Earth and Life

Global Biodiversity, Extinction Intervals and Biogeographic Perturbations Through Time

John A. Talent (Ed.)

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Earth and Life

International Year of Planet Earth

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Executive Director International Secretariat
International Year of Planet Earth

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Goodwill Ambassador
International Year of Planet Earth

The book series is dedicated to the United Nations International Year of Planet Earth. The aim of the Year is to raise worldwide public and political awareness of the vast (but often under-used) potential of Earth sciences for improving the quality of life and safeguarding the planet. Geoscientific knowledge can save lives and protect property if threatened by natural disasters. Such knowledge is also needed to sustainably satisfy the growing need for Earth's resources by more people. Earth scientists are ready to contribute to a safer, healthier and more prosperous society. IYPE aims to develop a new generation of such experts to find new resources and to develop land more sustainably.

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John A. Talent
Editor

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Foreword

The International Year of Planet Earth (IYPE) was established as a means of raising worldwide public and political awareness of the vast, though frequently under-used, potential the earth sciences possess for improving the quality of life of the peoples of the world and safeguarding Earth's rich and diverse environments.

The International Year project was jointly initiated in 2000 by the International Union of Geological Sciences (IUGS) and the Earth Science Division of the United Nations Educational, Scientific and Cultural Organisation (UNESCO). IUGS, which is a non-governmental organization, and UNESCO, an inter-governmental organization, already shared a long record of productive cooperation in the natural sciences and their application to societal problems, including the International Geoscience Programme (IGCP) now in its fourth decade.

With its main goals of raising public awareness of and enhancing research in the Earth sciences on a global scale in both the developed and less-developed countries of the world, two operational programmes were demanded. In 2002 and 2003, the series editors together with Dr. Ted Nield and Dr. Henk Schalke (all four being core members of the Management Team at that time) drew up outlines of a science and an outreach programme. In 2005, following the UN proclamation of 2008 as the United Nations International Year of Planet Earth, the "year" grew into a triennium (2007–2009).

The outreach programme, targeting all levels of human society from decision makers to the general public, achieved considerable success in the hands of member states representing over 80% of the global population. The science programme concentrated on bringing together like-minded scientists from around the world to advance collaborative science in a number of areas of global concern. A strong emphasis on enhancing the role of the Earth sciences in building a healthier, safer and wealthier society was adopted – as declared in the Year's logo strap-line "Earth Sciences *for* Society".

The organizational approach adopted by the science programme involved recognition of 10 global themes that embrace a broad range of problems of widespread national and international concern, as follows:

- Human health: this theme involves improving understanding of the processes by which geological materials affect human health as a means identifying and reducing a range of pathological effects.
- Climate: particularly emphasizes improved detail and understanding of the non-human factor in climate change.
- Groundwater: considers the occurrence, quantity and quality of this vital resource for all living things against a background that includes potential political tension between competing neighbour nations.

- Ocean: aims to improve understanding of the processes and environment of the ocean floors with relevance to the history of planet Earth and the potential for improved understanding of life and resources.
- Soils: this thin "skin" on Earth's surface is the vital source of nutrients that sustain life on the world's landmasses, but this living skin is vulnerable to degradation if not used wisely. This theme emphasizes greater use of soil science information in the selection, use and ensuring sustainability of agricultural soils so as to enhance production and diminish soil loss.
- Deep Earth: in view of the fundamental importance of deep the Earth in supplying basic needs, including mitigating the impact of certain natural hazards and controlling environmental degradation, this theme concentrates on developing scientific models that assist in the reconstruction of past processes and the forecasting of future processes that take place in the solid Earth.
- Megacities: this theme is concerned with means of building safer structures and expanding urban areas, including utilization of subsurface space.
- Geohazards: aims to reduce the risks posed to human communities by both natural and human-induced hazards using current knowledge and new information derived from research.
- Resources: involves advancing our knowledge of Earth's natural resources and their sustainable extraction.
- Earth and Life: it is over 2½ billion years since the first effects of life began to affect Earth's atmosphere, oceans and landmasses. Earth's biological "cloak", known as the biosphere, makes our planet unique but it needs to be better known and protected. This theme aims to advance understanding of the dynamic processes of the biosphere and to use that understanding to help keep this global life-support system in good health for the benefit of all living things.

