discusses biogeography, mechanisms of dispersal of plants and animals, the potential for increase in population numbers, the regulation of population numbers, estimates of the rates at which species became extinct, etc. Indeed these are important precursors to much of Darwin’s reasoning in transferring the mechanistic approach of Lyell from Geology into Biology – even though at the time Lyell rejected evolution. Lyell’s understanding of ecology and biology was strongly influenced by the Swiss botanist Augustin de Candolle.

The influence of de Candolle can be seen in many extracts from Lyell: … the most fertile variety would always, in the end, prevail over the more sterile (p. 34); Unhealthy plants are the first which are cut off by the causes prejudicial to the species, being usually stifled by more vigorous individuals of their own kind. … In the universal struggle for existence, the right of the strongest eventually prevails (p. 55–56); All plants of a given country … are at war; one with another. The first which establish themselves by chance in a particular spot, tend … to exclude other species, the greater choke the smaller, the longest livers … the more prolific. In this continual strife, it is not always the resources of the plant itself… Its success depends, in a great measure, on the number of its foes and allies among the animals and plants inhabiting the same region (p. 131). (All quotes are from volume 2 of Lyell 1830–33)

These extracts, including intra- and inter-specific competition and the universal struggle for existence, are taken out of
so, and Lyell assumes a ‘Balance of Nature’. However, a student of Lyell would have found several precursors of Darwin’s mechanism for biological evolution within Lyell’s Principles of Geology. Darwin certainly went well beyond Lyell’s reasoning; three examples are: his acceptance of evolution, his move away from a deterministic science (accepting stochastic factors), and his elimination of purpose (or ultimate causes) from science.

It was accepted at the time that Lyell was strongly influenced by the approach of the earlier Scottish geologist, James Hutton. Both aimed to explain past geological events by mechanisms that could be studied in the present. It is in this sense that Darwin extended Lyell’s and Hutton’s mechanistic mode of reasoning from geology into historical biology, Hutton, too, carefully defined his approach to geology: how he was going to reason about unobserved geological events and processes – he was concerned about the ‘scientific method’. The following quotations are from his major geological treatise, Theory of the Earth (Hutton 1795). The first is a brief description of his approach with its requirement for searching for operations that actually exist in the modern world and which might account for changes in the past: But how shall we describe a process which nobody has seen performed, and of which no written history gives any account? ... first, ...; and, 2dly, In examineing the natural operations of the globe, in order to see if their now actually exist such operations, as, ... appear to have been necessary to their formation (p. 22, emphasis added). So we have to search for ‘natural operations of the globe’, the appropriate mechanisms.

Hutton made predictions from his theory of the earth, and sought to test these by experiments and observations. On the observational side he predicted an important cycle of uplift, erosion, deposition of new strata, and uplift again: ... when one day, walking in the beautiful valley above the town of Jedburgh, I was surprised with the appearance of vertical strata in the bed of the river, where I was certain that the banks were composed of horizontal strata. I was soon satisfied with regard to this phenomenon, and rejoiced at my good fortune in stumbling upon an object so interesting to the natural history of the earth, and which I had been long looking for in vain (p. 432, emphasis added). This was a discovery of an ‘unconformity’, where the two strata were formed at very different geological periods – with a period of uplift and erosion between the lower and the upper strata – just as Hutton had predicted.

He certainly recognised that his approach had hypotheses which he sought to test. For example: ... at present, I hold this opinion only as a conjecture (p. 442). And again: I have always conjectured that the waters of Giez[er ] [Iceland] must be impregnated with flinty material by means of an alkaline substance, and so expressed my opinion ... (p. 509); this was tested (and confirmed) when a traveller returned from Iceland with the samples for him to test. It is important to note that no claim was made that we knew all the mechanisms: ... there may be many causes of which we are as yet ignorant (p. 298). Thus we already see (in 1795) a strong emphasis on testing and hypotheses, combined with a search for mechanisms. Thus Hutton aimed at understanding the past in terms of processes that can be studied in the present, even though their knowledge of potential mechanisms was obviously very limited at the time.

Lyell had the advantage of another 35 years of research since Hutton, and was eventually able to persuade most geologists of the sufficiency (for geology) of mechanisms that could be studied in the present (the equivalent of Figure 1C for geology).

The conclusions that I draw from this section are as follows:

- It was significant that the young Darwin was a geologist – geology was a broader discipline than now, and included the biological effects on the physical environment.
- Both Hutton and Lyell were well aware of the need for conjecture, hypothesis, and testing, as well as measurement and experimentation in science.
- Both Hutton and Lyell sought to explain past events in geology by mechanisms that could be studied in the present (including biological effects on rates of erosion).
- Darwin’s insistence on a mechanism of evolution based on known causes is an application of Hutton’s and Lyell’s methods (including the necessity of a long time scale).
- Lyell (from de Candolle) already recognised competition in nature, and Darwin was already prepared for it when he read Malthus several years later.

Darwin’s attitude of searching for mechanisms seems largely set during the voyage of the Beagle when he convinced himself of the superiority of Lyell’s (and thus Hutton’s) approach of searching for mechanisms from the present that could help explain the past.

**Continuity to humans**

Perhaps the least accepted of Darwin’s claims in the 19th century was that humans had arisen by normal microevolutionary processes. As just one example, Darwin (1872) concluded (based on a very early use of questionnaires) that there were some human emotions and expressions that were ‘universal’ among humans. It is only in the last few decades (after 100 years of disbelief) that such conclusions are becoming accepted (see Jones 2009).

