

Macroevolution and macroecology for the biological synthesis

Martin L. Christoffersen¹

Abstract

I argue for a systems approach to Evolutionary Biology, urging for more attention at the higher levels of the biological hierarchies. An example is provided on how the higher levels may constrain and enhance our knowledge of lower level phenomena. The neo-Darwinian Evolutionary Synthesis is appropriate for the organismic and populational levels. I consider Historical Biology decoupled from the populational level and basic for the development of Macroevolutionary Theory. Such a theory may function as a paradigm for cladistics, having applications in both Macroevolution and Macroecology. Biosystematics deals with the history of species and monophyla (biodiversity), while Ecosystematics deals with the history of biotas (ecodiversity). The new insights into Historical Biology produced by macroevolutionary and macroecological studies are so startling and of such broad ontological and epistemological connotations that I boldly predict an approaching revolution in the area of Historical Biology and of our present understanding of Evolutionary Theory.

Key words: macroevolutionary theory; biological hierarchy; ecological hierarchy; biosystematics; ecosystematics; biodiversity; ecodiversity.

Resumo

MACROEVOLUÇÃO E MACROECOLOGIA PARA A SÍNTESE BIOLÓGICA. Eu adoto uma abordagem sistêmica para a Biologia Evolutiva, com maior atenção para os níveis superiores das hierarquias biológicas. Um exemplo de como os níveis hierárquicos superiores influenciam e aumentam nosso conhecimento dos fenômenos em níveis inferiores é apresentado. A Síntese Evolutiva Neo-Darwinista é apropriada para os níveis organizmicos e populacionais. A Biologia Histórica é independente do nível populacional e básica para o desenvolvimento de uma Teoria Macroevolutiva. Tal teoria poderá funcionar como um paradigma para a cladística, tendo aplicações na Macroevolução e na Macroecologia. A Biosistemática lida com a história de espécies e táxons superiores (biodiversidade), enquanto a Ecosystemática lida com a história de biotas (ecodiversidade). Os novos conhecimentos em Biologia Histórica produzidos pela macroevolução e pela macroecologia são inesperados e têm conotações epistemológicas e ontológicas significativas, antevendo uma revolução que se aproxima na Biologia Histórica e na nossa compreensão da Teoria Evolutiva.

Palavras-chave: teoria macroevolutiva; hierarquia biológica; hierarquia ecológica; biosistemática; ecosystemática; biodiversidade; ecodiversidade.

Introduction

The acceptance of emergent properties in system thinking is experiencing a renaissance among philosophers since the final decade of the twentieth century (McLaughlin, 1992).

For instance, species selection, punctuated equilibria, mass extinctions by extraterrestrial evolutionary transitions discussed by Maynard Smith & Szathamary (1995), represent emergent macroevolutionary phenomena.

This means that macroevolution is more than successive rounds of microevolution (Grantham, 2007), and that the Neo-Darwinian reductionist emphasis on lower level processes are no longer tenable for a complete version of evolutionary theory. Macroecology and Macroevolution are legitimate and

autonomous disciplines for a hierarchical expansion of evolutionary biology (Grantham, 1995). These new research areas deal with the larger temporal, geographical and taxonomic scales in biology. Taking Croizat's (1964) three factors for a biological synthesis, space, time, and form, we may consider that Macroevolution deals with the biology of species and monophyletic taxa, and with the evolution of form through time. Macroecology deals with the economy of communities and ecosystems, and the evolution of biotas through time.

Eldredge (1985, 1996) has argued that there are two distinct biological hierarchies in nature, the Evolutionary

¹ Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, 58059-900, João Pessoa, Paraíba, Brasil; mlchrist@dse.ufpb.br

Hierarchy and the Ecological Hierarchy. The evolutionary hierarchy consists of such levels as atoms, molecules, genes, cells, individuals, populations, colonies, species, and higher monophyletic taxa. In the ecological hierarchy, such levels as individuals, demes, populations, communities, ecosystems, and the whole biosphere (Gaia), may be recognized.

It is interesting to note that both these hierarchies imbricate at the population level, the level emphasized by neo-Darwinists. Macroevolution and Macroecology, in the expanded Biological Synthesis, deal with the higher levels in these ascending hierarchies.

