

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/226152979>

Prebiotic world, macroevolution, and Darwin's theory: A new insight

Article in *Biology & Philosophy* · June 2009

DOI: 10.1007/s10539-007-9072-z

CITATIONS

4

READS

94

3 authors:



Luis Boto

The National Museum of Natural Sciences

39 PUBLICATIONS 895 CITATIONS

[SEE PROFILE](#)



Ignacio Doadrio

Spanish National Research Council

672 PUBLICATIONS 8,359 CITATIONS

[SEE PROFILE](#)



Rui Diogo

Howard University

351 PUBLICATIONS 4,723 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Dissemination of Science @Rui_Diogo_Lab [View project](#)



Evolution and medicine [View project](#)

Prebiotic world, macroevolution, and Darwin's theory: a new insight

Luis Boto · Ignacio Doadrio · Rui Diogo

Received: 28 March 2007 / Accepted: 30 April 2007 / Published online: 28 June 2007
© Springer Science+Business Media B.V. 2007

Abstract Darwin's main contribution to modern biology was to make clear that all history of life on earth is dominated by a simple principle, which is usually summarised as 'descent with modification'. However, interpretations about how this modification is produced have been controversial. In light of the data provided by recent studies on molecular biology, developmental biology, genomics, and other biological disciplines we discuss, in this paper, how Darwin's theory may apply to two main 'types' of evolution: that occurring in the prebiotic world and that regarding the acquisition of major key-innovations differentiating higher-taxa, which makes up part of the so-called macroevolution. We argue that these studies show that evolution is a fascinating, complex and multifaceted process, with different mechanisms driving it on different occasions and in different places.

Keywords Darwin · Evolution · Key-innovations · Macroevolution · Prebiotic world

Evolution is change. Darwin's main contribution to modern biology was to make clear that the history of life on earth is dominated by this simple principle. However, interpretations about how this change is produced have been controversial. In these days, when Darwin's evolutionary theory and principles are confronted by supporters of a new form of creationism, intelligent design, it may seem a dangerous exercise to ask if the theories proposed by Darwin and their followers (e.g. Darwin 1859; Dobzhansky 1937; Mayr 1963) explain all types of evolutionary events.

L. Boto (✉) · I. Doadrio · R. Diogo
Departamento Biodiversidad y Biología Evolutiva, Museo Nacional de Ciencias Naturales (CSIC),
Calle Jose Gutierrez Abascal 2, 28006 Madrid, Spain
e-mail: mcnb119@mncn.csic.es

R. Diogo
Department of Anthropology, George Washington University, Washington, USA

It is, however absolutely necessary to do this if one would like to have a broader, contextual understanding of how life has been changing since the first macromolecules arose, to its current enormous diversification, in light of the recent data provided by works on molecular biology, developmental biology, genomics, and other biological disciplines.

In this essay, we will discuss how Darwin's theory may apply to two main 'types' of evolution: that occurring in the Prebiotic World, and that concerning the acquisition of major key-innovations differentiating higher-taxa, which makes up part of the so-called Macroevolution. We exclude in our discussion aspects related to another main 'type' of evolution, which is related to the diversification of extant species and is included in the so-called Microevolution, because it is, in general, the ground where Darwinism and Neo-Darwinism is less controversial.

Of course, we do not want to argue that these three main 'types' of evolution are really completely different, there is surely a significant overlap between them, and certainly different authors can refer to different main 'types' of evolution other than those mentioned here. Our aim is simply to briefly discuss how Darwin's theory explains certain evolutionary events, and it is for this reason, and to somewhat simplify a discussion of such a complex subject, that we undertook this division as a basis for the discussion below.

Prebiotic world

What mechanisms could explain the change from the early molecules to the early living forms? What forces have driven the changes in the prebiotic world?

Apart from the controversial Panspermia theory (Melosh 1988), which proposes an external planetary evolution of early life forms, recent studies have supported some theoretical models (e.g. Szathmari 2004, Robinson 2005; Koonin and Martin 2005) in order to try to explain how the first biomolecules arose and evolved. For example, it is currently accepted, on the basis of our knowledge (Gilbert 1986; Jeffares et al. 1998; Penny 2005) of the dual character of RNA (as catalytic and codifying molecules) and of interesting results from studies of 'in vitro evolution' (Bartel and Szostak 1993; Wright and Joyce 1997; Lawrence and Bartel 2005), that our DNA based biological world was predated by a RNA world.

