



Darwin's changing views on evolution: from centres of origin and teleology to vicariance and incomplete lineage sorting

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ABSTRACT

It is a strange fact that in many ways the first edition of Charles Darwin's *Origin of Species* is closer to modern neodarwinism than the sixth and last edition. Sometimes this is attributed to a decline in the quality of the argument, but the opposite interpretation is given here. It is suggested that Darwin's early work on evolution is naïve and based on the two creationist principles of centre of origin and teleology (panselctionism). This fusion later became the 'modern synthesis'. However, after the first edition of the *Origin*, Darwin developed a non-teleological synthesis that integrated natural selection with what he called 'laws of growth' – phylogenetic/morphogenetic trends or tendencies. Discussion of Darwin's later, more sophisticated model of evolution has been suppressed in the teleological modern synthesis, but similar ideas are re-emerging in current work on molecular phylogenetics and biogeography. This indicates that the ancestor of a group can be diverse in its morphology and its ecology, that this diversity can be inherited, and that groups usually originate over a broad region and not at a single point.

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INTRODUCTION

There are two evolutionary concepts that are familiar to all biologists as well as to the general public. First, in biogeography, taxa start at a centre of origin and disperse from there. Second, in morphology, structures have evolved in order to supply the needs of the organism and have often become exquisitely adapted for different purposes. These two concepts make up a model of evolution, the 'modern synthesis', which describes the evolution of form (by improved design) and evolution in time and space (by dispersal).

The evolution of a clade can be considered in terms of the *geographical space* it occupies through time, including its original area and subsequent modifications. Darwin (1859) proposed that a new species evolves at a localized centre and attains its distribution by dispersal from there. A group's evolution can also be discussed with reference to *morphological space*, with 'morphology' taken here to include both molecular and macroscopic structure. In Darwin's view, the ancestor of any group was a single individual, parent pair or species and was, above all, morphologically uniform. From this 'point' the

descendants evolved new forms to result in, say, a diverse genus occupying a broad sector of morphological space.

In this view, the biogeographical and morphological centres of origin are both always points. After arising in this way, a new species is 'wedged' (to use Darwin's term) into a new geographical space through dispersal, and into a new morphological and ecological space through adaptation and natural selection. The processes occur together, and evolutionary development comprises radiations away from centres.

An alternative view of evolution in space, supported here, involves vicariance. Here there is no point centre of origin in geographical space because new taxa evolve by the differentiation or splitting of widespread ancestors. The origin of new taxa does not involve movement, but rather the cessation of movement, and differentiation takes place *in situ*, over a wide area. For example, consider a genus comprising one species in the east of a continent and one in the west, with the two meeting in the middle. In dispersal theory, each species originated at an independent point and spread out by dispersal from there, eventually meeting the other species. In vicariance, a widespread ancestor split down the middle, and the mutual boundary of the

species represents this fracture. Each species evolved over a broad front and does not have a 'centre of origin'.

An alternative view of evolution in form, supported here, is emerging in molecular studies. Earlier morphological analyses showed incongruent character trees, and these were interpreted as evidence for ancestors being polymorphic. In the last few years, molecular analyses have begun to sequence more than one gene in studied taxa and often the genes have incongruent phylogenies. As with morphology, this suggests that the ancestor was polymorphic, with the polymorphism retained and recombined in the descendants. The taxa are not defined by unique novelties and the effect is similar to that produced by ancient hybridism. The process, termed 'incomplete lineage sorting' by geneticists, is well known in primates, *Drosophila* and many other taxa (Salem *et al.*, 2003; Pollard *et al.*, 2006; Wiens, 2008; Knowles & Chan, 2008). It is predicted to be most important in widespread, more or less sessile ancestral complexes in which evolution is rapid, and this may be a common situation. In evolution by incomplete lineage sorting there are no point centres of origin in morphological space, as the ancestor was not uniform and the polymorphism (with its geography) is retained in the modern descendants. Parallelism is often explained as the result of adaptation to local ecology. However, in most cases, such as the similarities in the teeth of some lemurs and rodents or the similar brain–eye systems of primates and fruitbats, this is not convincing. Widespread, diverse ancestors, rapid evolution, and retention of ancestral polymorphism are more likely to be the cause.

