



A Classification of Possible Routes of Darwinian Evolution

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A classification of four possible routes of Darwinian evolution is presented. These are serial direct evolution, parallel direct evolution, elimination of functional redundancy, and adoption from a different function. This classification provides a conceptual framework within which to investigate the accessibility by Darwinian evolution of complex biological structures.

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1. Introduction

It is generally assumed that Darwinian evolution must occur in a gradual, step-by-step manner, with natural selection acting at each step. A common argument used by anti-Darwinists involves the difficulty of explaining the origin of complex structures by such a process. However, there are several different mechanisms by which Darwinian evolution can occur. It is the purpose of this article to classify the different possible routes of Darwinian evolution. It is important to define four terms clearly before further discussion.

DEFINITIONS

Irreducible Complexity

The quality of a structure such that at least one of its components is essential, with its loss rendering the whole structure absolutely non-functional. This term was coined by Behe (1996a, p. 39).

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Functional Indivisibility

The quality of a component of a structure such that there is at least one alteration to it which would render the whole structure absolutely non-functional. This term was implied but not used by Behe (1996a, pp. 45, 142).

Darwinian Evolution

Descent of organisms in which the following criteria are met: (i) intergenerational differences are very much smaller than inter-specific ones; (ii) no intervention by conscious agent(s) occurs; (iii) the frequency of mutations or other heritable modifications is unrelated to functional utility; and (iv) selection is the sole means by which heritable modifications are accumulated to form functional structures.

Accessibility by Darwinian Evolution

The quality of a biological structure such that it could be generated by a sequence of very small changes, each of which is selectively neutral or advantageous (Darwin, 1859, p. 189; Dawkins, 1986, p. 91).

BACKGROUND

It was recently suggested that many biological structures are irreducibly complex, and therefore inaccessible by Darwinian evolution. Thus far, this is merely a restatement of the (fallacious) popular creationist argument about organs such as the eye. However, the new departure was to argue that the components of biochemical systems, unlike those of supramolecular structures, are single molecules, which are often functionally indivisible. The conclusion was that irreducibly complex structures of functionally indivisible components are inaccessible by Darwinian evolution. Eukaryotic undulipodia (cilia and flagella), bacterial flagella, intracellular vesicular transport, and the mammalian immune response and blood-clotting systems were given as examples (Behe, 1996a).

The above thesis is unsound, as it is not certain either that any biological structures are irreducibly complex, or that their component molecules are functionally indivisible (Coyne, 1996; Doolittle, 1997; Fulton, 1997; Ussery, 1999). However, the more theoretical question about the accessibility by Darwinian evolution of irreducibly complex structures of functionally indivisible components, if such exist, has not been thoroughly examined. One suggested mechanism for the evolution of such structures is the addition of advantageous but inessential components which become essential later as a result of the addition of further, interlocking, components (Orr, 1996). However, this could only produce a complex, rather than an irreducibly complex, structure.

One factor hampering examination of the accessibility of biological structures by Darwinian evolution is the absence of a classification of possible routes. A suggested classification is presented here.

2. Classification

Possible routes of Darwinian evolution can be classified into four fundamental categories, as outlined below.

2.1. SERIAL DIRECT DARWINIAN EVOLUTION

This means change along a single axis. Although it can generate complicated structures, it

cannot generate irreducibly complex structures. The components added may be functionally indivisible, having originated by either mutation or adoption (see below), with a probable example being the steps in an $A \rightarrow B \rightarrow C \rightarrow D$ metabolic pathway, such as the TCA cycle (Behe, 1996a, b). On the other hand, they may be functionally divisible, with an example being increments of giraffe neck length. A molecular example of the latter is the gradual change in enzyme specificity and activity resulting from single amino acid substitutions. An analogy can be drawn between this type of route and a gradual thermodynamically reversible change, as the process can be reversed at any stage without the formation of a vestigial structure.

2.2. PARALLEL DIRECT DARWINIAN EVOLUTION

This means approximately synchronous changes in more than one component, so that modification to other components always occurs before the total modification to any one component has become significant. For example, in the evolution of the eye of *Nautilus*, and of the vertebrate eye if this passed through a *Nautilus*-like stage (Land & Fernald, 1992), it would be necessary for the evolution of the retina to be approximately synchronous with that of the pinhole eye. The retina is accessible via small steps from a single photosensitive cell, with increments of photosensitivity, and the pinhole eye is likewise accessible from a minor concavity, with incremental advantages initially in physical protection and then in focusing (Nilsson & Pelger, 1994). However, neither component would function without the other, and, furthermore, the retina would be exposed to damage if not enclosed.