It is also somewhat accepted that the processes of natural selection have played some role in the molecular substitution events that occurred in the course of this prebiotic evolution (De Duve 2005), with a gradual variation from more simple to more complex mechanisms. In a world under construction all remains to be 'invented', and new molecules performing new functions arose as a consequence of simple physicochemical principles. New molecules would replace the older ones if they fit in the new requirements for complexity of these prebiotic entities.

An early step in this prebiotic world is the abiotic synthesis of nucleotides by mineral catalysis, today accepted as feasible (Miller 1998; Orgel 2004; Muller 2006). However, a problem that arose since the first studies on the origin of life is the so called 'chicken and egg' paradox; that is, which came first, heredity or metabolism (Haldane 1967; Oparin 1967; Fry 2006)? Is it necessary to have first a molecule able to catalyze some reactions? Or do we need to have first the presence of the codifying character in the original biomolecules before the development of metabolic capacities?

Recent studies (Mossel and Steel 2005) show that there is seemingly a high statistical probability that random biochemical networks supporting self-sustaining

autocatalysis would arise. They thus point out the possibility of the presence of both catalytic and hereditary properties in the first biomolecules, an idea that was in fact advanced by Troland (1914) before the Haldane-Oparin controversy (see Fry 2006). Once we accept the existence of a biomolecule of this type, a new question arises: if the efficiency in catalyzing the replication of all RNA molecules is similar, would not the molecule disappear at some time by degradation? It is necessary that this molecule performs its proper replication better than other RNA molecules. In this sense, it has been proposed that the presence of two domains in the first RNA replicase could make their proper replication easier, suggesting that the first ribozyme may have been an intramolecular replicase (Ma and Yu 2005).

When RNA is established as a pivotal molecule, able to code for new molecules performing new functions and to catalyze its proper replication, variants of RNA performing auto replication in a more consistent and faster way can be selected.

At some moment, at a certain degree of complexity, it is necessary to preserve acquired complex functions, and thus evolutionary constraints facilitating such a task may arise. From this moment, the codifying function of RNA should be highly efficient, copying the proper sequence with high fidelity. But new mutations should also arise in the sequence region with catalytic activity allowing their elongation and increasing their complexity. According to certain authors, it is the so-called Darwin-Eigen cycle that has allowed, and driven, prebiotic evolution (Poole et al. 1999). However, it is important to note that there are other possible models to explain prebiotic evolution in a RNA world, and that there are discrepancies among such models.

There are also different models to explain the transition from that RNA world to a RNP (Ribonucleoproteic) world, and, then, to a DNA world (Koga et al. 1998; Poole et al. 1998; Forterre 2005; Koonin and Martin 2005). Two recent papers (Forterre 2005; Forterre 2006) have advanced an interesting model, which proposes that at a certain moment the transition to a DNA world was mediated by the 'invention' of DNA in RNA viruses. In the model, RNA viruses arose as parasitic entities after the origin of the ribosome. The transformation of RNA into DNA might eventually have allowed the viruses to escape the restrictions imposed by the host, yielding the DNA molecules selectively favored by natural selection. In a subsequent step, the DNA molecules and the respective machinery for replication and transcription (evolving in the new DNA viruses) could be transferred to RNA cells, where eventually they would substitute the RNA itself. So, in this model natural selection is again proposed as an important evolutionary mechanism during the prebiotic phase of the history of life on Earth.

It is, however, interesting that in this prebiotic phase natural selection was seemingly exerted over molecules, contrasting with the original Darwinian proposal of selection acting over individuals and/or populations. So, for example, one RNA molecule eventually performing a new function or replicating more efficiently than another RNA molecule may have substituted for the latter in a relatively short time. Therefore, in a certain way prebiotic evolution may have been relatively faster than the somewhat slow, gradualist evolution by natural selection exerted over individuals and/or populations that is often defended by Darwinists.