Macroevolution includes Taxonomy, Paleontology, Phylogeny, and Biosystematics. Macroecology includes Community Studies, Conservation Studies, Paleobiology, Historical Biogeography, and Ecosystematics.

I define Biosystematics herein as the history of taxa (biodiversity), and Ecosystematics as the history of biotas (ecodiversity).

Biological systems

Evolutionary Biology studies open, interacting, self-replicating and self-regulating (steady state, autopoietic) organic systems, from cells to ecosystems. It deals with the most complex living products and processes of the more general phenomenon of Universal Evolution.

Our scientific heritage is strongly biased in its present tendencies to valorize studies at the more elementary levels of the hierarchies of nature (reductionism), rather than at the more complex levels (emergentism), to favour evolution (transformism) over stasis (homeostasis), to enhance process explanations (functionalism) over pattern reconstructions (structuralism), to think mostly in terms of primary causes and consequent effects (mechanicism), to the default of its converse (system theory), to preach optimal efficiency (adaptationism) over directed evolution (theleology), to search for physico-chemical principles (materialism) in detriment of distinct biological principles (organicism), to give priority to natural causes (naturalism) over final or transcendental causes (finalism), to glorify testable proposals (scientificism) and to excommunicate faith (metaphysics), to study nonhistorical (immanent) before historical (contingent) phenomena, to prefer chance (indeterminism) over regularity or necessity (determinism), to value accidental (random) over causal (purposeful) events, to reverence data (empiricism) over ideas (theory), to establish a one-way time arrow for

events (historicism) rather than a double-arrow (relativism), and, more recently, to valorize lower level molecular biology over higher level organismic biology.

A systems approach to science (Von Bertalanffy, 1952, 1968; Weiss, 1971; Bunge, 1979) does not instigate a radical opposite stance to these reductionist tendencies, but does tell us that a framework of complementarity for such philosophical dualisms may be rewarding and conducive to new insights (Folse, 1990). Like in all complex systems, feedback loops in both directions should be expected at all levels of the biological hierarchy. A systems approach also reminds us that at each successive level we should expect to discover emergent properties which cannot be fully explained by knowledge from the lower levels. Finally, information gained at the higher levels may help us to understand obscure points or indicate new perspectives for research at the lower levels, and vice-versa.

We should thus not be unduly surprised to learn that: (a) the future may well constrain past evolution (Campbell, 1985); see suggestion of the existence of anticipatory/cognitive genes (Campbell, 1982); (b) life may have no beginning or end, that is, living and nonliving things may be co-eternal in the universe (Haldane, 1954; Goudge, 1961), having only eternal self-maintaining properties (Margulis, 1990); (c) environments may be becoming adapted to their organisms, just as much as the other way round; (d) an embryo does not necessarily have to exist before the adult (the 'chicken and egg paradox' becomes non-existent); (e) ecosystems and their environments may significantly constrain lower-level evolutionary phenomena (Lovelock, 1979); (f) symbiotic interactions (symbiogenesis) strongly appear to have been responsible for the very emergence of eukaryotes (Margulis, 1981); (g) homeostatic (homeorrhetic) regulatory mechanisms may be an even more fundamental fact of life than evolutionary processes (Margulis, 1990); (h) stochastic speciation events may affect populational anagenetic transformations (Gould, 1989); (i) the "phenotype" may influence the "genotype" after all, notwithstanding the central dogma of genetics (Ho, 1986); (j) brains may function as replicators of our terrestrial Gaian superorganism - all we have to do is colonize space (Lovelock & Allaby, 1984; Turner, 1989); (k) consciousness and self-awareness may be the natural outcome of any sufficiently complex cybernetic system, including computers and robots (e.g., Asimov, 1970).

At least in principle such statements should not be more remarkable or awesome than relationships in the opposite

direction, like: (a) viruses may be the extreme paradigm of eternal selfish genes (Dawkins, 1976), which have discarded their mortal bodily interactors; (b) the shapes, sizes, growth patterns of such things from aardvarks and amino-acids to zebras and zygotes, are necessary consequences of exact physico-chemical laws (Thompson, 1917; Rensch, 1959; Lima-de-Faria, 1988); (c) phylogenies of the entire living world may be successfully reconstructed exclusively from a few selected molecular sequences (e.g., Li & Graur, 1990).

