Populations, ecosystems and global diversity: the scientific work of Antoni Hoffman

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Es gehört oft mehr Mut dazu, seine Meinung zu ändern, als ihr treu zu bleiben. (Friedrich Hebbel)

When I first met Antoni Hoffman in 1980 he had come to Tiibingen to work in the Department of Geology and Paleontology with a fellowship from the Alexander von Humboldt-Foundation. Dolf Seilacher was his host. Antoni Hoffman was already well-known for his extensive article 'Community paleoecology as an epiphenomenal science' published in Paleobiology in 1979. It was quite remarkable that a young, unknown scientist, who had not published much, set out to criticise a whole scientific discipline simply on the basis of a vast knowledge of the Literature and his ability to analyse scientific results and methodologies most succinctly. The reference section of that paper comprises 400 titles that cover large areas of paleontology and ecology but also the philosophy of science. As young paleontologists who learn the trade were supposed (and still are) to become very familiar with a taxonomic group and the analytical and descriptive methods of the discipline and do extensive field work Antoni Hoffman's strategy was quite unusual. Being five years older than he, I had about that much earlier (1974) risked my own reputation as a functional morphologist by pointing out in a purely theoretical and methodological article, that paleontologists in central Europe neglected evolutionary theory and that those who wrote about evolution still supported outdated orthogenetic speculations implicitly or explicitly. I knew quite well that the scientific establishment in the West resented such criticism and I was very curious to see how Antoni Hoffman would develop during his stay in Tübingen (1980 to 1982).

He did not join the Research Division (SFB)*53* 'Paleoecology' of the University of Tiibingen (founded and headed by A. Seilacher) but wrote theoretical articles on metascientific problems, on ecostratigraphy, on methods of paleobiology and on Punctuated Equilibria. He contributed a review of the methods of community paleoecology to a report of the SFB (Hoffman 1982b) in which he criticised the work of the community paleoecologists of the SFB and in which he suggested that there were other fruitful problems for community paleoecology than were done in Tubingen.

Antoni Hoffman and I soon found out that we had many interests and opinions in common, for example on macroevolution, on methods of paleontology and on phylogenetic systematics and we had many fruitful discussions. However, during Antoni's stay in Tübingen we did not publish together partly because I wrote my habilitation thesis on a topic in vertebrate paleontology. When I started a project on the history of paleontology he told me that he was not interested in the history of science. Apparently he wanted to stay in the main-stream of research instead of looking at it from the perspective of a historian. Nevertheless he knew the history of ideas well which is shown in his introductory article to the book *Mass* Extinctions. Processes and Evidence edited by Stephen K. Donovan in 1989 and in all the historical expositions of his book Arguments (Hoffman 1989a). I have no doubts that our discussions influenced me significantly. After Antoni Hoffman had left for the USA in spring 1982 I gave an inaugural lecture as a Privatdozent that dealt with the inability of paleontology finding macroevolutionary laws in the fossil record. On the basis of our discussions I had thought that it was important to introduce such a topic – that was discussed already at that time in international fora – to the academic public in Tubingen. After my lecture, however, it was pointed out to me that it was bad style to show in an inaugural lecture what a science can not do, instead to show what it can do.

Only after Antoni's return to Poland in 1986 did we start a joint project that attempted to defend paleontology against the physics-envy-driven view that paleontology and all other natural sciences could only then be regarded seriously as science if they were thoroughly nomothetic. We tried to show how important the narrative, idiographic side and its methods are in paleontology, ecology and many other fields of the earth and life sciences. We hoped to make clear that the history of earth and life had to be read and interpreted from the data and told in a long narrative in the same hermeneutical way as a scholar reads and interprets old texts. The hermeneutical circle played the central role in our methodology. It says that no detail can be understood without an understanding of the whole and the whole cannot be understood without an understanding of the details. This project produced three publications preceding Antoni Hoffman's death.

Social background

Antoni Hoffman once told me that he had learned English from his father, who was an important political intellectual in post-war Poland. I assume that his father influenced his whole thinking strongly and thus must have contributed to Antoni's characteristic view of science. In the preface to his book Arguments on Evolution Antoni Hoffman said that he had grown up in a tradition of the questioning of all authority. 'Perhaps this is a by-product of the school that, as a rule, expected us, students, to believe without any second thoughts whatever the authority – the teacher, the text-book, you name it – gave us to believe, while it was often quite obvious that the authority was wrong. Scepticism has thus become my nature' (1989a: p. vi). I do not think that this is a sufficient explanation and that he probably was not aware of influences that must have come from his family, because if the explanation were true, all

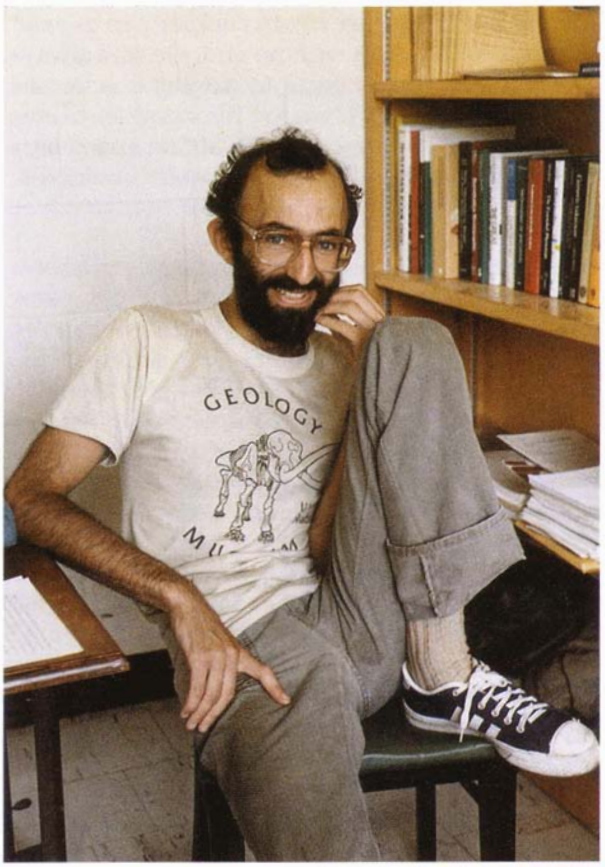

Fig. 1. Professor Antoni Hoffman (1950–1992) as we remember him.

members of authoritarian, ideological systems would become sceptics. Rather I think that Antoni was already a critical thinker when he entered school.