CENTRES OF ORIGIN IN BIOGEOGRAPHY

Darwin wrote:

It is obvious that the individuals of the same species... must have proceeded from *one spot*, where their parents were first produced... Undoubtedly there are many cases of extreme difficulty in understanding how the same species could possibly have migrated from some *one point* to the several distant and isolated points, where now found. Nevertheless the simplicity of the view that each species was first produced within a *single region* captivates the mind. He who rejects it, rejects the vera causa of ordinary generation with subsequent migration, and calls in the agency of a miracle.

(Darwin, 1859, p. 352, italics added)

In this view, a species has a single centre of origin and migrates from there, just as an individual organism does. Each species had its own independent centre, unlike the case for vicariance theory, in which new species come into existence together with at least one other.

The year after the *Origin of Species* was published, Hooker expressed reservations regarding Darwin's concepts of centre and origin. He wrote that the 'points of affinity' between the floras of Australia and New Zealand are

so numerous and decided as to render the dissimilarities all the more singular... under whatever aspect I regard the flora of Australia and New Zealand, I find all attempts to theorise on the possible causes of their community of feature frustrated by anomalies in distribution such as I believe no two other similarly situated countries in the globe present... Everywhere else I recognise a parallelism or harmony in the main common features of

contiguous floras, which conveys the impression of their generic affinity at least being effected by migration from centres of dispersion in one of them, or in some adjacent country. In this case it is widely different.

(Hooker, 1860, p. lxxxviii)

Hooker, unlike Darwin, envisaged the pattern originating by vicariance, not by dispersal from a centre of origin.

The American ecologist Frederic Clements was more forthright than Hooker and noted that Darwin's (1859) assumption that species evolved at one spot 'seems to be little more than inheritance from the special creationists' (Clements, 1909, p. 145; Gadow, 1909, p. 326, made a similar observation). Darwin, trying to bring in the idea of evolution, appealed to what he thought was a 'captivating' argument: species are like individuals and originate at a single point. However, this is an old concept of the mediaeval Church, which interpreted the Eden story as a development in history, with a centre of origin and a dispersal event by a morphologically uniform parent-pair ancestor. In his later years, Darwin admitted the influence of creationism on his earlier work, writing that 'I was not... able to annul the influence of my former belief, then almost universal, that each species had been purposely created...' (Darwin, 1888, p. 61; see also Llorente *et al.*, 2001, on the garden of Eden and the centre of origin).

In the passage quoted at the start of this section, Darwin (1859) acknowledged that the means of dispersal in many taxa seem insufficient to explain the distributions, and that this constitutes an 'extreme difficulty' for the dispersal model. Most authors have ignored the problem and many continue to propose dispersal events for which there is no known analogue in the current ecology. For example, it is still widely believed that primates rafted across vast areas of open ocean (Fleagle, 1999), although this has never been observed (Stankiewicz *et al.*, 2006, and Masters *et al.*, 2007, have provided good critiques). Biologists have come to accept the idea that distribution and dispersal are often mysterious and paradoxical. Another serious problem is represented by the many taxa in which the 'means of dispersal' are *too* effective. Given the vast extent of geological time and the powers of movement that all taxa have, all species, even those with rather poor means of dispersal, should occur throughout the world, at least in areas of suitable ecology. However, they hardly ever do. Molecular studies indicate that regional and local endemism is the rule in all groups, despite, not because of, the movement in communities.

Many biologists, such as Huxley, Hooker and Clements, rejected the centre of origin and this led to an early flowering of what would later be called vicariance biogeography. By the close of the 19th century, biologists had described most of the genera in groups such as birds and mammals and were well aware of the main biogeographical patterns. Distributions in the Southern Hemisphere were explained in terms of more or less simultaneous biological and geological breaks (cf. Hooker on the flora; Huxley and F.W. Hutton of New Zealand on the fauna). Many of the modern groups were known by fossils to be Mesozoic, or assumed to be so from the fossil record of relatives. T.H. Huxley

grouped the mammals into Prototheria, Metatheria and Eutheria, and proposed that major geological changes in the Mesozoic, especially in the Pacific region, had led to their differentiation and biogeography. A.E. Ortmann of the Carnegie Museum in Pittsburgh gave a similar account for Crustacea and stressed that the aim of zoogeography was to explain the geological evolution of faunas. C.H. Eigenmann of Indiana University related the rise of the Andes to vicariance in freshwater fishes. Knud Andersen of the British Museum produced vicariance analyses of bats in work that is still widely used.