Macroevolution

With independence of the nature of the LUCA (Last Universal Common Ancestor), once the complexity of the new life world arose (with a DNA coding to RNA and this latter coding to proteins, with a compartmentalized metabolism, etc.), evolutionary constrictions

have seemingly grown (Woese 1998; Galtier et al. 1999; Penny and Poole 1999; Forterre 2005; Koonin and Martin 2005; Ciccarelli et al. 2006). As this moment, specific mutations alone seem to not be enough to explain the numerous key innovations leading to the enormous differences seen for example between major higher clades. Therefore, different authors have proposed different mechanisms acting at different evolutionary events to try to explain how such differences have arisen (e.g. lateral gene transfer, gene or genome duplications, chromosomal rearrangements, co-option of gene products for new functions, changes in regulatory networks, paedomorphism, hybridization, etc.). Here we briefly discuss some of them.

Although this is still the subject of much controversy, it seems that lateral gene transfer (Brown 2003; Philippe and Douady 2003; Ge et al. 2005; Kurland 2005) may play an important role in the evolution of microbes (Bacteria, Archaea), allowing evolutionary innovations at this level (Gogarten et al. 2002; Pal et al. 2005). Genes transferred between different organisms may therefore allow the host to acquire new functions present in the donor without losing its own original functions. Such a mechanism is not Darwinian in the sense that the new configuration of the host it is not the result of a gradual transformation and is not directly inherited from the ancestors of that host (Darwin 1859). But, of course, Darwinian natural selection may then act on the host with the new configuration and select for it against organisms not exhibiting this configuration. There is a significant amount of data suggesting that several genes have been transferred between bacteria (Kroll et al. 1998; Ginolhac et al. 2005), between Archaea and Bacteria (Wolf et al. 1999; Nesbo et al. 2001), between bacteria and eukaryotes (Aravind and Koonin 1999; García-Vallvé et al. 2000) and even between eukaryotes (Raz and Van Luenen 1997). Interestingly, Lan and Reeves (2000) have stressed the strong pressure (because of a single origin of replication) to lose genes that are not of immediate utility for a specific bacterial strain in a particular environment. However, it should be noted that the genes lost will vary between strains, depending on the local environment. These authors therefore consider that as long as there is a mechanism of occasional transfer of genes, allowing colonization of new environments from new combinations, then there is no long-term 'loss' of the genes. It is just that each strain is specializing for its environment, but still retains its adaptability. As such, lateral gene transfer among related strains is just a part of the normal mechanisms. In summary, it can be said that, despite the controversies about their extent and importance, lateral transfer events effectively seem to play a significant role in general macroevolution, as they do in microbial evolution. In this regard, some authors go as far as to suggest that a new revolution in Biology is arising (see e.g. Goldenfeld and Woese 2007; Doolittle and Baptiste 2007).

Another example of macroevolutionary changes that are not necessarily Darwinian, but for different reasons, are those related with paedomorphism. A well-known vertebrate group in which such changes seem to have played an important role is, for instance, the Dipnoi, or lungfishes. Bemis (Bemis 1984) reviewed some seemingly paedomorphic morphological transformations that occurred from the most basal lungfish forms to extant dipnoans. Examples of these are the loss of heterocercal tail, the fusion of medial fins, the reduction of fin rays, the loss of cosmine, the changes in scale shape, the reductions in ossification and the increase of cell size. According to that author, all these features are very likely related to a paedomorphic event, which may well be due to selection for one of these features, or may even be related to any another reason (genetic, physiological, etc.). Therefore, the evolutionary transformations leading to many of the features listed above was not necessary 'Darwinian' in the sense that these transformations were probably not related to the direct adaptive value of, or to a direct selection towards, those features (see

e.g. Gould 2002). In other words, if for example feature A resulting from paedomorphism turns out to be adaptive, selection will favor that feature, and therefore paedomorphism will be selected, with the paedomorphic features B, C, D, for example, being present in the selected organism but not because they were directly selected. As recently stressed by Diogo (Diogo in press), paedomorphism has seemingly not only played an important role in lungfish evolution, but also in several other groups, and seems in fact to be a rather common macroevolutionary event. If this is so, several features now seen in many different taxa may effectively not be related to a direct Darwinian selection towards those features.