The first task of the leading Earth scientists appointed as theme leaders was the production of a set of theme brochures. Some 3500 of these were published, initially in English only but later translated into Portuguese, Chinese, Hungarian, Vietnamese, Italian, Spanish, Turkish, Lithuanian, Polish, Arabic, Japanese and Greek. Most of these were published in hard copy and all are listed on the IYPE web site.

It is fitting that, as the International Year's triennium terminates at the end of 2009, the more than 100 scientists who participated in the 10 science themes should bring together the results of their wide ranging international deliberations in a series of state-of-the-art volumes that will stand as a legacy of the International Year of Planet Earth. The book series was a direct result of interaction between the International Year and the Springer Verlag Company, a partnership which was formalized in 2008 during the acme of the triennium.

This IYPE-Springer book series contains the latest thinking on the chosen themes by a large number of earth science professionals from around the world. The books are written at the advanced level demanded by a potential readership consisting of Earth science professionals and students. Thus, the series is a legacy of the science programme, but it is also a counterweight to the earth science information in several media formats already delivered by the numerous national committees of the International Year in their pursuit of worldwide popularization under the outreach programme.

The discerning reader will recognize that the books in this series provide not only a comprehensive account of the individual themes but also share much common ground that makes the series greater than the sum of the individual volumes. It is to be hoped that the scientific perspective thus provided will enhance the reader's appreciation of the nature and scale of earth science as well as the guidance it can offer to governments, decision makers and others seeking solutions to national and global problems, thereby improving everyday life for present and future residents of planet Earth.

Eduardo F.J. de Mulder
Executive Director International Secretariat
International Year of Planet Earth

Edward Derbyshire
Goodwill Ambassador
International Year of Planet Earth

Series Preface

This book series is one of the many important results of the International Year of Planet Earth (IYPE), a joint initiative of UNESCO and the International Union of Geological Sciences (IUGS), launched with the aim of ensuring greater and more effective use by society of the knowledge and skills provided by the earth sciences.

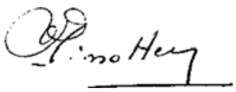
It was originally intended that the IYPE would run from the beginning of 2007 until the end of 2009, with the core year of the triennium (2008) being proclaimed as a UN Year by the United Nations General Assembly. During all 3 years, a series of activities included in the IYPE's science and outreach programmes had a strong mobilizing effect around the globe, not only among earth scientists but also within the general public and, especially, among children and young people.

The outreach programme has served to enhance cooperation among earth scientists, administrators, politicians and civil society and to generate public awareness of the wide ranging importance of the geosciences for human life and prosperity. It has also helped to develop a better understanding of Planet Earth and the importance of this knowledge in building of a safer, healthier, and wealthier society.

The scientific programme, focused upon 10 themes of relevance to society, has successfully raised geoscientists' awareness of the need to develop further the international coordination of their activities. The programme has also led to some important updating of the main challenges the geosciences are, and will be confronting within an agenda closely focused on societal benefit.

An important outcome of the work of the IYPE's scientific themes includes this thematic book as one of the volumes making up the IYPE-Springer Series, which was designed to provide an important element of the legacy of the International Year of Planet Earth. Many prestigious scientists, drawn from different disciplines and with a wide range of nationalities, are warmly thanked for their contributions to a series of books that epitomize the most advanced, up-to-date and useful information on evolution and life, water resources, soils, changing climate, deep earth, oceans, non-renewable resources, earth and health, natural hazards, and megacities.