When he first came to Tübingen in 1980 at the age of 30, he already appeared as a mature scientist who was fully aware of methodological issues of paleontology and of philosophical and metascientific options (see Hoffman 1981b). During the years he spent in Germany and the USA he may have changed his mind about scientific issues and widened the spectrum of his research interests, but from the very beginning his publications seem to follow a logical chain of thought. In a contribution to Marjorie Grene's symposium (Hoffman 1983a) he mentioned three main inspirations as a student, the evolutionary ecologists in Cracow (Adam Łomnicki and his coleagues), the philosophers of science in Warsaw (Stefan Amsterdamski and his coleagues), and the paleobiological community of Warsaw.

Science was for Antoni Hoffman an intellectual enterprise where the written word, the exact wording of a theory counted most – much more than illustrations, diagrams or specimens. For him the central aim of a scientist was to test theories, despite knowing that 'facts' in science could never be seen outside of a theoretical context. He rejected the Popperian asymmetry that theories can only be falsified but never verified. For him there was no single falsifying

death-blow to a theory but also no final verification. He, in comparison to most of his colleagues, regarded science more as a task with no end. He was always willing to devote his untiring, uncompromising efforts to solving a scientific problem. He did not cling to a favourite idea but changed his mind whenever necessary and expected the same of his colleagues. He was highly suspicious of any attempt to persuade the scientific community, not with well-considered, well-formulated arguments, but with the selling-methods of the market-place or with journalistic skills.

Field work, experiments, descriptions, diagrams, illustrations, measurements, accumulation of data, comparisons, statistical analyses, computer simulations etc. were only tools for him to arrive at general conclusions to support or reject an assumption. It goes without saying that he knew the classical works of all modem philosophers of science – Popper, Hempel, Feyerabend, Duhem, Quine, etc. – but he was also familiar with the writings of philosophers such as Descartes, Hegel, Marx, Husserl, etc. Such a deep interest in philosophy may represent a family trait if one considers that his brother is a professor of philosophy in the USA. Despite such knowledge Antoni avoided the strategy of some of his contemporaries, namely throwing the names of philosophers or their descriptions or prescriptions of scientific method into the face of an opponent instead of using clear and well-formulated arguments. Of course he expected his colleagues to be as well-read in the philosophy of science as he was. When for instance, he wrote in a certain context that he was referring to the K.R. Popper of the *Poverty of Historicism* and not to the K.R. Popper of the *Logic of Scientific Discovery*, as a reader one had to be aware of the difference and one had also to remember that the *Poverty of Historicism* takes a strict stance against Marxism.

A command of English became Antoni Hoffman's most important scientific tool, because he used it unlike most of his colleagues, who read simply what was necessary in order to work in a narrowly defined scientific field. He translated from Polish into English for Polish scientific journals when he was unemployed as a political dissident (1976–1980) in order to make a living for himself and his family. In 1980 the English language opened for him a door to the West at a time when any idea of a collapse of the Iron Curtain was still absolutely utopian. (The scholarship of the Alexander von Humboldt-Foundation ended that difficult time of unemployment. Within weeks after arriving in Tübingen he learned German and from then on spoke only German with us.)

Reading English (including a few other languages) also opened to him the all-important door to the intellectual world. He was proud of what literature was available in Polish (some books had been translated from the English into Polish even earlier than into German) and he and his wife with their own translations of scientific books and articles contributed much to that literature. It was an extremely wide spectrum of scientific and philosophical books published in English that he read carefully and that contributed to his scientific world. He reviewed many of these books, but they were book-reviews of outstanding quality. They are long, hardly ever under 400 words but often up to 3000 words. He did not only evaluate the merits of the books but also placed them into context – informing the reader but also demanding much concentration and knowledge of the reader. As he wrote most reviews in English for the German *Zentralblatt für Geologie und Palaontologie* it is not certain how

many readers he had, but from reading the reviews myself I know that they were also collections of material and ideas for himself (a kind of reading-diary), which he used in future projects and major review articles.

His excellent command of the English language was the prerequisite for his careful analysis of those publications on ecological and evolutionary theory that were at the center of his interests. He read them so carefully that he found out that the reason for a scientific debate in the literature often was that there existed several different formulations of the same hypothesis. For instance, probably no one has traced the different versions of the hypothesis of Punctuated Equilibria and studied their implications as carefully as Antoni Hoffman in his book Arguments on Evolution.

The English language was of course also his major tool for scientific communication. He knew a large number of scientists personally or from letters and it is impressive to see in the 'Acknowledgments' of his publications that he always sent his manuscripts to several such experts before he submitted them to a journal. His complete work in English comprise one book, two more that he edited, more than 80 publications and progress reviews and more than 160 book reviews and abstracts.