This research programme came to a halt with the First World War and the death of pioneers such as Andersen: there seems to have been a loss of intellectual will or nerve, and research on vicariance ceased. Authors returned to the older, easier ideas of centres, origins, and chance dispersal over familiar, modern geography. These were the ideas that Darwin had supported half a century earlier in his first synthesis. Matthew (1915) represented a revival of this Victorian view and included a critique of the vicariance biogeographers. Instead of focusing on tectonics, Matthew concentrated on locating the oldest fossils and deducing phylogenies, centres of origin and dispersal routes. Any tectonic changes were regarded as too old to be relevant for biogeography; instead, changes in Cenozoic climate and sea level were proposed as the drivers of evolution.

The requirement for massive amounts of dispersal in the Darwin–Matthew model follows from accepting a point centre of origin: 'It is evident that [Darwin's] position in regard to single origin caused him to turn to migration as the necessary solution of all the problems of distribution' (Clements, 1909, p. 146). Despite the fundamental importance of the centre of origin, there does not appear to be any account devoted to the concept that concludes in its favour. This may indicate that the idea is the 'hard core' of the dispersalist research programme and so is protected from any examination. McDowall (2004, p. 347) wrote that centres of origin were 'certainly of interest' and 'this is because whatever were the causal mechanisms generating species distributions, the overall patterns we observe are the accumulation of the individual patterns'. But this avoids the issue of whether or not centres of origin exist. One detailed analysis by a palaeontologist concluded that data from living and fossil groups in Europe 'refute the applicability of the centre of origin concept' (López Martínez, 2003, p. 504). (Note that human-mediated introductions and hybrids, such as the well-known grass *Spartina anglica*, are not considered here.)

CENTRES OF ORIGIN IN ECOLOGY

Taxa that occur in more than one habitat type are often assumed to have originated in one habitat and from there colonized new habitat. A new habitat, such as a landslide, is colonized. However, in many cases the different habitats and the taxa in them may have evolved together, by differentiation, as in geographical vicariance. For example, in dispersal theory mountain ranges first rise and are then colonized by suitable

taxa. However, it is now thought that ranges such as the Andes rose together with the populations already in the area before any orogenesis, and that the montane flora and fauna evolved by passive uplift (Croizat, 1976; Craw *et al.*, 1999; Ribas *et al.*, 2007; Thomas *et al.*, 2008). Here there is no empty niche or dispersal, only *in situ* evolution.

Current attempts to integrate ecology and phylogeny still interpret a phylogenetic tree in terms of centres of origin and dispersal. For example, a pattern: [tropical America (tropical America + temperate North America)] is assumed to indicate dispersal from tropical America to temperate North America (Wiens & Donoghue, 2004). Instead, this pattern can, and probably often does, indicate vicariance within a widespread American ancestor. This produced three allopatric taxa – two in tropical America, one in North America – followed by secondary overlap of the two southern clades (in practice, overlap is generally far from complete). In the general case, a phylogenetic tree with all the basal clades in the tropics has been interpreted as support for a centre of origin in the tropics, with the branches indicating paths of dispersal (Wiens & Donoghue, 2004, figure 1). However, the tree can also represent a sequence of differentiation in an already global ancestor.

A remarkable map of phylogenetic structure in the American bird fauna showed that local faunas through all Latin America (from southernmost South America to southern Mexico) are dominated by members of basal clades (Hawkins *et al.*, 2006; figure 2). This trend is strongest in the Amazon basin and Patagonia. In contrast, avifaunas from a northern region centred on the Appalachians (central Mexico/Colorado, north-east to Newfoundland) are dominated by groups in less basal clades. This pattern could be interpreted as northward dispersal. Alternatively, it could result from differential extinction of basal clades in North America as a result of Cenozoic cooling or orogeny and changes in sedimentation there, but this is contradicted by the dominance of basal clades in Patagonia. Extinction has, of course, been widespread but may not have erased the underlying pattern. The third, most likely, possibility is that the phylogenetic structure again represents a sequence of differentiation in a pan-American ancestor, beginning in the south and moving north. The differentiation within American bird faunas shown by Hawkins *et al.* (2006) mainly occurs at a phylogenetic/geographical node in Mexico (cf. Heads, 2009), not between the tropics and the non-tropics. Hawkins *et al.* (2006) also show a minor centre of basal clade dominance in northern Alaska, indicating that North America has been 'invaded' by two separate waves of differentiation that passed through its avifauna, one from the north-west and one from the south.