Parallel direct Darwinian evolution can generate irreducibly complex structures, but not irreducibly complex structures of functionally indivisible components (Fig. 1), and this is the valid conclusion to draw from Behe's thesis. As with serial direct Darwinian evolution, single steps in any of the parallel routes may be functionally either divisible or indivisible. Most complex supramolecular biological structures have primarily this type of accessibility by Darwinian evolution, with examples being bat echolocation,

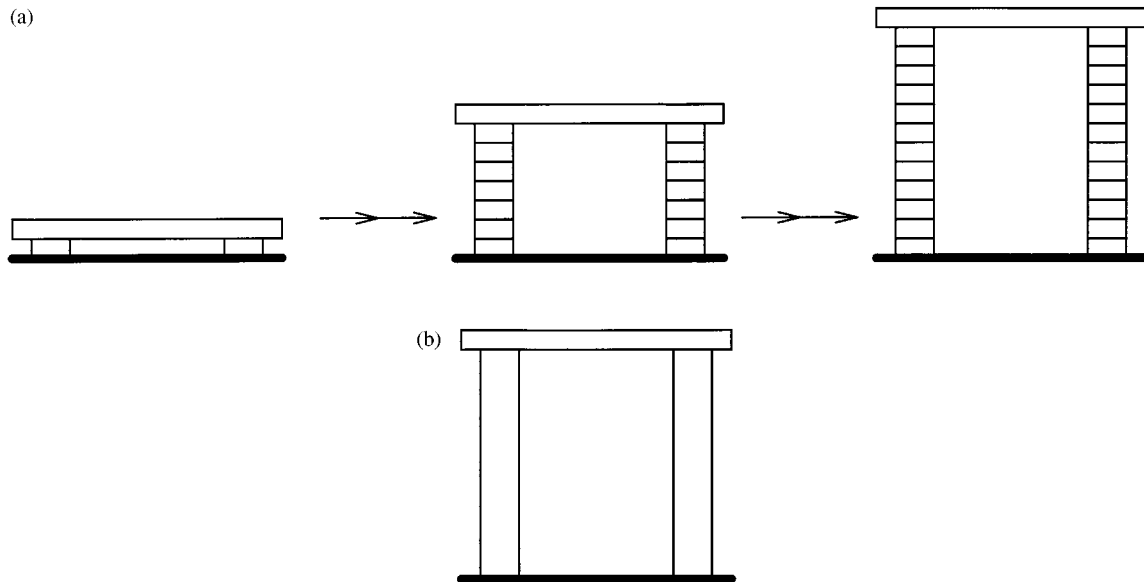


FIG. 1. Irreducibly complex tables. *Definition of table:* Structure consisting of a horizontal surface with a space beneath. The tables shown are two-dimensional, and are composed of uncemented blocks which are subject to gravity. The tables are irreducibly complex, as removal of either leg would cause loss of function of the table. (a) The legs in the right-hand structure are not functionally indivisible, as removal of one block from each leg results in only a minor decrease in height. The sequence shows a route to this structure, with many steps omitted, which is analogous to Darwinian evolution because all steps are small and each involves an improvement in the selection criterion (height). The permitted single step is the addition of two small blocks, one in each leg. However, if the blocks were very small relative to the table height, which would be a more realistic analogue of supramolecular biological structures, the permitted single step would be the addition of one small block, as the tilt caused would be negligible. (b) The legs in this structure are functionally indivisible. The derivation of this structure from a simpler structure would necessitate large steps, such as addition of large blocks or rotation of blocks, and/or an indirect route.

spiders' web construction, honeybee waggle dances, and insect mimicry by orchids (Dawkins, 1986, 1995). Some complex (but not irreducibly complex) molecular systems, such as the globin proteins (Ptitsyn, 1999; Satoh *et al.*, 1999), could also have evolved in this manner.