This legacy opens a bridge to the future. It is published in the hope that the core message and the concerted actions of the International Year of Planet Earth throughout the triennium will continue and, ultimately, go some way toward helping to establish an improved equilibrium between human society and its home planet. As stated by the Director General of UNESCO, Koichiro Matsuura, "Our knowledge of the Earth system is our insurance policy for the future of our planet". This book series is an important step in that direction.



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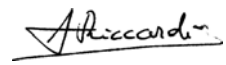

Alberto C. Riccardi
President
IUGS

We cling to a sort of magical thinking about the impending ecological disaster. It is too easy to accept the assertions of the World's professional optimists, or the pronouncements of those who noisily deny scientific facts. If more of us cared to experience the natural world unmediated by anything at all – to simply sit, quietly, open to its sublime beauty – we might take better care of it – our heritage with its almost incomprehensibly long history!

From Sara Maitland in *A Book of Silence*, published by Granta, 2008

This volume is dedicated to my son Ross who, on the point of submitting his PhD, died in a car accident near Allora, southern Queensland, on 21 September 1991. A mathematician, biologist and statistician, his research on statistical modelling of complex ecosystems would have complemented this volume perfectly. He would have relished many of the contributions here.

Preface to this Volume

This volume is one of a series of volumes, Springer's Legacy Series, produced as a tangible by-product of the activities of UNESCO's International Year of Planet Earth. The volume was directed towards considering the broad pattern of increasing biodiversity through time, and recurrent events of minor and major ecosphere reorganization, some regional, such as the swiftly developing collapse of reef systems: or local, exemplified by the 79 AD disaster about Pompei. Intense scrutiny was sought on the pattern of physical (including isotopic), sedimentary and biotic circumstances through the time intervals during which life crises occurred. These events affected terrestrial, lacustrine and estuarine ecosystems, locally and globally, but also affected continental shelf (including intertidal) ecosystems and even deep ocean ecosystems. The pattern of such events is an important part of the backdrop against which modelling the pattern of future environmental change needs to be evaluated.

A broad spectrum of authors was sought but, inevitably, recently published exhaustive surveys resulted in lacunae in this particular volume. Authors who felt they could usefully contribute were encouraged to take liberties with subject, organization and point of view. As a consequence, some of the contributions are highly personal and digressive (such as the concluding chapter of this volume); some are essays, others are reflective overviews of broad topics, and yet others present the detailed results of specialized scholarship undertaken over many years. It is anticipated that all have adroitly balanced scientific data and inference. Writing is often a slippery commodity. An author's voice and the readability of his/her contribution can be easily lost by over-editing. Care has been taken to maintain the personal voice and viewpoints of the authors.

Every fossil, large or small, can be viewed as a time-capsule or as a data bank – as my late friend, Paul Tasch, insisted nearly 40 years ago in his *Paleobiology of the Invertebrates: Data Retrieval from the Fossil Record.* Paul's thesis was that all fossils may be viewed as parts of an infinitely larger data bank of transcendental scale and that the information each fossil can deliver (alone or in conjunction with other fossils) can answer many questions concerning the fossils themselves and the environments in which they lived. There have been countless trillions of such tiny time-capsules. Their stories – as individuals or as members of former communities, supplemented by information about the sediments on or in which they lived and were buried – provide us with grand panoramas of deep time, and provide much information about the context of the recent past, and help explain the present-day ecosphere of our planet. In this volume, 74 authors contributed 36 manuscripts that present 'snapshots' of that grand saga – the vast array of patterns, and a mind-numbing panorama of tiny events leading up to the present day – and have thereby contributed a special standpoint from which to consider our planet's immediate future.

Many scientists have interpreted parts of this saga. Some are painstakingly probing how life could have originated from the simple chemicals present on the early Earth – a long, almost intractable endeavour, developing understanding of how protocells could have formed and then imported RNA building blocks into their structure. Others – the majority – have concentrated on aspects of the 'tree of life' such as the relationships of now-extinct organisms. Though most of the trunk and branches of this 'tree' disappeared long ago, all living species are ultimately twigs of a single tree. Others have focused on reconstructing ancient environments. Such reconstructions, especially their cyclicities, gain significance as we approach the present day and consider the contribution of humankind to atmospheric chemistry, ecosystem degradation and global warming – and how the impact of these might be mollified.

