In summary, Caswell[2] and I[1] differ philosophically, but my Eqn 9 is absolutely correct and reduces to Caswell's Eqn 1 if $R = \varnothing$. The trouble is that R is not in general empty – except by decree.

Michael Mesterton-Gibbons
Dept of Mathematics, Florida State University, Tallahassee, FL 32306-4510, USA (mmestert@mailer.fsu.edu)

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A new evolutionary synthesis: do we need one?

Robert Carroll[1] has given an excellent account of some major evolutionary transitions and has discussed the role that abiotic, as well as biotic, factors play in these transitions. However, regardless of how instructive his treatment of this topic is, Carroll's conclusion – that we are in need of a new evolutionary synthesis – does not follow from it for two reasons.

First, biology is one of the sciences that is both nomothetic and idiographic – it is aimed at both discovering laws of nature (e.g. the theory of natural selection or the red queen hypothesis) and explaining historically singular events (e.g. the identification of key innovations of a taxon or the unravelling of the food web of an ecosystem). For a complete understanding of the history of life on earth, results obtained in nomothetic and in idiographic branches of biology have to be communicated and interpreted in conjunction[2], an activity that has not really started yet. On pp. 28–30 of his recent *TREE* perspective[1], Carroll makes an important step in this direction (see also Ref. 3); one can hope that many others will follow. However, this will succeed only when it is realized that nomothetic and idiographic science have different aims and methodologies. Ghiselin[2] has provided an excellent survey of the various misconceptions that originated (and originate!) because of failures to distinguish between laws of nature and spatiotemporal singularities.

The developmental, geophysical and systematic findings discussed by Carroll are spatiotemporal singularities, inferences of idiographic science: *Hox* genes originated only once, the Proterozoic supercontinent broke up only once, and the Eukaryota, Metazoa and Chordata are unique taxa. By contrast, the evolutionary synthesis is the main nomothetic framework in biology. In order not to be falsified, it has to be compatible with findings of idiographic science, but it cannot incorporate them because laws of nature cannot be about a single individual (such as a taxon or an event). Because the current evolutionary synthesis is compatible with the facts mentioned by Carroll, there is no need to revise it, only to apply it in neglected contexts.

Second, Carroll discussed the patterns of evolution above the species level. He maintains that they are 'clearly distinct in all taxonomic groups'. If correct, this would indeed be a lawlike phenomenon requiring a modification of the evolutionary synthesis. However, Carroll fails to document this bold claim (see also Ref. 4). His Fig. 1, which is meant to illustrate 'the most obvious contrast between the darwinian [and Carroll's] view of the patterns and the rates of evolution', is unable to do just that: continual divergence and morphological gaps between higher taxa can be explained by simple speciation and extinction processes[5]. Therefore, before rejecting the evolutionary synthesis on such speculative grounds one has to make sure that the patterns observed are not taxonomic artefacts, because Carroll compares 'phyla' by counting their 'families'. However, Linnean categories are not comparable across different taxa (as for instance brilliantly discussed by Ax[6], who is even quoted by Carroll; see also Ref. 2).

Hanno Sandvik
Norwegian Institute for Nature Research (NINA), Polar Environmental Centre, 9296 Tromsø, Norway; and Dept of Biology, University of Tromsø, 9037 Tromsø, Norway (hanno@ibg.uit.no)

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Reply from R. Carroll

Hanno Sandvik's[1] comments reflect a general reluctance to recognize the significance of recent advances in molecular developmental biology, and knowledge of large-scale changes in the earth and its biota in understanding the patterns and processes of macroevolution. His most crucial statement is that I have failed to demonstrate that the fossil record of the metazoan phyla provides an obvious contrast with the darwinian view that '…continual divergence and morphological gaps between higher taxa can be explained by simple speciation and extinction processes'. These factors can explain much of what has occurred *within* the individual phyla, but they do not explain their origins nor the maintenance of the distinct body plans that have characterized the phyla since their appearance in the fossil record 530 million years ago[2].

What differentiated the initial stages in the evolution of the metazoan phyla in the late Neoproterozoic was the emergence of an entirely new system of genetic control necessary for the embryological development of multicellular organisms. This involved a new capacity for the differentiation of numerous cell types and the origin of the *Hox* cluster, which controls the regional organization of the metazoan body and its individual parts. Also restricted to this period was the establishment of the distinctive body plans of the individual phyla, which have remained highly conserved for the entire Phanerozoic. According to Gerhart and Kirschner[3], the constancy of body plan early in ontogeny might be a necessity for effective change later in development, which has characterized metazoans since the Early Cambrian.

As in the Phanerozoic, darwinian selection must have resulted in differential survival among the multitude of incipient structures and body designs, but the generation of variation was manifestly different. The capacity for differentiation of distinct cell types expanded exponentially, accompanied by the emergence of a complex hierarchical system of genetic control. The amount of duplication of individual genes and their functional divergence, especially those of the *Hox* complex, was never again matched, and the entire genome was duplicated twice in the lineage leading to jawed vertebrates[4].

Knowledge of the genetic basis of change during the origin of metazoans does not contradict the concept of natural selection, but it does provide an entirely different understanding of the basis for the inheritance of quantitative characters than arose from classical genetics. It also demonstrates that the emergence of entirely new genes and genetic networks generated morphological and physiological change at a scale far beyond that explained by the alteration of allele frequencies within populations whose importance is so strongly emphasized in the evolutionary synthesis and most recent textbooks[5].