CENTRES OF ORIGIN IN FORM (MORPHOLOGY AND MOLECULES): ADAPTATION AND TELEOLOGY

In Darwin's early view, a new species moves out from its centre of origin into the world just as an individual does, making

space for itself and outcompeting others. Adaptations such as hands, eyes, or whatever, develop for this purpose. The reason for the evolution of eyes, for example, may seem obvious – they are for seeing; that is their purpose and why they exist. However, explaining the presence of the eyes by appealing to their ability to see involves citing an effect (an end, or *telos*) to explain a cause and is simply not logical. Astronomers do not talk about the purpose of Jupiter's moons and physicists do not discuss what gravity or hydrogen could be for. The evolution of eyes has nothing to do with the fact that they ended up seeing, and, in its unconscious teleology, modern biology reveals its ancient affinity with mediaeval scholasticism rather than with modern (Renaissance) science. School children and university students have learned for thousands of years that we have eyes so that we can see and that they are perfectly designed for that purpose. In fact, teleological reasoning is about the only thing all first-year biology students, everywhere, know about analysing organic structure: the *purpose* of lungs is to exchange gases, trees grow *in order to* reach the light, rabbits' teeth grow continuously *so that* they can feed on abrasive grasses and everything is for the best. Voltaire exposed the superficiality and naivety of this approach but modern biology has yet to accept his conclusions.

Laws of growth and morphological trends

In mammals, parallel evolution has led to unrelated clades of 'ant-eaters' in Africa and, above all, in Australasia and South America, in which the skull is highly reduced and almost tubular. In these animals, features such as the zygomatic arch have disappeared and the snout or rostrum forms a long tube with a minute mouth at the end. Owing to the great reduction of the jaws and the formation of the rostrum, it is no longer possible for these animals to feed in any other way than by evert and retracting their tongue, which just fits through the mouth. In a teleological explanation, the need for the ant-eating diet came first and led to selection for a longer, narrower, more fused rostrum, better for catching ants; the skull became tubular, the rostrum formed and the mouth almost closed over, all for the animals' own good. In a non-teleological explanation, prior structural trends in the evolution of the vertebrate skull (mainly reduction and fusion, especially in the pharynx and jaws; cf. Sidor, 2001, 2003) led to the tubular rostrum. With its evolution, the ant-eater had no choice but to change to a diet of ants and worms, and the structure determined the function. Any further reduction will lead to extinction. Likewise, the long neck of the giraffe is not a marvellous adaptation for feeding on high branches: the neck grew longer and so the giraffe was forced to feed higher up.

In primates, Szalay & Delson (1979, p. 1) argued that evolution consists of 'a molding of... structure... for various biological roles...' and that 'Most evolutionary changes in teeth are the result of selective forces derived from a specific dietary regime' (p. 11). This is very close to Lamarckism: morphological features are accounted for in terms of their

'role', and the structure of teeth is caused by diet, rather than vice versa. The focus is on understanding the particular group in terms of its own ecology rather than in terms of broader structural trends.

Average social group size in primates is directly related to the degree of neocortex development (Fleagle, 1999). In one school of thought, brain size is driven by social interactions, but, instead, increasing social interactions are probably driven by increasing brain size; complex social interactions are impossible without the ability to remember individuals but with this ability become virtually inevitable. Another theory holds that neocortex evolution in primates was originally for remembering food trees, but all the functions of the neocortex are epiphenomena determined by its structure, which itself is determined by broader trends in encephalization found throughout birds and mammals, the 'higher' vertebrates.

Consider a standard phylogenetic reduction series in a hypothetical organ: (1) a complex, branched gamete- or spore-producing structure, (2) a sterile, spiniferous organ, (3) a glandular emergence producing a secretion, such as a physiologically active substance, nutritive substance or a poison, (4) a simple, non-glandular emergence, and (5) a blotch of colour, a single layer of pigmented cells. A teleologist would concentrate on the adaptations of the individual stages, and what the structure at a particular point in history does (what it is 'good for'). These functions may be, with respect to the stages described: (1) reproduction, (2) defence, (3) internal physiology, nutrition of offspring, or defence, (4) nothing, and (5) attracting mates or pollinators. This static, morphological approach is important for the description of current ecology. However, as an interpretation of evolutionary morphogenesis it fails because it misses the most important fact, namely that the series conforms to a single trajectory of reduction. This trend is likely to be under the control of a simple genetic variation, playing itself out over tens of millions of years and countless taxa.