The history of our biosphere, now under serious threat, is a stunningly complex story. Many ancient environments, seemingly little changed through hundreds of millions of years, are still with us. These include the environments of oceanic trenches (hadal regions) and abyssal plains, where oozes slowly form from the tests of microscopic organisms (radiolarians and foraminifers). Other environments, if not being destroyed, are changing rapidly.

If used quantitatively, exhaustive palaeontologic databases can be used not only for deciphering grand-scale patterns in the history of the biosphere, but can also be brought to bear on gross global tectonic problems – especially by quantitative analysis of biogeographic data for inferring the relative disposition and motions of crustal blocks, major and minor, during the past 550 million years or so. This has considerable potential value: being able to use data from the foldbelts of the globe where palaeomagnetic data has lost value from overprinting by subsequent tectonic episodes (intervals of intense earth movements).

Five of the nine chapters at the beginning of this volume present a fresh look at the data and methods of palaeontology (Martin Aberhan and Wolfgang Kiessling), 'coordinated stasis' (Carlton E. Brett), the possible impact of periodic astronomical phenomena on the history of life (Bruce S. Lieberman and Adrian L. Melott), a background chapter on climate change through time (John Dodson) and a major synthesis of much data on the development of intertidal biotas through the last 550 million years (Markes E. Johnson and B. Gudveig Baarli). Two chapters focus on marine encrusting and endolithic communities (sclerobiofacies) (Carlton E. Brett et al., and Bruno Mistiaen et al.) – the first with experimental data from shells positioned at various depths in the deep sea, the second a statistical study of Devonian epibionts. This sequence of nine chapters ends with a contribution on the significance of taphonomy and fish microfossils ('fish-bits') in unravelling the history of Devonian vertebrates (Carole J. Burrow and Susan Turner), and another on one of palaeontology's most spectacular 'windows' on deep time, the Eocene-age Messel Pit near Darmstadt in Germany (Stephan Schaal).

John Dodson maintains that the components and processes of Earth's climate system are subject to the same physical laws as the rest of the Universe. Climate change occurs in response to changes in Earth's orbit about the Sun. The behaviour of the climate system can therefore be understood and predicted through careful, systematic study. On a grand scale, rearrangements of continents through plate-tectonic motions have surely wrought massive changes in global climate during deep time.

The first four of the next nine chapters present a survey of latest Precambrian embryos and the Early Cambrian Chengxiang faunas from China and explain their evolutionary significance (Jun-yuan Chen); grand-scale evolution during the

Ordovician is chronicled by Arnold I. Miller; Jiří Frýda details the revolution in gastropod classification that has come from ontogenies revealed by SEM photography; and Philippe Steemans et al. discuss innovations in the micro- and megafossil plant record, from earliest plant spores to earliest seeds. Three chapters provide a panorama on the appearance and disappearance of a unique group, the tentaculitids (Eberhard Schindler), results of intensive investigation of shell morphology of Palaeozoic ammonoids (Dieter Korn and Christian Klug) and the outcomes of statistical studies of Late Palaeozoic trilobites (Rudy Lerosey-Aubril and Raimund Feist). The sequence ends with an overview of the evolution of cladid crinoids (Gary D. Webster) and an elegantly illustrated synthesis of the aerodynamics and origin of flight during the dinosaur–bird transition (Sankar Chatterjee and R. Jack Templin).