To illustrate how insights obtained from higher levels of the hierarchy may help to open new perspectives at the lower levels and produce feed-back loops in both directions, I briefly comment on the paper of Amorim et al. (1993). These authors concluded that two distinct evolutionary events are involved at distinct hierarchical levels: (a) one involving the molecular modification of a pre-existing gene at a single locus (syntrepty); (b) the other involving the process of plesiomorphic allele elimination at that locus in the population (synapousy). Their conclusion has important effects on the parsimony concept as applied to allele matrices. But their conceptual resolution is also interesting for providing a plausible theoretical basis for the intuitive concept of “underlying synapomorphy” (Saether, 1979) found at the higher levels. As there is no reason to believe that the event of synapousy will be necessarily completed at the species level, many cases now interpreted as homoplasies between taxa may be found to correspond to independent events of synapousy.

Thus Evolution has to be studied on different spatial and temporal scales, at different hierarchical levels, and in both directions within and between biological levels. The scientific theories, perspectives, models, philosophical premises, working hypotheses, methodologies of investigation and expected results may differ depending on these scales, levels and directions.

Such a growing awareness has led an increasing number of researchers to realize that the neo-Darwinian program for the study of evolution, centered mainly on the organismic and populational levels, has generated a Synthetic Theory of Evolution which is largely incomplete and unsatisfactory as a general paradigm for Evolutionary Theory.

At the molecular level, the Genetic Theory of Natural Selection (Dobzansky, 1970; Maynard Smith, 1989) has been growingly contested in favour of a model of molecular evolution of effectively neutral mutations (Kimura, 1983). It

should also be noted that Molecular Biology is distinct from organismic Biology in the sense that its study objects represent nonliving parts of living organisms. Furthermore, modern biology is still far from understanding the details of transcription of the “genotype” into the “phenotype” and the mutual interactions between these two levels.

At the other extremity, it is not possible to adequately extrapolate models developed at the populational level to taxa above the species level, because of the stochastic events of an historical nature which are involved in the process of speciation.

Consequently, present biology leads with three broad levels which are still relatively independent of each other: Molecular Biology, Organismic-Populational Biology and Historical Biology.

Organismic Biology has experienced its greatest revolutionary periods in the 1850s, when Darwin (1859) provided a mechanism and convincing evidence for evolution, and in the 1900s, with the acceptance of Mendelian heredity (Bateson, 1902, 1908). In the 1950s, Molecular Biology commemorates its revolution of the DNA (Watson & Crick, 1953), while Population Biology sees its zenith as a consequence of major breakthroughs provided by the neo-Darwinian Program (Mayr & Provine, 1980).

But in the 1950s also the seeds of a new research program were being sown: The Macroevolutionary Program, integrating the traditional disciplines of Systematics, Paleontology and Biogeography. The intense debate and development of Hennigian principles and methods (Hennig, 1950) in the 60s and 70s, and their application in a widening scale in the 80s and 90s, have provided the main stimulus for a profound renewal in the field of Historical Biology. If research continues to grow as exponentially and as excitingly as at present in this area, I venture to boldly predict that in this first decade of this millennium Historical Biology will provide the next biological revolution. By the way, Campbell (1982) suggested year 2009, the bicentenary of Darwin’s birth - and of the very idea of organic evolution (Lamarck, 1809) - as a hopeful date for a grand Evolutionary Synthesis.

Macroevolution

The Hennigian movement has not been restricted to Systematics, but has influenced the remaining historical disciplines with equally profound consequences.

Paleontology has lost its sovereignty for phylogeny reconstruction. The traditional view of fossils as providing direct hard evidence on ancestors, primitive characters, absolute ages and ordered sequences of taxa has been strongly debated, with organized approaches such as stratophenetics (Gingerich, 1979) being bitterly questioned. After a tumultuated period (Thomson, 1985), and the realization that Paleontology presently has no distinct phylogenetic method to offer to Historical Biology, this discipline may now focus more clearly on its truly unique dimensions: The study of (a) life manifestations extending eons of time into the past, (b) creatures unimaginable even to the wildest science fiction creators as we go back in time (Gould, 1990), and (c) dazzling successions of biotas through the Phanerozoic, representing an estimated total diversity several orders of magnitude larger than that known for our present biotas. All these facets ensure that Paleontology and Paleobiology will never die hard and fossilize: these disciplines will not lose their fascination and importance for those interested in the history of life.