Methodological attitude

It is to these scientific articles and the book that I now turn in order to trace the development of his ideas during the short time that he had available. (I cannot comment on his Polish publications and I shall not give all individual references of the papers I refer to. They easily can be identified in Antoni's bibliography in this volume.) This will not be a scientific biography let alone a description of his life but I will try to analyse how he gradually picked up all those topics and ideas that he so masterly presented in his Arguments on Evolution and how it came that he introduced himself as a 'sceptic' even in the title of one of his papers. This epithet was used later in a derogatory way by others in order to characterize him at a time when his enthusiasm about new ideas and scientific projects in paleooceanography and stable isotopes already outweighed his scepticism regarding the merits of macroevolutinary theories and generalizations.

All his publications and book-reviews address not the specialist of any kind, but a wider audience. However, reading them requires a considerable knowledge. How important the written word was for him – in a science like palaeontology that virtually lives from pictures – is shown by the fact that virtually none of his publications contains an illustration, but only tables and statistical diagrams. Antoni Hoffman's book Arguments on Evolution has no illustrations and no diagrams at all. His publications and reviews are still important and worthwhile reading today because they were written as contributions to the scientific discourse of paleontology and not as technical communications.

Antoni Hoffman soon found that the number of readers who would be willing to engage with him in a scientific discourse was not very large. Unlike most other paleontologists he was regarded as a 'mere theorist' who was not a specialist on any taxonomic group and who had little field experience. Many colleagues reacted negatively to his criticism. The different attitudes towards him can be clearly seen through a comparison of the reviews of his Arguments

on Evolution (1989)in Nature and Science. As he knew both reviewers, Richard Dawkins and David Jablonski, quite well, their different reactions could not have surprised him much. Jablonski's review is critical and rather negative. In addition the review received the headline (by the author or by an editor of Science) 'Neoconservative paleobiology'. This clearly reveals the view evidently supported by Science that scientific judgements are considered as a matter of persuasion and politics rather than of argument and conviction.

Of course Antoni Hoffman shared with all 'paleontological theorists' the criticism of the descriptive paleontologists namely, that they were uncritically using data from the literature (for example the Treatise on Invertebrate Paleontology) and were not able to evaluate the uncertainties of such a data set.

Despite the fact that he never attacked any fellow scientist personally he was regarded as a court-jester, a *Till* Eulenspiegel or an owlglass who confronted his colleagues with a mirror which showed them their weaknesses. Others criticized him as a kill-joy who trampled upon the favourite ideas of his colleagues and hence they spitefully avoided quoting him in their own publications.

To be sure, Antoni Hoffman took a clear and explicit stance with respect to scientific methodology. He did not agree with some of his colleagues who thought it was sufficient from a Popperian perspective of science that one had to be very bold in inventing new ideas. He demanded that new hypotheses were to be tested most rigorously before they could be taken seriously. He also did not agree with the view that it was time to overthrow the 'dull' normal science (in the sense of T.S. Kuhn) of neo-Darwinism by a paradigm shift towards a hierarchical theory of evolution in which neo-Darwinism was to play only a small role. He not only thought that neo-Darwinism still presented a very large number of interesting problems but argued from the perspective of 'pragmatic reductionism' (a term that he coined in 1983 in order to specify Occam's Razor – that theories should employ as few terms as possible – in the context of narrative and idiographic science) that there were no empirical reasons to expand neo-Darwinism by adding new evolutionary 'laws', let alone to demolish this theory.

Paleoecological works

Antoni Hoffman appeared in 1974 in the arena of publishing paleontologists as a community paleoecologist (or a paleosynecologist) with a full command of the literature and also of statistical methods who set out to test methods and hypotheses of this science. The field of community paleoecology had won great attention since the late 60s. In his review in Marjorie Grene's symposium volume (Hoffman 1983a: p. 243) he described Everett Olson, J.A. Shotwell, Jim Valentine, Peter Bretsky, and Arthur Boucot as the classic writers of this discipline. '...they did not restrict the scope of their empirical analyses and theoretical considerations to ecological time. They regarded community paleoecology as something more than, or at least different from community ecology projected into the geological past' (Hoffman 1983a: p. 244). Hence this discipline was regarded by many earth scientists as the most promising area of all paleontology because it combined very different approaches and aspects and gave direct access to the history of the whole biosphere and the principles

that ruled its evolution. In other words Antoni chose the most challenging field of paleontology for his own research.

His first published papers are based on his unpublished dissertation on the Korytnica clays (Miocene). He published a detailed synecological study (based on factor analysis) of the assemblages and their environmental control, stability and evolution (Hoffman 1976a–b, 1977a–f). He regarded the six assemblages that he identified as indicators of an ecological succession, but he remarked that his data did not help him to corroborate some common ecological hypotheses that he knew from the classical literature and that related ecological complexity, taxonomic diversity, ecological maturity, and environmental predictability to each other. The fact that such an important field had failed to withstand his scrutiny was very disappointing for him and must have formed the basis for his developing scepticism with respect to theory-formulation in ecological and evolutionary paleontology.

Individual autoecological studies from the Korytnica clays were published as a basis for synecology. There are statistical analyses of predation by muricid and naticid gastropods (Hoffman *et al.* 1974) and several studies on character displacement in gastropods and on growth and on mortality patterns in gastropods and bivalves (Hoffman 1976a–b, 1978a–b). In these studies empirical data were not at the center of interest but rather the general concepts such as environmental control of life history strategies and r-and-K-selection regimes. Not surprisingly Antoni was always explicit about the methodological problems of applying ecological methods to paleontological material.

Together with colleagues he analysed Miocene kelp-associated macrobenthic ecosystems from Poland (Hoffman *et al.* 1978), Permian marine assemblages from Spitsbergen (Małkowski & Hoffman 1979) and benthic foraminiferal associations (Hoffman & Pisera 1979).