I will consider just two aspects here, genomics and recent work on mental powers of young children and young apes. The first, genomics, is relatively straightforward now that human and chimpanzee genomes (Mikkelsen et al. 2005) are available for comparison, and I have already commented (Penny 2004) that the genetic differences between the two species are all the standard types of microevolutionary changes that we would see within and between populations, and between varieties and sibling species. We find large numbers of single point mutations, many small insertions and deletions, differences in copy number of some genes, different transposable elements activated in the two species, one chromosome fusion, and so on (Figure 2).

Biologists need to stress this more strongly. That is, genetically, the human genome is derivable from a common ancestor with the apes by normal genetic processes. That is an amazing, powerful conclusion that should be taught in every school, and used in interactions with the public about evolution. Of course, there is a huge amount to learn about which genetic changes have effects (most genetic changes are expected to be neutral – ‘neither beneficial nor injurious’, in Darwin’s words). Some changes will be critical for our human-ness, but which ones?
In principle there were alternatives. We tell the students that it was possible that some ‘Kind Friendly Creator’ (the KFC model), or a group of itinerant space travellers (the Douglas Adams model) might have inserted into the human genome a whole lot of genes for wisdom and intelligence. Just think – we say a whole lot of new genes for wisdom and intelligence in the human genome; then, after the appropriate pause, we add that if that were true, all we would have to do now is find out how to turn those genes on! Yes, it is intended as a joke, but it has a very serious purpose: our human genome is derivable by normal microevolutionary processes – other possibilities are eliminated.

The second aspect here is the continuity of the human mind from a common ancestor with the Great Apes – there is no absolute and unbridgeable difference between the two. One aspect, certain general features of human expression preserved across cultures, has already been referred to (Jones 2009) – but there are many others. It has long been known (for example, Patterson & Linden 1981) that the Great Apes (chimps, gorillas and orang-utans) can be taught sign language. The mental abilities of apes are increased under environmentally rich conditions in captivity (Ijzendoorn et al. 2009), and some elaborate tool use is found in the wild (Boesch et al. 2009).

In the first few years of life, ‘mental’ abilities of the Great Apes are comparable with humans of the same age (Ijzendoorn et al. 2009), but then their increase in abilities appears to slow down – while young humans keep developing. Some classic morphological data (Figure 3) support this – both monkeys and apes seem to have a similar brain/body ratio during development – but in apes, and especially in humans, the juvenile phase with its continued brain growth just keeps on going. Thus basically we have similar genes, and similar brain/body growth early on, so we expect there to be many fundamental similarities. Certainly there are differences; humans are considered more co-operative than the other apes (Hirata 2009). But just as we accept the continuity of the human mind from early childhood into adulthood, the same applies to comparing the mental abilities of young apes and young humans. It was over 100 years from the time Darwin made his claim about the continuity from apes to humans, and it has only been the last few decades that the data have been available. Darwin’s claim was certainly a bold one, but modern work is supporting it – though we still have so much to learn.

Discussion

A conclusion from this study is that Charles Darwin worked in a way that is surprisingly consistent with the ideas of Karl Popper on how the best scientists work. This conclusion was not expected at the start of the study when Darwin was often considered a poor theoriser who simply collected a lot of data and just happened to be in the right place at the right time, and Popper was considered somewhat hostile to evolutionary theory as being unfalsifiable (Penny et al. 1982). Rather, we find Darwin as well aware of the philosophy of knowledge of his time, an excellent theoriser, well aware of the necessity of hypotheses, and perhaps even ahead of most scientists and philosophers of knowledge of his time in trying to falsify hypotheses. Then there is the aspect, borrowed from geology, of searching for the mechanisms that might explain past changes. Finally, there is the recent work on the continuity from ape ancestors to humans – it is now a very active area of work. This area again shows just how innovative the thinking of Darwin was (Dennett 2009).

Does the analysis here answer our initial question on why in several aspects Darwin was well ahead of his biological contemporaries? At best it is an incomplete answer, but I venture that it is an important part of an answer. His theoretical/mechanistic approach from his geological background was not shared generally by biologists seeking to understand the origins of biodiversity. Even today we find significant resistance to Darwin’s claim that the processes of microevolution are sufficient for all of macroevolution, especially for humans.

It is important that in our teaching of science we give our students a feeling for the excitement of science, the hypotheses,
counter-hypotheses, tests and failed tests, imagination, caution and critical analysis. We have seen that excellent science of proposing and testing hypothesis has been practised over many centuries, and that the search for mechanisms that can explain the past has been a focus over that time. Describing patterns in nature is useful, but without attempting to understand the underlying mechanisms leading patterns we are very limited. Perhaps, for example, the teaching of evolution today focuses too much on the description of patterns and relationships, and still needs to get more to the underlying mechanisms. Integrating micro- and macro-evolution is still a key issue.

In an evolutionary theory of knowledge we must emphasise the importance of our current knowledge as our building blocks but must also discuss the unsolved questions. I hope that examples of great scientists testing and rejecting their own hypotheses, and searching for mechanisms, will help the education of the next generation of scientists. Will they be able to answer Darwin’s claim, and demonstrate the sufficiency of microevolutionary processes for macroevolution, including for humans?

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