Gene duplication has also been postulated (Muller 1936; Ohno 1970; Zhang 2003) as a way to acquire new functions in macroevolution; this view has been reinforced by the knowledge derived from the sequencing and comparison of genomes from a wide range of living organisms. Such a gene duplication allows one of the copies to maintain its original function, while the other copy may thus accumulate mutations and eventually gain a new function (neofunctionalization). The neofunctionalization of genes allowing new functions in molecular evolution is, in a certain way, mechanistically somewhat similar to the morphological functional uncouplings leading to the performance of new functions by certain structural systems, which seem to play a crucial role in morphological macroevolution (e.g. Diogo and Vandewalle 2003; Diogo 2004).

Obviously, molecular neofunctionalization is not the only destination of the new copy of a gene (Lynch and Conery 2000; Lynch and Katju 2004). This can be subfunctionalized, making a part of the original function, or be completely eroded remaining in the genome as a pseudogene. Subfunctionalization of genes can be the first step in the construction of genetic networks and gene families (Hancock 2005), and combination of different modules can allow the rise of a new function (see below). Neofunctionalization and subfunctionalization are 'Darwinian' in the sense that they are based in gradual modifications of gene copies over which natural selection can act, but they do not seem to explain the rapid functional changes associated with the rapid environmental changes undertaken by certain microbes, for example. Such rapid environmental changes are thus perhaps a good example in which lateral gene transfer (see above) may play an important role (see e.g. Gogarten et al. 2002).

Partial or complete genome duplication (Ohno 1970; García-Fernández and Holland 1994; Holland et al. 1994; Panopoulou and Poustka 2005) has been proposed as a relevant mechanism in the acquisition of major evolutionary novelties, allowing the somewhat simultaneous neofunctionalization and/or subfunctionalization of several genes. For example, it has been proposed that genome duplication likely played a central role in plant and fungi evolution (Bowers et al. 2003; Kellis et al. 2004; Coghlan et al. 2005). Also, the idea has been advanced that the two genome duplications that occurred in the lineage leading to vertebrates, and one additional duplication that occurred within teleostean fishes, may be linked to a burst of phenotypic complexity (Dehal and Boore 2005; Meyer and Van de Peer 2005; Christoffels et al. 2004). However, certain authors argued that the hypotheses favoring such a link are weakened when both the extant taxa and the fossil taxa, and not only the former, are taken into consideration (Donoghue and Purnell 2005).

Others genomic rearrangements, such as chromosomal inversions, deletions or translocations, have been proposed as possible candidates to explain the acquisition of novelties. But many authors consider that the occurrence of such rearrangements is probably not so much related to macroevolution of higher taxa, but more likely with mechanism involved in speciation (see e.g. Coghlan et al. 2005).

Both co-option of genes in new functions and change in regulatory networks during the developmental process emerge now as the seemingly more reliable candidates to explain

the acquisition of evolutionary novelty and the emergence of body plans during evolution. Changes in the regulatory regions of the genome can drive changes in regulation of gene expression of particular genes, affecting other genes downstream in the regulatory network with lethal results if the change stops a fundamental step of the developmental process. But, in certain cases, these can result in developmental changes compatible with the adult life form. In such cases the developmental changes can therefore lead to a significant phenotypic change in the adult organism, over which selection can thus act. In such cases, evolutionary novelties could eventually be relatively fast.

A recent seminal review (Davidson and Erwin 2006) has focused on the modifications in developmental regulatory networks, its authors arguing that these modifications can affect evolution at different taxonomic levels depending of the type of network affected. These authors suggest that modifications in the so named “kernels” (networks regulating more universal steps of development and thus more impervious to change) can affect the macroevolution of higher taxa, while changes in other networks can affect the evolution of other, lower taxa, depending on the dispensability of the network.

Co-option of a particular gene involved in a particular network operating during the developmental process to other genetic interactions can eventually constitute a complementary mechanism to generate evolutionary novelties. Examples of this mechanism can be found in the *Bicoid* based anterior patterning exclusive of *Drosophila* and other dipterans (Stauber et al. 1999; Dearden and Akam 1999; Lynch and Desplan 2003), which arose after the duplication of an ancestral regulatory gene by co-option of the duplicate gene to new regulatory functions, and in the functional changings of the *Distal-less*, *Engrailed* and *Orthodenticle* genes occurring during the derived developmental process of echinoderms with respect to other Bilateria (Loewe and Wray 1997).