Antoni Hoffman's major observation during these years was that ecological and paleoecological terms and concepts were rather 'vague and cloudy' (his own words). Consequently he did not regard it as sufficient to test ecological generalizations rigorously with empirical examples. Rather, he submitted the discipline to a methodological analysis and proposed that only a clear system-theoretical approach could help to analyze patterns and processes in community paleoecology. He developed a systems-model for the kelp-associated macrobenthic ecosystem and presented his general ideas in his first major theoretical paper in *Lethaia* (Hoffman 1978e).

In 1979 he came back to the assemblages in the Korytnica clays. He showed that – depending on the ecological theory one chooses – the assemblages could be interpreted in different ways. This justified grave doubts with respect to the community-paleoecological approach.

The conclusion of all this was summarized in 'Community paleocology as an epiphenomenal science', a long article in *Paleobiology* (Hoffman 1979e). The central problem he discussed was the ontological status of communities. He doubted that communities represented a distinct, real level of biotic organization achieved through ecological integration of, and coevolution among, species. He had two arguments: (1) The actual degree of community integration is in general insufficient to induce any driving forces for a structural development as predicted by the system theory. (2) The concept of biological reality and distinctness of the community level of biotic organization implies assign-

ment of a significant role to group selection. Yet group selection had never been empirically demonstrated and had to be rejected for theoretical reasons. Empirical studies had refuted the assumption that communities have a typical behaviour by developing gradually towards an equilibrium state representing an optimum habitat partitioning among component species. There was no intrinsic, biotic mechanism inducing community dynamics in either ecological or evolutionary time. In other words communites are not 'superorganisms' that show a predictable behaviour in ecological time nor can they be regarded as units that evolve. These are the reasons why Antoni regarded ecological communities as descriptive conventions, as merely epiphenomena of the overlap in distributional patterns of various organisms. Compared to the problems of ecologists additional methodological problems arise for a paleoecologist due to all the taphonomic biases. Nevertheless Antoni regarded paleocommunity studies as valuable tools for paleoenvironmental reconstructions and for the analysis of environmental factors influencing niche dimensions and longevity of species.

Despite the fact that he regarded communities as epiphenomena Antoni Hoffman continued to give rigour to the study of changes of communities in ecological and evolutionary time by applying systems concepts (Hoffman 1980a). His doubts that communities are units that are subject to independent selective forces not reducible to the individual level, led to three papers (Hoffman 1980b, 1981a, and 1982a) on the concepts of ecostratigraphy. His conclusion was that as ecosystems do not evolve autonomously they also cannot be used as stratigraphical indices in the same way as guide-fossils. Nevertheless paleocommunities can be used within narrow geographical regions, e.g within basins, to demarcate important geohistorical events.

Theoretical evolutionary works

A paper by Tom Schopf on stochastic approaches to paleontology led Antoni Hoffman to write a metascientific analysis of paleonlology in 1981. He showed that stochastic and deterministic approaches are both based on a number of metaphysical options that one decides upon before attacking a scientific problem. Both are equally valid and may provide law-like–principles and may lead to complementary results.

Around 1980 Antoni Hoffman became more and more aware that not only systematists, stratigraphers and evolutionary theorists but also paleoecologists like himself had something to say in the context of the wave of discovery of macroevolutionary 'laws' that had started with the Punctuated Equilibria of Niles Eldredge and Stephen Jay Gould in 1972 and Leigh Van Valen's Red Queen hypothesis in 1973. The discussion and criticism of macroevolution was to become his major subject for the next decade.

In three papers (Hoffman 1978f, 1981c, and 1982c he discussed possible developmental and ecological mechanisms (and their paleontological tests) that control gradualism, stasis and punctuation in the evolution of a species lineage. He argued that developmental canalization and plasticity may be adaptive and genetically determined. Hence Punctuated Equilibria cannot serve as an argument for macroevolution being decoupled from microevolution as had been claimed by the macroevolutionists.

The Red Queen Hypothesis of Van Valen says that taxonomic survivorship curves are log-linear in various organic groups, which means that extinction rates are constant in an order or class and independent of the age of that taxonomic group. Other authors had tried to relate species durations to various ecological characteristics. In 1982 and 1983 Antoni Hoffman (Hoffman & Szubzda-Studencka 1982; Martinell & Hoffman 1983) showed together with coauthors that bivalve species with a wide geographic distribution had a significant longer duration than species with a small distribution. Ecological characteristics have no influence on species longevity.

In a contribution to the work of the SFB 'Paleoecology' in Tübingen and in a long discussion for a symposium edited by the philosopher Marjorie Grene Antoni clearly expressed his disappointment in the current results of paleobiology. 'I myself shared the hope and enthusiasms with the most fervent adherents to the research concept of community paleoecology. This may explain why I perceive its achievements so critically, but also why I am so desperately attempting to appreciate its actual promises... no biological problems have thus far been found which could be solved by analysing the fossil record of ecosystems.' (Hoffman 1982b: p. 252).

In the paper of 1982 he said that community paleoecology had still fruitful problems in paleoenvironmental reconstruction, the study of niche differentiation, ecological succession and intrapopulation variability, but these were not specifically paleo-ecological ones.

In the contribution to the symposium (Hoffman 1983a) he not only criticised community paleoecology but he elaborated on several macroevolutionary topics. He criticized the model of the development of global diversity in the Phanerozoic as well as the attempt to explain this curve by an equilibrium model and argued that the hypothesis of Punctuated Equilibria cannot serve as an argument for the statement that macroevolution is decoupled from microevolution. He suggested that paleobiologists concentrate on fruitful projects like theoretical morphology, constructional morphology and biological responses to long-term environmental changes.