In all these examples, characters and taxa show general, parallel tendencies to evolve in certain ways rather than in others. Darwin's insightful later work (e.g. Darwin, 1875, 1888) stressed the primary importance of these trends, which he termed 'laws of growth', rather than morphological centres of origin and selection. Some of the most significant trends in evolution are reductions, fusions and the suppression of parts. This is seen, for example, in the telescoping and condensation that has led to the modern vertebrate skull and the angiosperm flower. These morphogenetic reduction series often involve changes in basic symmetry that follow standard sequences. For example, in plants the shoot has been reduced from a complex system with many parts and high orders of symmetry. Parallel reduction has led to many unrelated species, such as oaks and coconut palm, having leaves arranged in cycles of five, with the sixth leaf standing above the first. This pentaradial symmetry, first noticed by Leonardo da Vinci at the dawn of modern biology, is already quite simplified and one of the last members of a reduction series (the ultimate, minimal symmetries are

trilateral and bilateral). Reduction and fusion in the vertebrate limb have led to more or less bilateral structure with a trace of pentaradial symmetry, and limb reduction has continued further in sirenians and whales, to the point where the animals can no longer function on land and have been forced by their structure to live in water.

Recent work in morphology and palaeontology has stressed 'trends' (Sidor, 2001, 2003), 'tendencies' (Frohlich, 2006; Douglas & Manos, 2007) and 'iterative themes' (Rudall, 2003). In discussions on the evolution of diversity, many authors now emphasize prior aspects of the genome or the 'developmental-genetic architecture' that predispose it to evolve in certain ways and not others, rather than natural selection of advantageous traits and better-designed features (Burns *et al.*, 2002). This intrinsic, clade-specific 'propensity' (Lovette *et al.*, 2002; Davies *et al.*, 2004) is discussed in developmental genetics as 'evolvability' (Arthur, 2002) or 'tendency to evolve' (Frohlich, 2006).

Nothing important in biology happens just once. As Vermeij (2006, p. 1804) pointed out, 'Many events in the history of life are thought to be singular, that is, without parallels, analogs, or homologs in time and space...'. However, Vermeij (p. 1804) re-examined the appearance of major structural innovations of taxa in the fossil record and found that 'Claims of singularity are... not well supported by the available evidence'. He concluded that

The principle of parsimony, which in history mandates the simplest explanation of events and the fewest possible steps from initial state to observed outcomes, has made historical singularity both acceptable and expected. The metaphor of the evolutionary tree, with its single root and its many branches issuing from distinct, single nodes, further strengthens the expectation of unique phylogenetic events. But is uniqueness real, or is the appearance of historical singularity an artifact of retrospection and of sampling the inadequately preserved historical record?

(Vermeij, 2006, p. 1804)

History of teleology

Some writers have used laws (trends) to explain biological structure, whereas others have used teleology (Table 1). The earliest Greek philosophers were naturalists and materialists, and had made the breakthrough into science, explaining phenomena not with reference to the gods or teleology, but as the inevitable outcome of laws of nature. However, following the rise of Plato and Aristotle these views became unorthodox, heretical and finally illegal. Only after 15 centuries was the combined authority of the classics and the Church questioned by the sceptics of the Renaissance, the scientists. Bacon and Descartes banished teleology from science, Spinoza called it a refuge for ignorance.

For some reason, Hegel, the philosopher of nature, history, development and progress, is overlooked in most studies of evolution. However, the connection between Hegel's thinking and that of the early Darwin was discussed by Nietzsche, who recognized in both authors the teleology he rejected. (In contrast, Nietzsche wrote to a friend that he was 'amazed' and 'enchanted' to find that Spinoza, too, denied teleology;

Table 1 Protagonists for two traditions in western philosophy, defined by their use of teleology in biology (cf. Heads, 2005a).