Notwithstanding all the progress implied above for cladistic methods, it is remarkable how the theoretical foundations of phylogenetic inference continue insecure, despite the enormous conviction of the defenders of the cladistic school regarding the best methodology to be applied (Sober, 1988). To establish an entire practice on a methodological principle like parsimony (Farris, 1983) seems to strain the credulity of the incredulous. For this reason I am personally convinced that cladistics has to be based on a larger theoretical body of knowledge which may serve as a Metatheory (Tuomi, 1981) for cladistic practices. Further, as cladistic techniques are most appropriate for the hierarchical levels above populations, it seems to me that the new Macroevolutionary Theory, which is just starting to develop, represents the obvious candidate to function as a Paradigm for Historical Biology.

Historical Biology, the basis for the further development of Macroevolutionary Theory, are the subject of two distinct disciplines. Biosystematics, dealing with the history of species and monophyla through space and time (the study of biodiversity), and Ecosystematics, dealing with the history of ecosystems and biotas through space and time (the study of ecodiversity).

Biosystematics

Historically, the study of biological diversity has been centered around the compilation and description of living beings, grouped into the lowest identifiable groups of organisms. Even with the acceptance of Evolution (Darwin, 1859), taxonomic practices have changed little until the middle of the 20th century. The New Systematics (Huxley, 1940, 1942) stimulated the development of populational thinking and of “biological” concepts for the smallest taxonomic units (Mayr, 1942). Unfortunately, evolutionary thinking has, until recently, remained restricted to these lower taxonomic levels. Macrotaxonomy continued to be practiced under a largely typological perspective.

Under the domain of neo-Darwinism, systematics overlapped largely with Population Genetics, Evolutionary Ecology, Behavioral Biology and Developmental Biology. The evolutionary history of taxa in geological time and global space has been approached largely by reductionist extrapolations derived from data of population biology and autoecology.

Since Darwin’s (1859) insight that “our classifications must be, as far as possible, genealogical”, few taxonomists have realized that degrees of similarities and differences are not adequate criteria on which to infer the evolutionary history of organisms. Hennig (1950) finally established a consistent method to infer phylogenetic relationships among species and among monophyletic taxa.

Biosystematics was originally a populational concept, used largely by botanists (Johnson, 1970; Böcher, 1970). Griffiths (1974) uses this term in a broader context which includes all of the higher taxa of the biological system, but still placed Biosystematics within the populational level of the biological hierarchy.

But in this hierarchy of living elements, species are very gradually being recognized as forming a level distinct from populations and monophyletic taxa. First the appropriateness of the biological definition of species - an atemporal relational concept - has been questioned (Simpson, 1961; Wiley, 1978), then the individual-like nature of species has been fought for (Ghiselin, 1975; Hull, 1976), and finally the gradual accumulation of anagenetic changes in populations has been challenged as an adequate explanation for speciation, in favour of the primacy of stochastic cladogenetic events (Eldredge & Gould, 1972).

I thus consider species to be finally decoupled from populations (Stanley, 1979) and, consequently, Biosystematics to be decoupled from Population Biology. Species become the smallest individual lineages of ancestral-descendant populations separated by two stochastic cladogenetic events (speciations), while higher taxa are nested sets of monophyla which include an ancestral species and all of its descendants. Biosystematics includes the systematization of both living and fossil taxa.

Ecosystematics

In Historical Biogeography, which developed on a scientific basis starting with the insights of Croizat (1952, 1958, 1964) on vicariant events before the Geologic Revolution of Plate Tectonics in the 60s (Hallam, 1973), cladistic methods were introduced by Nelson (1970). This generated new techniques, new theoretical models and a new outlook for Historical Biogeography. Today an intense debate in this area is still taking place (Myers & Giller, 1990), analogous to that between pheneticists and cladists in the 60s and 70s. The polarization occurs, respectively, between the schools of Panbiogeography (Craw, 1987) and Vicariant Biogeography (Humphries & Parenti, 1986).

Ecosystematics deals with the history and systematization of the various levels of the ecological hierarchy. Amorim (1992) has recently proposed a practical system for naming biogeographic components. Such a biogeographical reconstruction relates more to space than to ecosystems. I suggested (Christoffersen, 1995) that the broad basis upon which to develop Ecosystematics may start with the identification of areas in which a community of populations have interacted through a period of time. It will evidently be necessary to refine such a system so as to reflect precise ecosystem information, all the way down to the basic units of our Gaian system.