Also in the contribution to Marjorie Grene's symposium, Antoni Hoffman indicated that the fossil record may be good enough to test the Red Queen Hypothesis which he saw clearly as a neodarwinian theory and not as an antidarwinian theory. In that same year Niels Stenseth and John Maynard Smith had clarified the discussion on the Red Queen hypothesis by developing two alternative evolutionary models of multispecies systems. Evolution is either driven principally by biotic interactions (this would be in accordance with the Red Queen) or evolution is propelled primarily by abiotic factors and will stop in the absence of changes in abiotic parameters (Stationary Model). The authors concluded that a decision between the two theories can only be made by tests of the fossil record. In 1984 Antoni Hoffman and Jennifer Kitchell published an extensive test by using data on Tertiary planktic species. As far as I know this test which used more than 950 species has been the biggest one published so far. They came to the conclusion that the two theories of multispecies evolution had to be reformulated and more specific predictions had to be made before a test can be carried out successfully. After this paper Antoni Hoffman did not drop the subject but wrote other papers with J. Kitchell and with J. Uchmański on the testing of the two models, but also on the

theoretical refinement of the models. In a review (Hoffman 1991a) he emphasized that the status of the Red Queen Hypothesis was still uncertain because the theoretical formulations were still not refined enough and hence not yet open to rigorous empirical testing.

Antoni Hoffman devoted himself also to the problem of species selection (Hoffman 1984a–b). He had long before rejected the idea that selection acts on the level of ecosystems; hence they could not be regarded as autonomous unities, i.e. 'superorganisms'. Species selection, a kind of selection acting on species and not reducible to individual selection had been proposed by the macroevolutionists (Eldredge, Gould, Stanley, etc.) in order to show the independence of macroevolution. Antoni clarified several terminological and empirical issues and came to the conclusion that other than possibly sexual-reproduction no species-level properties have been identified that would not be reducible to the individual level. Hence, species selection may occur in nature, but so far it has no empirical basis.

Knowing that the narrative side of evolutionary biology is at least as important as the generalizing, statistical, nomothetic side Antoni Hoffman published several papers with Joe Ghiold on the issue of vicariance biogeography using data from irregular echinoids (Ghiold & Hoffman 1984, 1986, 1989). Not surprisingly they came to the conclusion that historical biogeography must remain narrative.

Antoni Hoffman doubted that paleobiology could ever achieve the status of a thoroughly nomothetic science. On the one hand, he saw no evidence for insufficiency of the neo-Darwinian microevolutionary theory. On the other hand – he emphasized – those aspects of biological phenomena which are investigated by paleobiologists on a higher taxonomic level are summary effects of unique, historical events concerning individual species. The interest in the approaches, concepts and methods of paleontology as a historical science with a strong idiographic, narrative side led to a joint project between Antoni and I. We could complete only three papers before his untimely death, a general methodological analysis (Hoffman & Reif 1988), a discussion of the study of species-level lineages in the fossil record (1990) and a reconsideration of Rudolf Kaufmann's data on iterative evolution in Cambrian trilobites (Hoffman & Reif, in press).

By the middle-1980s Antoni Hoffman had expanded his attention gradually from ecosystems to the global diversity through the Phanerozoic and its controlling factors including mass extinctions. Knowing the ecological basis of the Theory of Island Biogeography quite well he argued in several papers that the equilibrium assumption of species diversity derived from that theory was not valid for an explanation of the development of the generic diversity on a continental scale let alone global family diversity through the Phanerozoic. Antoni Hoffman showed that the assumption that rates of origination and rates of extinction of families through the Phanerozoic are diversity dependent is contradicted by empirical data. He found no evidence to support the claim that the evolutionary faunas proposed by Jack Sepkoski are anything more that abstract statistical constructions (Hoffman 1985a, d).

In a progress report (Hoffman 1984d) he pointed out the weaknesses of new publications on mass extinctions. He argued that a qualitative difference of mass extinctions from background extinction could not be shown with statis-

tical means, that the statistics of extinction events depended on the absolute geological time scale used and that the assumption of periodic mass extinction events depended on the culling of the data and the definition of mass extinctions. He also showed that it was by no means certain that all mass extinctions were instantaneous events and that marine extinctions were synchronous with terrestrial extinctions. In a statistical analysis in Nature (Hoffman 1985b) he demonstrated that the apparent periodicity of mass extinction (that had been proposed by Dave Raup and Jack Sepkoski) resulted from stochastic processes.

Together with Joe Ghiold, Antoni (Hoffman & Ghiold 1985) developed a neutral model in which the average probabilities of origination and extinction of marine and nonmarine invertebrate families varied independently and had equal chances of going up and down from one stage to another. The basic assumptions of the model simply implied that the average rates of speciation and species extinction are abstract statistical constructions reflecting each a myriad of independent biological processes operating at the underlying, microevolutionary level; they also reflect the essential unpredictability of any biological process. This model was not refuted by the available data and it automatically led to the alleged periodicity of mass extinctions of 26 million years in the late Phanerozoic. In a later simulation in the context of this neutral model Antoni together with Eugene Fenster (Hoffman & Fenster 1986) showed that the shape of the curve of global family diversity during the Phanerozoic as well as the pattern of Sepkoski's evolutionary faunas could be mimicked if one took into consideration only two extraordinary events, the Late Cambro-Ordovician radiation and the Late Permo-Triassic extinction. The rest of the curve was explained sufficiently by the independent random walks of family origination and family extinction.