The mix of genomes or hybridization may also be related to the acquisition of macroevolutionary novelties. A hybrid origin of the eukaryotic cell (Gupta and Golding 1993; Ribeiro and Golding 1998; Rivera and Lake 2004) has for example been proposed, with this cell arising as consequence of hybridization between a Bacteria and an Archaea. This hypothesis is the subject of controversy (Poole et al. 1999; Lester et al. 2005; Kurland et al. 2006), but if it could be demonstrated this could effectively provide one of the best examples of how the mixing of two genomes may result in a radically new organism. Hybridization has also been proposed as a possible mechanism operating in the evolutionary radiations observed in several phases in the history of life (Lewontin and Birch 1966; Seehausen 2004; Kearney 2005), namely during the evolution of land plants (Riddle and Birchler 2003), but also in animal evolution (Mallet 2005). The mixing of genomes obtained by hybridization can therefore be a source of macroevolutionary innovations in times of for example rapid environmental changes, allowing a fast adaptation of the resultant hybrid to the changing conditions. In such a mechanism the evolutionary changes would not be slow and gradual, but relatively fast.

In fact, it is interesting to notice that many authors today tend to defend the position that most major macroevolutionary events, even those that are ‘Darwinian’ in the sense that they are driven by natural selection, are probably much easier and faster than was predicted by the Darwinian and Neo-Darwinian theories. An illustrative example of this is the new theory of ‘facilitated variation’, which, as stated by its authors, was precisely proposed with the aim of ‘resolving Darwin’s (macroevolutionary) dilemma’ (Kirschner and Gerhart 2005). According to these authors, this theory can effectively explain why many macroevolutionary changes may occur faster than previously thought. The theory basically argues that macroevolution is constrained, but that paradoxically it is precisely this that allows significant, relatively fast macroevolutionary changes. Examples given by the

authors are the *Hox* genes, which seem to be highly constrained in evolution, but at the same time have allowed the rise of an impressive number of different anatomies, from miniature fishes to enormous dinosaurs. Other examples concern the way development is constrained, in the sense that many structural systems are interconnected, in a somewhat 'self-organization', e.g. if limb primordia develop in a certain place, limb muscles will develop too, limb nerves also, and so on, until a functional limb is developed. But such 'self-organization', constrained on the one hand, allows, on the other, that in certain specific cases it is possible to develop limbs with muscles, nerves, and other associated structures in a new place due to a simple changing of the place of origin of the first limb primordia (Kirschner and Gerhart 2005).

Concluding remarks

As the works referred to above illustrate, recent developmental, comparative, phylogenetic and genetic studies, among others, are therefore showing that, like the fascinating eye of a *Drosophila*, evolution is a remarkably complex and multifaceted process, with different mechanisms driving it on different occasions and in different places. These recent studies are also challenging the traditional Darwinian theories. With some exceptions, which, it is important to stress, should not be overlooked, it can be said that works mainly focused on the acquisition of new macroevolutionary innovations tend to be those in which these theories are more challenged; works on microevolution, and namely on speciation, tend to be those challenging them less. It is precisely hoped that this paper may help to stimulate future works that may, in turn, allow the opening of new doors for the understanding of the complex, but highly fascinating, multifaceted evolutionary process that has led, and continues to lead, to the amazing biological diversity of this planet.

Acknowledgments This paper is dedicated to the memory of Prof. Pere Alberch. We specially acknowledge A. García Valdecasas, N. Lonergan, Kim Sterelny, and an anonymous referee for the improvement of this manuscript, as well as F. Meunier, D. Adriaens, M. de Pinna, P. Skelton, F. Poyato-Ariza, T. Grande, H. Gebhardt, M. Ebach, A. Wyss, J. Waters, G. Cuny, L. Cavin, F. Santini, J. Briggs, L. Gahagan, M. Gayet, J. Alves-Gomes, G. Lecointre, L. Soares-Porto, P. Bockmann, T. Roberts, G. Arratia, L. Taverne, C. Ferraris, C. Borden, E. Parmentier, P. Vandewalle, M. Chardon, B. Richmond, B. Wood, B. Hall and F. Galis and many other colleagues for their helpful advice and assistance and for their discussions on evolution.