Ecosystematics is still a young science, but its potential contribution to Macroevolutionary Theory seems enormous. At this stage it is important that the basic units of ecosystems be identified and systematized. I also suggested (*op. cit.*) that monophyla may finally be categorized into relative taxonomic ranks most conveniently based on biogeographic systems. These biogeographic ranks would gradually substitute the Linnean ranks and would convey the system structure of monophyletic biotas evolving through time (Christoffersen, 1995).

Conclusions

Macroevolutionary Theory thus involves both the study and explanation of the diversity of taxa and biotas through space and time. It concerns the origination, expansion, diversification, interaction, coevolution, competition, extinction, homeostasis and evolutionary rates of such taxa as man to the whole of Life (named Biotae by Christoffersen, 1989) and of such associations from a particular pathogenesis or root nodule to Gaia.

Still lacking in most macroevolutionary hypotheses are efficient retrospective tests, which may serve to corroborate such hypotheses (Giere, 1984), once there is presently no possibility of applying experimental tests in the historical dimension. But, irrespective of the outcome of macroevolutionary hypotheses such as (a) the symbiotic theory of the origin of eukaryote organization and meiosis (Margulis, 1981, 1990), (b) punctuated equilibria (Eldredge & Gould, 1972), (c) the cyclic pattern of biotic extinctions (Raup & Sepkoski, 1988), (d) the existence of an intelligent Universe (Hoyle, 1985; Minsky, 1985), (e) the “Mesozoic model”, instead of the refuge theory, for the evolution of the neotropical biota (Amorim, 1991), (f) the existence of internal constraints on developmental pathways (Alberch et al. 1979), etc., the important point is the following. The search for new evolutionary theories has permitted the development of complementary models for the interpretation of evolutionary pattern and processes that would never have been dreamt of within the neo-Darwinian straitjacket.

It is now time to integrate Macroevolution and Macroecology into the New Biological Synthesis.

Acknowledgements

A continued scholarship from CNPq has been my true blood-line for the ontogeny of my research up to this point.

References

- ALBERCH, P., GOULD, S.J., OSTER, G.F. & WAKE, D.B. 1979. Size and shape in ontogeny and phylogeny. *Paleobiology* 5:296-317.
- AMORIM, D.S. 1991. Refuge model simulations: testing the theory. *Revista Brasileira de Entomologia* 35:803-812.