In the context of mass extinction Antoni Hoffman repeatedly emphasized that it was important to study individual events in detail rather than subjecting the fossil record of the late Phanerozoic or even the whole Phanerozoic to statistical analyses in the expectation of finding macroevolutionary laws or principles. He also doubted that a curve of the development of the global diversity on a family level was at all biologically meaningful even if the uncertainties of the fossil record and of the absolute geological time-scale could be overcome. Even if paleontologists could ever compile the development of species diversity of the shallow marine realm through the Phanerozoic one could not expect that this would reveal macroevolutionary laws.

The study of mass extinctions found not only great interest in the public press but it also led worldwide to sizable research programs in geology in order to find geochemical and mineralogical indicators of singular or periodic impact events and to find traces of impact craters. Astronomers began to search for the causes of periodic bolide impacts and for a dark companion of the sun on the basis of the alleged 26-million year extinction periodicity. In 1985 Antoni Hoffman together with Matthew Nitecki carried out a survey among paleontologists and geophysicists from North America, Britain, Germany, and Poland in order to find out how the attitudes of scientists differed toward the hypothesis that an extraterrestrial impact had really caused mass extinctions at the K/T-boundary. They found that there were wide differences between scientific disciplines and different countries thus raising the questions of

significance of the cultural and educational background in development of scientific opinions.

'Why not neo-Darwinism?' can be regarded as the headline to all of his papers that deal with evolutionary biology and paleontology. It also is the title of a review paper (Hecht& Hoffman 1986) that he published together with Max Hecht and which carries the subtitle 'A critique of paleobiological challenges'. The conclusions of the authors are short and pithy and they set the stage for Antoni Hoffman's book Arguments on Evolution: 'Our conclusions are obvious: **(1)** at the present stage of knowledge, the claims that neo-Darwinism is inadequate to explain macroevolutionary patterns are unjustified; (2) the interplay of microevolutionary processes and their environmental framework can account for macroevolutionary patterns actually observed in nature; (3) macroevolutionary theories, which postulate the reality of uniquely macroevolutionary processes (species selection, species drift, biotic diversification at supraspecific levels, mass extinctions), are unfounded' (Hecht & Hoffman 1986: p. 34).

Arguments on evolution

Antoni Hoffman's Arguments on Evolution. A Paleontologist's Perspective is a remarkable book. Already in the first lines of the preface he left no doubt that his writing of the book had been provoked not only by the large number of published challenges of the neo-Darwinian paradigms (S.J. Gould had declared this paradigm in 1980 as 'effectively dead') but also by his observation 'that to challenge this paradigm has become a way to gain the scientific fame and fortune, to achieve an intellectual authority' (Hoffman 1989a: p. v). Hence the book is one big argument to show that none of these challenges really undermine the status of the neodarwinian paradigm. In retrospect it appears to us as Antoni Hoffman's scientific legacy, even more so than his article on the future of paleontology which I will mention below. More than anything else the book renders an acount of Antoni's own view of evolutionary paleontology. Hence the book does not either address specifically the specialists in macroevolutionary theory or a general reader. Rather Antoni found it necessary lay down extensively his thinking about the philosophy of science, about evolution as a fact or as a theory, the neodarwinian paradigm (individual variation, evolutionary forces, initial and boundary conditions, evolution), the fossil record as data on evolution (the nature of paleontological data, reconstruction of phylogeny, other questions than phylogeny to ask of the fossil record, geological time, time correlation), and evolutionary inference from the fossil record (evolution as explanation, description of historical biological phenomena, the search for an explanation, the dilemma of multiple explanations). I have found it necessary to extract all these key words from the table of contents of the book in order to show the spectrum of topics that the reader is confronled with.

In the introductory chapters we find remarkable statements about the rejection of the fact of evolution by creationists (Hoffman 1989a: p. 4), but also by pattern cladists (Hoffman 1989a: p. 11}, on the historical aspects of rationality and other paths of cognition (Hoffman 1989a: p. 12), on religion and evolution (Hoffman 1989a: p. 13) and very clear evaluations of the methodo-

logical problems biostratigraphy, evolutionary palaeobiology and phylogenetic systematics face. The exposition on historical explanations and on neutral models (Hoffman 1989a: p. 76) are very important to read.

Only then after this long chapter called 'Background' do we get to the main parts of the book, namely his 'unabashed criticism' (Hoffman 1989a: p. v) of the macro- and megaevolutionary challenges of the neodarwinian theory. Some of the 'Background' may seem to a perfunctory reader as an elaboration on standard knowledge of an earth and life scientist. This, however, is not the case because Antoni Hoffman took pains to show that if one accepts this 'Background' view of the theory of evolution, of the interpretation of the fossil record etc. one must concur with him on the rejection of the modern macro- and megaevolutionary theories. In order not to arrive at a premature conclusion he ended the 'Background' with the statement There is no apriori reason to believe that the fossil record will never provide any data that would force evolutionists to supplement the neo-Darwinian paradigm with theories of some other evolutionary forces and processes. It is the task of the paleobiologists to see whether such data can be found.' (Hoffman 1989a: p. 85).

This last statement is the motto for the two main parts of the book on macroevolution and on megaevolution. The theories that had been proposed during the preceding 20 years (Punctuated Equilibrium and Species Selection as macroevolutionary mechanisms and mass extinctions and other controls of global diversity as megaevolutionary processes) are first analysed carefully with respect to their claims, contents and logical structure. Then predictions are derived and compared with the fossil record. In other words Antoni Hoffman first took all theories seriously and then rejected them (in the face of the vidence of empirical data). **As** he first seemed to accept the theories this may have led David Jablonski to warn the readers of 'internal contradictions' in the book.