References

- Aravind L, Koonin EV (1999) The fukutin protein. *Curr Biol* 9:836–837
- Bartel DP, Szostak JW (1993) Isolation of new ribozymes from a large pool of random sequences. *Science* 261:1411–1418
- Bemis W (1984) Paedomorphosis and the evolution of Dipnoi. *Paleobiology* 10:293–307
- Bowers JE, Chapman BA, Rong JK, Paterson AH (2003) Unraveling angiosperm genome evolution by phylogenetic analysis of chromosomal duplication events. *Nature* 422:433–438
- Brown JR (2003) Ancient horizontal gene transfer. *Nat Rev Genet* 4:121–132
- Ciccarelli FD, Doerks T, von Mering C, Creevey CJ, Snel B, Bork P (2006) Toward automatic reconstruction of a highly resolved tree of life. *Science* 311:1283–1287
- Christoffels A, Koh EGL, Chia J-M, Brenner S, Aparicio S, Venkatesh B (2004) Fugu genome analysis provides evidences for a whole genome duplication early during the evolution of ray-finned fishes. *Mol Biol Evol* 21:1146–1151
- Coghlan A, Eichler EE, Oliver SG, Paterson AH, Stein L (2005) Chromosome evolution in Eukaryotes: a Multi-kindom perspective. *Trends Genet* 21:673–682

- Davidson EH, Erwin DH (2006) Gene regulatory networks and the evolution of animal body plans. *Science* 311:796–800
- Darwin C (1859) *On the origin of species by means of natural selection, or the preservation of the favored races in the struggle for life*. D Appleton, New York, USA
- Dearden P, Akam M (1999) Developmental evolution: axial patterning in Insects. *Curr Biol* 9:591–594
- de Duve C (2005) The onset of selection. *Nature* 433:581–582
- Dehal P, Boore JL (2005) Two rounds of whole genome duplication in the ancestral vertebrate. *Plos Biol* 3:314
- Diogo R (2004) Morphological evolution, adaptations, homoplasies, constraints, and evolutionary trends: catfishes as a case study on general phylogeny and macroevolution. Science Publishers, Enfield, USA
- Diogo R In press. On the origin of higher clades: osteology, myology, phylogeny and evolution of bony fishes and the rise of tetrapods. Science Publishers, Enfield, USA
- Diogo R, Vandewalle P (2003) Catfishes as a case study for discussions on general evolution: the importance of functional uncouplings in morphological macroevolution. *Eur J Morphol* 41:139–148
- Dobzhansky T (1937) *Genetics and the origin of species*. Columbia University Press, New York
- Donoghue PCJ, Purnell MA (2005) Genome duplication, extinction and vertebrate evolution. *Trends Ecol Evol* 20:312–319
- Doolittle WF, Bapteste E (2007) Pattern pluralism and the tree of life hypothesis. *Proc Natl Acad Sci US* 104:2043–2049
- Forterre P (2005) The two ages of the RNA world, and transition to the DNA world: a story of viruses and cells. *Biochimie* 87:793–803