- AMORIM, D.S. 1992. An empirical system of ranking of biological classifications using biogeographic components. *Revista Brasileira de Entomologia* 36:281-292.
- AMORIM, D.S., ARAÚJO, M.E. & SOLÉ, A.M. 1993. Origin and evolutionary novelties and elimination of plesiomorphic alleles: some comments on limitations of the concept of synapomorphy. *Revista Brasileira de Genética* 16:245-252.
- ASIMOV, I. 1970. *I, robot*. Connecticut: Fawcett Crest Book.
- BATESON, W. 1902. *Mendel's principles of heredity*. Cambridge: Cambridge University Press.
- BATESON, W. 1908. *The methods and scope of genetics*. Cambridge: Cambridge University Press.
- BÖCHER, T.W. 1970. The present status of biosystematics. *Taxon* 19:3-5.
- BUNGE, M. 1979. *A world of systems*. Dordrecht: Reidel.
- CAMPBELL, J.H. 1982. Autonomy in evolution. In: MILLIKAN, R. (ed.), *Perspectives on evolution*. Sunderland: Sinauer. p. 190-201.
- CAMPBELL, J.H. 1985. An organizational interpretation of evolution. In: DEPEW, B.H. & WEBER, B.H. (eds.). *Evolution at a crossroads: the new biology and the new philosophy of science*. Cambridge: Bradford Books. p. 133-167.
- CHRISTOFFERSEN, M.L. 1989: Proposta de um novo táxon para o conjunto dos seres vivos. In: CHRISTOFFERSEN, M.L. & AMORIM, D.S. (eds.). *Resumos do XVI congresso brasileiro de zoologia*. João Pessoa: Gráfica Santa Marta. p. 252.
- CHRISTOFFERSEN, M.L. 1995. Cladistic taxonomy, phylogenetic systematics, and evolutionary ranking. *Systematic Biology* 44:440-454.
- CRAW, R.C. 1987. Panbiogeography and structuralist biology. *Rivista di Biologia, Biology Forum* 80:226-229.
- CROIZAT, L. 1952. *Manual of phytogeography or an account of plant dispersal throughout the world*. The Hague: Junk.
- CROIZAT, L. 1958. *Panbiogeography, or an introductory synthesis of zoogeography, phytogeography, and geology; with notes on evolution, systematics, ecology, anthropology, etc.* Vols. 1, 2a-b. Caracas: Published by the author.
- CROIZAT, L. 1964. *Space, time and form; the biological synthesis*. Caracas: Published by the author.
- DARWIN, C.R. 1859. *On the origin of species by means of natural selection, or the preservation of favored races in the struggle for life*. London: Murray.
- DAWKINS, R. 1976. *The selfish gene*. New York: Oxford University Press.
- DOBZHANSKY, T. 1970. *Genetics of the evolutionary process*. New York: Columbia University Press.
- ELDREDGE, N. 1985. *Unfinished synthesis: biological hierarchies and modern evolutionary thought*. New York: Oxford University Press.
- ELDREDGE, N. 1996. Hierarchies in macroevolution. In: JABLONSKI, D., ERWIN, D.H. & LIPPS, J.H. (eds). *Evolutionary paleobiology. In honor of James W. Valentine*. Chicago: The University of Chicago Press.
- ELDREDGE, N. & GOULD, S.J. 1972. Punctuated equilibria: an alternative to phyletic gradualism. In: SCHOPF, T.J.M. (ed.), *Models in paleontology*. San Francisco: Freeman. p. 82-115.
- FARRIS, J.S. 1983. The logical basis of phylogenetic analysis. In: PLATNICK, N.I. & FUNK, V.A. (eds.). *Advances in cladistics*. Vol. 2. New York: Columbia University Press. p. 7-36.
- FOLSE, H.J., Jr. 1990. Complementarity and the description of nature in biological science. *Biology and Philosophy* 5:211-224.
- GHISELIN, M.T. 1975. A radical solution to the species problem. *Systematic Zoology* 23:536-544.
- GIERE, R.N. 1984. *Understanding scientific reasoning*. 2nd ed. New York: Holt, Reinhart and Winston.
- GINGERICH, P.D. 1979. The stratophenetic approach to phylogeny reconstruction in vertebrate paleontology. In: CRACRAFT, J. & ELDREDGE, N. (eds). *Phylogenetic analysis and paleontology*. New York: Columbia University Press. p. 40-72.
- GOUDGE, T.A. 1961. *The ascent of life: a philosophical study of the theory of evolution*. Toronto: University of Toronto Press.
- GOULD, S.J. 1989. Punctuated equilibrium in fact and theory. *Journal of Social and Biological Structures* 12:117-136.