For Punctuated Equilibria, Antoni Hoffman found that five different versions had been proposed in the literature without clear demarcations. He showed that these different versions were either trivial, or 'blatantly false' (Hoffman 1989a: p. 109), or untestable, or seemingly wrong or unsupported by any evidence. 'Punctuated equilibrium cannot therefore force the evolutionary biologist to rethink, and go beyond, the neo-Darwinian paradigm' (Hoffman 1989a: p. 123).

The chapter on Species Selection starts with the important finding that contrary to the claims of the macroevolutionists the relationships between Punctuated Equilibria and Species Selection are highly questionable. Species Selection is hence regarded by the author as an independent theory that 'can in principle present a serious challenge to the neo-Darwinian paradigm because it is supposed to act upon entities fully separated from one another and each having a number of features that vary among but are invariant within species and that can be transmitted in the process of speciation to all daughter species' (Hoffman 1989a: p. 144). 'Species selection is by now firmly established as a potential evolutionary force. And if it really operates in nature, then the neo-Darwinian paradigm of explaining historical biological phenomena by evolution must be expanded to encompass at least a twofold hierarchy of levels of biological causality, two kinds of units of selection – genes and species. The ultimate proof, however, must come from hard evidence. Until a compelling evidence is found, species selection will be nothing but an explanation in search

for phenomena to explain – very much like the theatrical characters in search for an author who would write about them in the famous drama by Luigi Pirandello' (Hoffman 1989a: p. 167).

In the chapter on mass extinctions Antoni Hoffman entertained the same approach, namely to take all proposed theories very seriously. He stated: ' If mass extinctions are different from the background extinction in their biological effects – as suggested by David Jablonski – then a general theory of mass extinctions as a separate class of megaevolutionaryphenomena might be called for. As put by Stephen Jay Gould (1985), such a theory of mass extinctions should go beyond the neo-Darwinian paradigm...' (Hoffman 1989a: p. 183). After a long discussion he found no evidence of such a difference (Hoffman 1989a: p. 190). As we have seen above Antoni Hoffman had also developed a strong neutral model to show that there is no compelling evidence of periodic mass extinctions. In his book he gave a revised interpretation of this model (Hoffman 1989a: p. 194). In his final conclusion he was very careful to state: This is not to say that periodicity of extinctions is ruled out but only that it is not at this point the best among currently available interpretations of the historical pattern' (Hoffman 1989a: p. 196).Then follows a discussion of bolide impacts and the question of whether there is any evidence for them and whether they could really have caused mass extinctions. The author found that there was no evidence that mass extinctions have one common cause and are hence a separate class of megaevolutionary phenomena. He also found no evidence that they are single events, global in scope and geologically instantaneous in time (Hoffman 1989a: p. 202).

In the last chapter, on global diversification, Antoni Hoffman took the problem (the family-diversity curve of J.J. Sepkoski and the various explanations proposed for it) very seriously. 'One might argue – and many paleontologists in fact do – that because of all the inherent shortcomings of the data base, any research aimed at analysis of the megaevolutionaryphenomenon of biotic diversification in the Phanerozoic is, and must be, a purely academic exercise, very far removed from the real world. I believe, however that this argument is clearly insufficient to deny value to such research' (Hoffman 1989a: p. 216). 'I view the multiphase logistic model proposed by Sepkoski as a challenge to the neodarwinian paradigm because it portrays the pattern of diversification as resulting from action of specifically megaevolutionary processes rather than as a product of historical contingencies of species originations and extinction' (Hoffman1989a: p. 220). Sepkoski's model and also the model developed by Jennifer Kitchel and Timothy Carr are based on the assumption that diversification and extinction rates were diversity dependent. The third model which the author discussed was Joel Cracraft's suggestion that the primary controls on the rates of speciation and species extinction are not the standing diversity but are exerted by a plexus of physical environmental factors. All three models are megaevolutionary models because they explain the pattern of biotic diversification in the Phanerozoic by reference to a single set of general laws. 'However, there is at present no need for a megaevolutionary theory of biotic diversification' (Hoffman1989a: p. 233), because the empirical pattern can be accounted for by the double random walk model that Antoni Hoffmanhad developed in earlier publications. This neutral model cannot be rejected, as a statistical null hypothesis, by the avaiable evidence. 'The average

rates of species origination and extinction for the global marine fauna are determined at each geological stage by myriads of independent factors, and hence the patterns of their change through geological time conform to randomness' (Hoffman 1989a: p. 231).

The conclusion in the epilogue of the book is rather short: 'No order has thus far been discovered in the historical patterns of biological evolution that would call for an explanation in terms of specifically macro- or megaevolutionary laws... The neo-Darwinian paradigm provides the best currently available explanation for macro- and megaevolutionary patterns. From a paleontologist's perspective, therefore, there is at present no reason to regard neodarwinism as either flawed, or at least incomplete' (Hoffman 1989a: p. 235). The epilogue then goes on to remind the reader that paleontology is a historical science and that in it, historical contingencies are by far more important than possible high-level laws. Whereas physics and chemistry are uniformistic sciences (electrons, atoms or molecules do not have individual characters), Hoffman emphasized that evolutionary biology is an individualistic science; each organism, population, and species have their own historically established individual features. Megaevolutionary patterns are found by the application of uniformistic approaches and they can be described in stochastic terms. The whole book then is a suggestion to return to individualistic approaches in paleontology and that rather than lumping events they should be studied individually.