2.3. ELIMINATION OF FUNCTIONAL REDUNDANCY

For example, it is difficult to hypothesize a direct route by Darwinian evolution from mammalian to reptilian jaws, as they consist of different pairs of bones. However, the fossil intermediates *Morganucodon* and *Kuehneotherium* had both quadrate-articular and dentary-squamosal articulation. The following postulated evolutionary sequence from reptilian to mammalian jaws, for which there is considerable fossil evidence, involves selective advantage at each step (Kermack & Kermack, 1984):

- (i) A tympanum evolved on a ventrally directed process of the lower jaw. Species without this

structure, such as pelicosaur, were only able to hear ground-carried sound, whereas those with it, such as *Thrinaxodon*, were also able to hear airborne sound.

- (ii) The ability to masticate evolved, resulting in the cynodont jaw. This offered an advantage for carnivory, but the requirement for the canines to clear each other necessitated a slight rotation of the jaw about its longitudinal axis, which weakened it. This weakening, involving the loss of sutural connection between the dentary and the accessory bones, may also have been in part because it improved sound conduction from the tympanum to the inner ear.
- (iii) A second joint evolved from accessory bones, strengthening the jaw without inhibiting its rotation. In *Morganucodon*, for example, the quadrate and articular acted as the hinge to guide opening and closing, whereas the squamosal and dentary prevented dislocation by acting as a thrust bearing.

- (iv) In a process of elimination of functional redundancy, the quadrate and articular became less massive and more loosely connected, and thus lost their functions as jaw bones. This may have been tolerated either because the squamosal-dentary jaw was inherently stronger than the quadrate-articular, or because there was a relaxation of selection pressure for jaw strength, due to a dietary change, for example.
- (v) The modification of the quadrate and articular enabled transmission of higher frequency sound, leading ultimately to their conversion into the incus and malleus. This process constitutes adoption (see below) rather than elimination of redundancy.

Redundancy elimination can generate irreducibly complex structures of functionally indivisible components, and a Darwinian evolutionary route of this type has been suggested for biochemical cascades, such as the blood-clotting system (Robison, 1996).

2.4. ADOPTION FROM A DIFFERENT FUNCTION

For example, scale-feather intermediates would offer no aerodynamic advantage, but one can hypothesize a sequence from scales to primitive but airworthy feathers in which each step offers an increased advantage as insulation. Their use for proto-flight motility would therefore only begin after this sequence. Recently discovered fossil evidence suggests that feather evolution did indeed follow such a sequence, with proto-feathers, composed of the same proteins as feathers, in *Sinosauropteryx* (Chen *et al.*, 1998; K. Padian, pers. comm., 1999), probably marginally airworthy feathers in the non-flying *Caudipteryx* and *Protarchaeopteryx* (Ji *et al.*, 1998), and feathers in the flying *Archaeopteryx* (Padian, 1998). The proto-feathers and feathers probably also possessed functions in display, camouflage, recognition, etc. and it is possible that the actual sequence was more complicated than the above hypothetical one, with evolution at some stages being driven primarily by selection for such functions (Padian & Chiappe, 1998). However, the proto-feathers in *Sinosauropteryx* were so thickly distributed that they almost certainly

did function as insulation (K. Padian, pers. comm., 1999).

Adoption from other functions, whether generating an irreducibly complex structure or otherwise, appears to be widespread at the molecular level. The following are a few examples: (i) Many bacteria and yeasts contain chimeric flavohaemoglobins, consisting of a haem domain which is homologous to non-chimeric haem proteins, and a flavin-binding domain which is homologous to NADPH sulphite reductase, toluate 1,2 dioxygenase, cytochrome P450 reductase, and nitric oxide synthase (Moens *et al.*, 1996). (ii) Antifreeze glycoprotein in the blood of Antarctic notothenioid fishes, which enables them to survive in icy seas, is considered to have evolved from a functionally unrelated pancreatic trypsinogen-like protease, and the recent discovery of chimeric genes which encode both the protease and an antifreeze glycoprotein polypeptide strongly supports this theory (Cheng & Chen, 1999). (iii) Crystallins (proteins with refractive functions in the eye lens) are closely related or identical to stress-protective proteins in non-ocular tissues (e.g. *Drosophila* α -crystallins and small heat-shock proteins are homologous). Piatigorsky uses the term "gene-sharing" for the encoding in a single gene of a protein with two or more functions, and suggests that this may be a widespread evolutionary "strategy" (Piatigorsky, 1998).