- Forterre P (2006) The origin of viruses and their possible roles in major evolutionary transitions. *Virus Res* 117:5–16
- Fry I (2006) The origins of research into the origins of life. *Endeavour* 30:24–28
- Galtier N, Tourasse N, Gouy M (1999) Non hyperthermophilic common ancestor to extant life forms. *Science* 283:220–221
- Garcia Fernandez J, Holland PW (1994) Archetypal organization of the *Amphioxus* Hox gene cluster. *Nature* 370:563–566
- Garcia-Vallve S, Romeu A, Palau J (2000) Horizontal gene transfer of Glycosyl Hydrolases of the rumen fungi. *Mol Biol Evol* 17:352–361
- Ge F, Wang L-S, Kim J (2005) The cobweb of life revealed by genome-scale estimates of horizontal transfer. *Plos Biol* 3:316
- Gilbert W (1986) The RNA world. *Nature* 319:618
- Ginolhac CA, Jarrin C, Robe P, Perriere G, Vogel TM, Simonet P, Nalin R (2005) Type I polyketide synthases may have evolved through horizontal gene transfer. *J Mol Biol* 60:716–725
- Gogarten JP, Doolittle WF, Lawrence JG (2002) Prokaryotic evolution in light of gene transfer. *Mol Biol Evol* 19:2226–2238
- Goldenfeld N, Woese C (2007) Biology's next revolution. *Nature* 445:369
- Gould SJ (2002) *The structure of Evolutionary theory*. The Belknap Press of Harvard University Press, Cambridge, MA, London
- Gupta RS, Golding GB (1993) Evolution of Hsp70 gene and its implications regarding relationships between Archaeobacteria, Eubacteria, and Eukaryotes. *J Mol Evol* 37:573–582
- Haldane JBS (1967) The origin of life. In: Bernal JD (ed) *The origin of life*. Appendix II, Weidenfeld and Nicolson, London, UK, pp 242–249
- Hancock JM (2005) Gene factories, microfunctionalization and the evolution of gene families. *Trends Genet* 21:541–545
- Holland PW, Garcia Fernandez J, Williams NA, Sidow A (1994) Gene duplications and the origin of vertebrate development. *Dev Suppl* 43:125–133
- Jeffares DC, Poole D, Penny D (1998) Relics from the RNA world. *J Mol Biol* 46:18–36
- Kearney M (2005) Hybridization, glaciation and geographical parthenogenesis. *Trend Ecol Evol* 20:495–502
- Kellis M, Birren BW, Lander ES (2004) Proof and evolutionary analysis of ancient genome duplication in yeast *Saccharomyces cerevisiae*. *Nature* 428:617–624
- Kirschner MW, Gerhart JC (2005) *The plausibility of life: resolving Darwin's dilemma*. Yale University Press, London, UK
- Koga Y, Kyurai T, Nishihara M, Sone N (1998) Archaeal and Bacterial cells arise independently from noncellular precursors? A hypothesis stating that the advent of membrane phospholipids with enantiomeric glycerophosphate backbone caused the separation of the two lines of descent. *J Mol Evol* 46:54–63
- Koonin EV, Martin W (2005) On the origin of genomes and cells. *Trends Genet* 21:647–654