Authors who favour teleology in biological explanation	Authors who favour non-teleological explanation in biology
	Pre-Platonic Greek philosophers: Empedocles 490–430 BC Democritus 460–370 BC
Plato 428–348 BC Aristotle 384–322 BC Hellenistic biologists: Erasistratus 304–250 BC Cicero 106–43 BC	Epicurus 341–270 BC Lucretius 99–55 BC
Medical writers: Galen 129–199 Plotinus 204–270 St Augustine 354–430 Mediaeval schools, churches and universities Scholastic philosophers: St Thomas Aquinas 1225–1274	[This view became unorthodox, heretical, and finally illegal]
	RENAISSANCE Bacon 1561–1626 Descartes 1596–1650 Spinoza 1632–1677 Voltaire 1694–1778 Hume 1711–1776 Goethe 1749–1832 Schopenhauer 1788–1860
Kant 1724–1804 Hegel 1770–1832 The younger (centre of origin) Darwin 1809–c. 1860.....	The older (laws of growth) Darwin c. 1860–1882 T.H. Huxley 1825–1895 Nietzsche 1844–1900 Croizat 1894–1982 'structural' morphologists: W. Troll 1897–1978
Wallace 1823–1913 J. Huxley 1887–1975 Simpson 1902–1984 Mayr 1904–2005	Gould 1941–2002
Modern schools and universities	

Kaufmann, 1971.) Nietzsche's critique of Darwinian evolution was expounded in many of his books and focused on teleology. The analysis is unsparing and very clear; teleology is exposed and ridiculed. Richardson (2004), a philosopher of science and a good neodarwinist has responded, insisting that Nietzsche's critique is 'a jumble of mistakes about Darwin and mistakes about biology' (p. 18) and even 'amateurishly wrong' (p. 21). But after this promising start Richardson could not produce a coherent argument, only the ludicrous claims that Nietzsche (1) did not mean what he said about Darwin, and (2) was himself a Darwinist without realizing it. (Forber, 2007 has written a rebuttal, if one is needed.) Grene & Depew's (2004) deeper analysis revealed the history: with the fall of the Roman Empire, a universal teleology of organic form derived from

Plato and Aristotle was 'the view inherited by the Scholastic philosophies of Judaism, Christianity and Islam'. Subsequently, it was assumed by the German Idealists and early evolutionists.

Darwin's two views on teleology

The official, modern view of evolution has adopted the ideas of the first edition of the *Origin of Species* rather than Darwin's mature ideas, as expressed in the sixth and last edition. What is the reason for this 'strange fact' (Dawkins, 2009)? Is Darwin's later work of a lower standard than his 1859 *Origin of Species*, or, as suggested here, on a much higher level? In his own origins, Darwin was a churchman and a teleologist, then an adaptationist (see Gotthelf, 1999, on Darwin and Aristotle). But as his knowledge of biology and laws of growth deepened, Darwin learned to avoid teleology. Through this process he left his background behind and evolved into a modern (Renaissance) scientist. Nevertheless, Darwin's later work has been ignored whereas his earlier arguments have been co-opted as support for teleology, panselctionism and centre of originism. The ideas in Darwin's books, letters and notebooks on teleology can be confusing, and Grene & Depew (2004, p. 208) suggested that Darwin was 'irredeemably ambiguous'. However, there is a trend in his work, and over time his main focus changed from centres of origin and teleology to laws of growth.

In an 1872 letter Darwin wrote:

It has been an error on my part, and a misfortune to me, that I did not largely discuss what I mean by laws of growth at an early period in some of my books. I have said something like this in my two new chapters in the last [i.e. sixth] edition of the *Origin*... Endless other changes in structure in successive species may, I believe, be accounted for by various complex laws of growth [without the aid of natural selection].

(Darwin & Seward, 1903, p. 343)

In this later, non-teleological synthesis, natural selection is no longer a primary force but only prunes what laws of growth (later interpreted as genetic predispositions and propensities) produce in the first place.

Discussing his earlier work, Darwin described: 'my tacit assumption that every detail of structure, excepting rudiments, was of some special, but unrecognized, service. Anyone with this assumption in his mind would naturally extend too far the action of natural selection...' (Darwin, 1888). Again, Darwin's later view is an embarrassment to the neodarwinists and is seldom discussed, but has direct relevance to contemporary views on 'trends' in morphology and developmental genetics.

The distinction between Wallace's crude panselctionism and the sophisticated synthesis of trends and selection that Darwin developed was obvious. Darwin's friend Romanes termed Wallace's theory 'neodarwinism', but 'palaeodarwinism' would have been more accurate, as Darwin himself soon left this simplistic view behind, with his shift away from adaptation and teleology towards structural analysis.