- GOULD, S.J. 1990. *Wonderful life. The Burgess Shale and the nature of history*. London: Hutchinson Radius.
- GRANTHAM, T. 1995. Hierarchical approaches to macroevolution. *Annual Review of Ecology and Systematics* 26:301-321.
- GRANTHAM, T. 2007. Is macroevolution more than successive rounds of microevolution? *Palaeontology* 50 75-85.
- GRIFFITHS, G.C.D. 1974. On the foundations of biological systematics. *Acta Biotheoretica* 23:85-131.
- HALDANE, J.B.S. 1954. The origins of life. *New Biology* 16:12-27.
- HALLAM, A. 1973. *A revolution in the earth sciences; from continental drift to plate tectonics*. Oxford: Clarendon Press.
- HENNIG, W. 1950. *Grundzuge einer theorie der phylogenetischen Systematic*. Berlin: Deutscher Zentralverlag.
- HO, M.-W. 1986. Heredity as a process. Towards a radical reformulation of heredity. *Rivista di Biologia, Biology Forum* 79:407-447.
- HOYLE, F. 1985. *The intelligent Universe*. London: Joseph.
- HULL, D.L. 1976. Are species really individuals? *Systematic Zoology* 25:174-191.
- HUMPHRIES, C.J. & PARENTI, L.R. 1986. *Cladistic biogeography*. Oxford: Clarendon Press.
- HUXLEY, J.S. 1940. *The new systematics*. Oxford: Clarendon Press.
- HUXLEY, J.S. 1942. *Evolution, the modern Synthesis*. London: Allen and Unwin.
- JOHNSON, L.A.S. 1970. Biosystematics alive? - A discussion. *Taxon* 19:152-153.
- KIMURA, M. 1983. *The neutral theory of molecular evolution*. Cambridge: Cambridge University Press.
- LAMARCK, J.P. de. 1809. *Philosophie zoologique*. Paris: Dentu.
- LI, W.H.; GRAUR, D. 1990. *Fundamentals of molecular evolution*. Sunderland: Sinauer.
- LIMA-DE-FARIA, A. 1988. *Evolution without selection. Form and function by autoevolution*. Amsterdam: Elsevier.
- LOVELOCK, J.E. 1979. *Gaia: a new look at life on Earth*. Oxford: Oxford University Press.
- LOVELOCK, J.E. & ALLABY, M. 1984. *The greening of Mars*. London: St. Martin's Press.
- MARGULIS, L. 1981. *Symbiosis in cell evolution. Life and its environment on the early earth*. San Francisco: Freeman.
- MARGULIS, L. 1990. Kingdom Animalia: the zoological malaise from a microbial perspective. *American Zoologist* 30:861-875.
- MAYNARD SMITH, J. 1989. *Evolutionary genetics*. Oxford: Oxford University Press.
- MAYNARD SMITH, J. & SZATHAMARY, E. 1995. *Major transitions in evolution*. New York: W. H. Freeman.
- MAYR, E. 1942. *Systematics and the origin of species*. New York: Columbia University Press.
- MAYR, E. & PROVINE, B. (eds). 1980. *The evolutionary synthesis: perspectives on the unification of biology*. Cambridge: Harvard University Press.
- MCLAUGHLIN, B. 1992. the rise and fall of British emergence. In: BECKERMAN, A. & FLOHR, H.J. (eds.). *Emergence or reduction?* Berlin: DeGruyter.
- MINSKY, M. 1985. Why intelligent aliens will be intelligible. In: REGIS, E. (ed.), *Extraterrestrials*. Cambridge: Cambridge University Press. p. 117-128.
- MYERS, A.A. & GILLER, P.S. 1990. Biogeographic reconstruction. Introduction. In: MYERS, A.A. & GILLER, P.S. (eds). *Analytical biogeography. An integrated approach to the study of animal and plant distributions*. London: Chapman and Hall. p 301-310.
- NELSON, G.J. 1970. The problem of historical biogeography. *Systematic Zoology* 18:243-246.
- RAUP, D.M. & SEPKOSKI, J.J., Jr. 1988. Testing for periodicity of extinction. *Science (Washington D.C.)* 241:94-96.
- RENSCH, B. 1959. *Evolution above the species level*. London: Methuen.
- SAETHER, O.A. 1979. Underlying synapomorphies and anagenetic analysis. *Zoologica Scripta* 8:305-312.

- SIMPSON, G. 1961. Principles of animal taxonomy. New York: Columbia University Press.
- SOBER, E. 1988. Reconstructing the past: parsimony, evolution, and inference. Cambridge: MIT Press.
- STANLEY, S.M. 1979. Macroevolution. Pattern and Process. San Francisco: Freeman.
- THOMPSON, d' A.W. 1917. On growth and form. Cambridge: Cambridge University Press.
- THOMSON, K.S. 1985. Is paleontology going extinct? *American Scientist* 73:570-572.
- TUOMI, J. 1981. Structure and dynamics of Darwinian evolutionary theory. *Systematic Zoology* 30:22-31.
- TURNER, F. 1989. Life on Mars: cultivating a planet and ourselves. New York: Harper.
- VON BERTALANFFY, L. 1952. Problems of life. An evaluation of modern biological thought. New York: Harper.
- VON BERTALANFFY, L. 1968. General system theory. Foundations, developments, applications. New York: Brazillier.
- WATSON, J.D. & CRICK, F.H.C. 1953. Molecular structure of nucleic acids: a structure for deoxyribose nucleic acid. *Nature (London)* 171:737.
- WEISS, P.A. (ed.). 1971. Hierarchically organized systems in theory and practice. New York: Hafner.
- WILEY, E.O. 1978. The evolutionary species concept reconsidered. *Systematic Zoology* 27:17-26.