- Kroll JS, Wilks KE, Farrant JL, Langford FR (1998) Natural genetic exchange between *Haemophilus* and *Neisseria*: Intergeneric transfer of chromosomal genes between major human pathogens. *P Natl Acad Sci USA* 95:12381–12385
- Kurland CG (2005) What tangled web. Barriers to rampant horizontal gene transfer. *Bioessays* 27:741–747
- Kurland CG, Collins LJ, Penny D (2006) Genomics and the irreducible nature of eukaryote cells. *Science* 312:1011–1014
- Lan R, Reeves PR (2000) Intraspecies variation in bacterial genomes: the need for a species genome concept. *Trends Microbiol* 8:396–401
- Lawrence MS, Bartel DP (2005) New ligase-derived RNA polymerase ribozymes. *Rna* 11:1173–1180
- Lester L, Meade A, Pagel M (2005) The slow road to the eukaryotic genome. *Bioessays* 28:57–64
- Lewontin RC, Birch RC (1966) Hybridization as a source of variation for adaptation to new environments. *Evolution* 20:315–336
- Lowe CJ, Wray GA (1997) Radical alterations in the roles of homeobox genes during echinoderm evolution. *Nature* 389:718–721
- Lynch M, Conery JS (2000) The evolutionary fate and consequences of duplicate genes. *Science* 290:1151–1155
- Lynch J, Desplan C (2003) Evolution of development: beyond bicoid. *Curr Biol* 13:557–559
- Lynch M, Katju V (2004) The altered trajectories of gene duplicates. *Trends Genet* 20:544–549
- Ma W, Yu C (2005) Intramolecular RNA replicase: possibly the first self-replicating molecule in the RNA world. *Origins Life Evol B* 36:413–420
- Mallet J (2005) Hybridization as an invasion of the genome. *Trends Ecol Evol* 20:229–237
- Mayr E (1963) Animal species and evolution. Harvard University Press, Cambridge, UK
- Melosh HJ (1988) The rocky road to Panspermia. *Nature* 322:687–688
- Meyer A, van de Peer Y (2005) From 2R to 3R. Evidence for a fish-specific genome duplication (FSGD). *Bioessays* 27:937–945
- Miller SL (1998) The endogenous synthesis of organic compound. In: Brack A (ed) The molecular origins of life: assembling pieces of the puzzle. Cambridge University press, Cambridge, pp 59–85
- Mossel E, Steel M (2005) Random biochemical networks: the probability of self-sustaining autocatalysis. *J Theor Biol* 233:327–336
- Muller HJ (1936) Bar duplication. *Science* 83:528–530
- Müller UF (2006) Re-creating an RNA world. *Cell Mol Life Sci* 63:1278–1293
- Nesbo C, L'Haridon S, Setter KO, Doolittle WF (2001) Phylogenetic analyses of two “archaeal” genes in *Thermotoga maritima* reveal multiple transfers between Archaea and Bacteria. *Mol Biol Evol* 18:362–375
- Ohno S (1970) Evolution by gene and genome duplication. Springer, Berlin, Germany
- Oparin AI (1967) The origin of life. In: Bernal JD (ed) The origin of life. Appendix I, Weidenfeld and Nicolson, London, UK, pp 199–235
- Orgel LE (2004) Prebiotic chemistry and the origin of the RNA world. *Crit Rev Biochem Mol Biol* 39:99–123
- Pal C, Papp B, Lercher MJ (2005) Adaptative evolution of bacterial metabolic networks by horizontal gene transfer. *Nat Genet* 37:1372–1375
- Panopoulou G, Poustka AJ (2005) Timing and mechanism of ancient vertebrate genome duplications. The adventure of a hypothesis. *Trends Genet* 21:559–567
- Penny D (2005) An interpretative review of the origin of life research. *Biol Phil* 20:633–671
- Penny D, Poole A (1999) The nature of the last universal common ancestor. *Curr Opin Genet Dev* 9:672–677
- Philippe H, Douady CJ (2003) Horizontal gene transfer and phylogenetics. *Curr Opin Microbiol* 6:498–505
- Poole AM, Jeffares DC, Penny D (1998) The path from the RNA world. *J Mol Evol* 46:1–17
- Poole A, Jeffares A, Penny D (1999) Early evolution: prokaryotes, the new kids in the blocks. *Bioessays* 21:880–889
- Raz E, van Luenen GAM (1997) Transposition of the nematode *Caenorhabditis elegans* Tc3 element in the zebrafish *Danio rerio*. *Curr Biol* 7:82–88
- Ribeiro S, Golding GB (1998) The mosaic nature of the eukaryotic nucleus. *Mol Biol Evol* 15:779–788
- Riddle NC, Birchler JA (2003) Effects of diverged regulatory hierarchies I allopolyploids and species hybrids. *Trends Genet* 19:597–600
- Rivera MC, Lake JA (2004) The ring of life provides evidence for a genomic fusion origin of eukaryotes. *Nature* 431:152–155
- Robinson R (2005) Jump-starting a cellular world: Investigating the origin of life, from soup to networks. *Plos Biol* 3:396
- Seehausen O (2004) Hybridization and adaptative radiation. *Trends Ecol Evol* 19:198–207

- Stauber M, Jäckle H, Schmidt-Ott U (1999) The anterior determinant bicoid of *Drosophila* is a derived Hox class 3 gene. *P Natl Acad Sci USA* 96:3786–3789
- Szathmari E (2004) From biological analysis to synthetic biology. *Curr Biol* 14:145–146
- Troland LT (1914) The chemical origin and regulation of life. *Monist* 24:92–133
- Woese C (1998) The universal ancestor. *P Natl Acad Sci USA* 95:6854–6859
- Wolf YI, Aravind L, Grishin NV, Koonin EV (1999) Evolution of aminoacyl-tRNA-synthases. Analysis of unique domain architectures and phylogenetic trees reveal a complex history of horizontal gene transfer events. *Genome Res* 9:689–710
- Wright MC, Joyce GF (1997) Continuous in vitro evolution of catalytic function. *Science* 276:614–617
- Zhang J (2003) Evolution by gene duplication: an update. *Trends Ecol Evol* 18:292–302