Current ideas on teleology

Ayala (2004, p. 65) argued that 'many features of organisms are teleological, a bird's wings are *for* flying; eyes are *for* seeing...' (italics in original). But this is only one way of looking at organic structure – the mediaeval, scholastic way, not the Renaissance, scientific way that Darwin started to employ after 1859. Ayala continued (p. 65): 'the wings of birds came about precisely because they permitted flying...'. Non-teleological science argues that flight was the result, not the cause, of the wings. Wings, and thus flight, developed because of prior structural tendencies in the vertebrate limb and thorax. Ayala imagined (p. 67): 'There was nothing in the constitution of the remote ancestors of birds that would necessitate the appearance of wings in their descendants.' Non-teleological science suggests that birds developed wings *because of* the genetic architecture and evolutionary predisposition of their ancestors.

Ruse's (2003, p. 8) book focused on a paradox: although teleological thinking and language 'would not be deemed appropriate in physics or chemistry', they 'fully permeate evolutionary biological science'. Even now 'we still go on using and seemingly needing this way of thinking'. Ruse is defending neodarwinism and teleology – hence the insinuation that all biologists are neodarwinists and use teleological language. However, this ignores Darwin's later work and also contemporary discussion in developmental genetics.

Ruse (2003, p. 33) argued that 'A rock may not have a purpose but an eye does. Eyes and hands do not just happen for no reason.' But nor do rocks. Ruse implies that the only reason for the evolution of the eye was its end purpose. Again, this overlooks morphological trends in phylogeny. Ruse (2003, p. 12) described the pre-Platonic philosophers' concept of 'natural law' as 'blind law, that is, pure chance without plan'. But he has misunderstood their position because, along with Aristotle and the creationists, he has accepted 'pure chance' and purpose as the only alternatives. So did the younger Darwin. However, Darwin's later version of evolution, like science in general, relies neither on teleology nor on 'pure chance', but explains particular cases with reference to general laws and regularities.

Mayr (1982), unlike Ruse, recognized that the teleology in biology was a serious problem. His solution was to suggest that the modern synthesis is not really teleological, and that it uses teleological language but not teleological thinking (Mayr, 1982). Ruse (2002, 2003) avoided using this weak argument and took a novel approach to the problem – he admitted that Darwin (1859) was teleological, but claimed that this was a good thing. This completely overlooks the epochal writings of Bacon and Hume, together with Darwin's own later synthesis.

Ruse (1989) denied suggestions that the use of teleology in biology might be a 'cause for concern'. Instead, he concluded that teleology should be 'cherished' as it is 'a vitally important tool for looking into the organic world' (Ruse, 2002, p. 47). 'Teleological thinking is important and powerful' and

teleological language is, in a phrase redolent of the high Middle Ages, 'perfectly pure and appropriate' (Ruse, 2002, p. 46).

Ruse (2002) based his analysis on the claim that organisms 'seem as if designed'. Laymen, TV show presenters, creationists and philosophers of science will all agree. However, many scientists – the non-teleological morphologists, physiologists and systematists active as a group since the 1500s, together with the modern molecular biologists – see things differently. Organic form does not look designed to these odd people. Rather than invoking the stale, mediaeval metaphors of perfect design and the wonders of adaptation, they explore structural trends, lineaments and repetitions in the evolution of genomes, organs and populations without any thought of purpose. Ruse (2002) argued that 'There is something distinctive about biological language, particularly evolutionary biological language. There one finds talk of "purposes" or "functions"...'. But this is not correct; nearly all human discourse is full of talk about purpose. It is the language of physics, chemistry and geology that is distinctive and unique, through its peculiar, unintuitive, scientific *absence* of any reference to purpose.

Critique of teleology

Gould & Lewontin's (1979) critique of teleology became one of the most cited papers ever published on evolution, but the ideas were regarded as unusual and in practice had little impact on the modern synthesis. However, mainstream biologists are now acknowledging problems with teleology. The editor of one journal, *Evolution and Development*, advised authors: 'be careful about using teleological words to describe biological entities' (Raff, 2005). This advice could also be given to school teachers. Raff warned that statements such as 'x is well-designed to do y' will be seized on by creationists. However, Bacon, Voltaire and the others all avoided teleological words and thinking, not because of the tactical reason that creationists might use them but because teleology is not valid in science.