Arguments on Evolution has remained a unique book. As far as I can see no other book by a single author challenges the non-darwinian macroevolutionary theories so extensively and competently. Jeff Levinton's book *Genetics, Paleontology and Macroevolution* was published almost at the same time. This book deals much with the fundamental issues, methods and approaches to the study of macroevolution (i.e systematics, phylogenetics, genetics, models of speciation, development and evolution, functional morphology). The empirical testing of macroevolutionary theories is dealt with in a comparatively small part of the book. Levinton's goal is the same as Antoni Hoffman's namely to show that macroevolutionary laws have not been found so far and that they are unlikely to exist.

Works in oceanic geochemistry

Antoni Hoffman had already in 1986 expressed his view that the Permo-Triassic boundary and its concomitant extinction was a unique event in the history of the Phanerozoic (Hoffman & Fenster 1986). This became the basis of his completely new interest and international cooperation in the late 1980s namely the study of stable isotopes to reconstruct paleooceanographic conditions and to explain individual global events in the biosphere. This shows how much Antoni Hoffman had paid heed to his own suggestion that paleontology should make use of individualistic approaches. *Arguments* had marked the end of a long and productive period of his life and Antoni began to collaborate with several Polish paleontologists and geochemists and a German geochemist. On the basis of the study of carbon and oxygen isotopes in a section in West Spitsbergen the group showed (Małkowski *et al.* 1989) that a drastic change in the state of the Earth's exosystem had occurred near the Permo-Triassic transition and must have caused major extinctions. A similar carbon isotopic

trend was later (1990) discovered by the group in China (Gruszczyński et *al.* 1990). Also in 1990 the group developed a general paleooceanographic model that is based on the variation of carbon isotopic composition of the seawater (Hoffman *et al.* 1990). *A* second topic of the group was the reconstruction of the life and burial environment of a Jurassic assemblage on the basis of isotopic and geochemical evidence. The third project of the group dealt with the paleooceanographic causes of the variation of carbon, oxygen and sulfur isotopes at the Ordovician-Silurian boundary and the evolutionary effects that could be predicted from the group's model.

Impact of Antoni Hoffman's work

In the late 1980s Antoni Hoffman was invited to contribute articles on macroevolution and on mass extinction to the now well-known books edited by J. Maynard Smith and G. Vida (Hoffman 1990) and by S. Donovan (Hoffman 1989d). This shows that he was regarded in many quarters as an important evolutionary paleobiologist. He wrote also a critical review of the last ten years of paleontology and its future for the 600-page text-book *Palaeobiology:* A *Synthesis* that was edited by Derek Briggs and Peter Crowther (Hoffman 1989c). His essay forms the last chapter of the book. Here he described progress in the various methods of descriptive paleontology ('palaeontography') and discussed the four most controversial issues of theoretical paleobiology (punctuated equilibrium, species selection, global diversity and mass extinctions). He pointed out that in spite of considerable efforts undertaken within the framework of theoretical paleobiology, no new biological laws, or even inductive generalizations, had been demonstrated by studies on the history of the biosphere. He emphasized that it was inevitable that the gap between paleontography and theoretical paleobiology would be closed in the future. The history of the biosphere ... may not be shaped according to a set of general biological laws. Karl Popper's *Poverty of historicism* should long have been obligatory reading for palaeontologists. The emphasis of palaeontological research must shift back (from the search for general macroevolutionary laws) to the study of unique, historical biological events and chains of events; it must follow the idiographic approach. Only then should we attempt to seek inductive generalizations about the evolution of lineages, the waxing and waning of clades, mass extinctions and explosive radiations of taxa, etc... For the future of palaeontology, I thus envisage a more humble focus on reconstruction of the history of life, rather than on attempts to discover the laws of this history; but I also envisage a considerable expansion of the scope of paleontology to include **all** aspects of the history of life on earth, rather than solely the history of particular lineages, clades, or communities. To this end, however, we must always be very explicit about the biological entities we undertake to describe and reconstruct – whether we talk of genotypes, phenotypes, or single traits, whether of phena, biological species, or phyletic lineages, whether of taphocoenoses, ecological communities, or taxocoenoses – and we must also be explicit about the limitations of our biological interpretations. Otherwise, paleontology will inevitably fall back to the stage of mere story-telling' (Hoffman 1989: 554–555).

It is too early to analyse the impact Antoni Hoffman's published work has had. There is no doubt that he made many readers worldwide aware of the fact that the question of whether neodanvinism describes the process of evolution adequately or not is a fundamental biological question and that all nondarwinian macroevolutionary hypotheses proposed so far have significant weaknesses.

I know of no other author who tested so many macroevolutionary assumptions and was so fruitful in proposing neodanvinian alternatives than Antoni Hoffman. In addition one should mention that he made a significant contribution to the discussion of the fundamentals of ecology, many of which are still very controversial. His methodogical and metascientific statements and analyses are not easy to read but they should be a challenge for all paleontologists.

If one knows that Antoni had a family, was unemployed from 1976 to 1980 – living on translations from Polish into English – that he had five different scholarships and grants from 1980 to 1986 in Tubingen, Chicago, Madison, Palisades, and again Tübingen and that after his return to Poland he not only worked as a paleobiologist for the Polish Academy of Sciences, but also as an academic and educational expert for the Polish Sejm (diet)and the Ministry of Education and that he developed curricula for a private Gymnasium that he had co-founded, one must admire his productivity, his interest in communication and his dedication to science. There is probably no other paleontologist in the world who had so full a command of the literature that spans so many individual disciplines in the earth sciences and there are very few thinkers as critical and as productive as he was. If one knew him closely one had to admire him for his integrity and his enthusiasm for science and for the future of Poland after the collapse of the Soviet empire. He was an outstanding person, but one also saw in him a very important ambassador of Polish science.

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