There are several apparent instances of adoption in one of Behe's examples, the blood-clotting system. One is the kringle domain, a structure of 90 amino acids with three characteristic disulphide bonds, which is present in various proteins of the blood-clotting cascade, and also in hepatocyte growth factor, which is not involved in blood clotting (Gerhart & Kirschner, 1997, pp. 220–222). A second example is epidermal growth factor, a 53 amino acid peptide with a characteristic motif of six cysteines, which is present in several blood-clotting proteins, and also in the epidermal growth factor precursor, the low-density lipoprotein receptor, laminin (an extracellular matrix protein), and several transmembrane receptors (Davis, 1990).

There are two ways by which irreducibly complex structures of functionally indivisible

components could result from adoption:

- (i) *Generation of an irreducibly complex structure by the joining of two or more non-irreducibly complex structures of functionally indivisible components.* A possible example is the *V(D)J* joining mechanism in the immune systems of jawed vertebrates, as the most primitive version of this may have been formed by the insertion of a transposon into the gene for a membrane-spanning receptor (Agrawal *et al.*, 1998; Hiom *et al.*, 1998; Plasterk, 1998). The receptor, which probably had a function in the non-adaptive defence system of jawless vertebrates, may not have been irreducibly complex. The product of the transposon, which had the non-defence-related function of transposing the transposon itself, was very simple, consisting solely of two transposases, and may not have been irreducibly complex. However, the insertion gave rise to irreducibly complex split antigen-receptor genes, and thus ultimately to the highly advantageous variable immune system.
- (ii) *Supply of an existing irreducibly complex structure of functionally indivisible components.* The structure would have evolved previously by either redundancy elimination or the joining of two or more non-irreducibly complex structures of functionally indivisible components. Undulipodia may be accessible by Darwinian evolution in this manner, as their two main hypothesized origins are from ectosymbionts (Szathmáry, 1987) and spindle tubules (McQuade, 1977; Cavalier-Smith, 1978, 1982). However, the most detailed published hypothetical pathway for the transformation of ectosymbionts into undulipodia was actually one of parallel direct Darwinian evolution. In this scheme, the connection between tubulin microtubules and dynein arms, which Behe suggested to be irreducibly complex, was absent at the initiation of the mutualist relationship between the eukaryote and the microtubule-containing spirochete, and its origin was explained, albeit incompletely, as part of the transformation from rotational to undulipodial motility (Szathmáry, 1987).

3. Discussion

The classification presented here probably covers all possible routes of Darwinian evolution, so that any biological structure should be accessible by some combination. It is hoped that it offers a useful conceptual framework for discussing accessibility by Darwinian evolution and responding to claims that certain structures are inaccessible.

Dawkins uses “brittleness” to mean the quality of a structure such that it must be perfect if it is to work at all, and “brittle” is therefore close or identical in meaning to irreducibly complex and composed of functionally indivisible components. He argues that no biological, and very few artificial, structures are “brittle”, and gives the arch as his sole example of one (Dawkins, 1995, pp. 82–83). Regardless of whether there really are no irreducibly complex biological structures composed of functionally indivisible components, the arch is an instructive example. The arch is irreducibly complex, and, assuming that cement does not set instantaneously, any arch one sees must therefore either have been built using scaffolding, analogously to redundancy elimination, or have been built elsewhere, perhaps horizontally, and moved into position when the cement had set, analogously to adoption. If the stones of an arch were capable of reproduction and mutation, and arches were selected for span, stability and parsimony of stone use, the arch would be accessible from a single cuboid by two routes of Darwinian evolution: (i) via a heap of stones, which is then removed (i.e. redundancy elimination); and (ii) from a lintel, by two lintels being positioned diagonally and end to end, followed by the insertion of a key stone, and then by the diagonals being replaced by stones increasingly trapezoidal along one axis (i.e. parallel direct Darwinian evolution). The latter is probably analogous to the actual Roman route of invention, but would require stone binary fission. Arches are irreducibly complex, and therefore inaccessible by serial direct Darwinian evolution, that is, by the stones being placed side by side *in situ*. Furthermore, if the stones were functionally indivisible, that is, capable of binary fission but not mutation, the arch would be inaccessible by parallel direct Darwinian evolution.

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