True believers in teleology, including most philosophers of biology, proclaim that natural selection is 'the light and the way' and 'in the beginning, natural selection created genes' (Cronin, 2005). In contrast, a down-to-earth account by a practising scientist, a plant physiologist, suggested that teleological explanation 'bedevils' biology (Hanke, 2004). Hanke illustrated his point with some amusing teleology from students' exam scripts, but the message was serious enough. Cummins (2002, p. 170) concluded in a similar way: the 'cheap trick' of teleology amounts to 'a license to bypass the messy and difficult details'. Grene & Depew (2004, p. 321) emphasized that Cummins' aim was to 'nudge [neo-teleology] to a well deserved extinction' and they 'can only hope that he succeeds'.

THE MODERN EVOLUTIONARY SYNTHESIS: CENTRES OF ORIGIN AND TELEOLOGY

Matthew's (1915) centre of origin-dispersalism and R.A. Fisher's teleology and panselectionism were fused in Sir Julian

Huxley's work, the first recognizable version of the 'modern evolutionary synthesis' (Wells *et al.*, 1931; Huxley, 1942). Huxley, in contrast to his grandfather T.H. Huxley and to Darwin's later work, stressed natural selection as the main, if not sole, cause of evolution (Table 1). Huxley was a Fellow at Oxford University, an Oscar winner (for the first wildlife documentary), President of the London Zoological Society, founder of IUCN and WWF, the first director of UNESCO, and, after the Second World War, an international leader in biological science administration and education. His grandfather's penetrating analyses of evolution were totally suppressed in the modern synthesis, and T.H. Huxley is now remembered only as 'Darwin's bulldog'.

In America the modern synthesis was taken up and promulgated by Mayr and G.G. Simpson, Matthew's protégé (Jepsen *et al.*, 1949). Mayr brought founder dispersal and the founder effect to the modern synthesis. Simpson contributed the concepts of orthoselection, sweepstakes dispersal, biogeographical barriers and filters, and the literal reading of the fossil record. The latter indicated that modern birds and mammals were Cenozoic groups. Any scientist, such as Wegener, who explained current groups or patterns in terms of Mesozoic tectonics (or any tectonics) was vilified and denounced as a 'landbridge builder'. Following the Second World War the modern synthesis became the official biology around the world and other views were discouraged. Gould (2002) has described the 'hardening' of the modern synthesis in the 1950s, when evolutionary teaching became 'almost blindly channelled' in its adaptationism, and this remained the situation until the molecular revolution.

Now, after 50 years, the modern synthesis is being undermined by new discoveries in molecular biology. First, most molecular clades have complex, precise biogeographical structure with vicariant patterns that repeat in many groups. Second, molecular clock dates show that clades are often tens of millions of years older than their oldest fossils, indicating that the fossil record is too unreliable for use in calibration. Fossil-calibrated molecular clocks do provide minimum dates though, and indicate that in mammals the orders and suborders, at least, are pre-Cenozoic. Clocks are best calibrated with reference to the distribution of molecular clades and associated tectonics (Sparks, 2004; Sparks & Smith, 2004; Heads, 2005b; Azuma *et al.*, 2008). Third, the phylogenies of different genes in a clade are often incongruent, indicating evolution by incomplete lineage sorting and vicariance. If ancestral polymorphism is retained through cladogenesis, it means that clades do not evolve from single points in biogeographical, morphological and ecological space, but from an ancestor that is widespread and always already diverse.

CONCLUSIONS

In his earlier 'neodarwinist' phase, Darwin (1859) accepted the idea of a single, restricted centre of origin in space and form and integrated this with teleology and pan-selectionism. However, he changed his ideas about modes of evolution as

he explored the subject and his knowledge grew. The synthesis of laws of growth and selection proposed in his mature work and accepted by recent writers on genetic predispositions and lineage sorting show that a point centre of origin in either morphology/molecules or biogeography is unrealistic. Unfortunately, it was Darwin's earlier, conformist views that were taken over by neodarwinism, and this school of thought has always avoided discussion of Darwin's own work on non-teleological laws of growth.

Darwin started out as a panslectionist neodarwinist whose method of analysis would be accepted as orthodox in any biology seminar today, but later he changed his mind. Gareth Nelson (personal communication) has pointed out that all biologists are dispersalists to begin with, and that it is only after actually studying biogeographical patterns that some develop an interest in vicariance. Perhaps everyone also starts out as a teleologist. However, if evolution takes place by vicariance and incomplete lineage sorting there is no need to assume either teleology or single, point centres of origin.

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