There were several important thresholds in the saga of life. The first of these was the origin of single-cell organisms on the surface of Earth, occurring as much as 3.7 billion years ago. The next great event, about 2.7 billion years ago, was development of photosynthesizing bacteria and production of their waste product, oxygen. Increasing levels of oxygen facilitated development of lowly multicellular organisms and, eventually (around 575 million years ago), the swift rise to prominence of bizarre soft-bodied creatures known as the Ediacara fauna. The name of another old friend, the late Martin Glaessner, is closely associated with elegant, early work on the strange Ediacaran animals. Martin drew analogies to present-day groups including jellyfish, sea pens and flat worms, but these assumptions were eventually, in large measure, discarded when it became clear that most were not related to Cambrian and younger groups. Dolf Seilacher was the great motivator in bringing about this rethinking.

Recent discoveries of phosphatised embryos of more than 100 taxa in the Duoshantou phosphate deposit (580 million years ago) at Weng'an, Guizhou, China, some so beautifully preserved that 'fact maps', the sequence of cell division, can be inferred. They include lineages closely related to living sponges, cnidarians and bilaterians (Jun-Yuan Chen, herein). Their discovery is consistent with the suggestion that several lineages of metazoan life (including the above major lineages), previously thought to be of Cambrian age or younger, flourished before the Cambrian explosion – despite not being known yet from fossilised mature individuals.

Close affinities between many of the appreciably younger Maotianshan Shale biota (c. 530 mya) found in the Chengjiang, Haikou and Anning areas near Kunming in Yunnan, China and the appreciably younger Burgess Shale biota (c. 505 mya) of British Columbia, Canada, accord with these lineages having rapidly become geographically (perhaps globally) widespread and, as suggested by Chen Junyuan, having possibly become less rapidly evolving following the Early Cambrian 'explosion'.

By the beginning of the Cambrian period (542 mya), the acme of the Ediacara fauna had passed, following the first readily recognisable mass extinction (perhaps a suite of associated sub-events) or grand-scale but gradual faunal turnover in Earth's history, referred to by some as the Kotlin Crisis. Though rare elements of the Ediacara fauna survived into the Cambrian, they declined dramatically in size, diversity and abundance of them through the Kotlin Crisis.

It was succeeded by the earliest Cambrian assemblages containing trace fossils and, finally, by the 'Big Bang' in animal evolution: the appearance of almost all groups of bilaterian animals – the groups that constitute nearly all of our present-day faunas. There had been rapid diversification of grazing animals with shells composed of phosphate or calcium carbonate – this is considered to be a response to the appearance of the first ‘predators’.

There is evidence from latest Precambrian (Ediacaran) trace fossils (burrows and trails) of organisms ingesting soft sediments and thereby obtaining nourishment from tiny organisms that lived in or very close to the surface of shallow-marine sands and silts. By Middle Cambrian time, tiny animals had begun to utilize the oozes of deep oceanic seafloors – specifically the ultra-fine soft, siliceous sediments on the abyssal plains – as a new food source. The first 60 million years of this saga (not elaborated herein) is presently being elaborated by Yoshitaka Kakuwa of the University of Tokyo.

Though the saga of life displays a broad pattern of increasing biodiversity through time, there have been recurrent events of minor and major ecosphere reorganisation. Scales range from minor and local events, scarcely discriminable from the normal ‘background’ pattern of extinctions, to the mother of all extinction events at the end of the Permian era when as much as 95% of all taxa became extinct, globally. Most, perhaps all, of these events including the end-Permian life crisis were not instantaneous but involved significant intervals of time with definable sub-events.

Though the Kotlin Crisis appears to have been spread over a substantial period of time, it could be regarded as the first of at least eight (rather than five) major events – if one includes the Hangenberg Extinction (360 mya) in the latest Devonian and the now swiftly developing Anthropogenic Event as well. They have been referred to as First-Order extinction events, but how one draws a line between these and the most devastating among the 85–90 other extinction events (many regional rather than global; compilation made by the late Otto Walliser) lacks consensus. Among these are the complex Ireviken Event (Silurian: Landovery–Wenlock boundary, about 428 mya), the Lau Event (mid-Late Silurian; Lennart Jeppsson et al., herein), the Klonk Event (spanning the Silurian–Devonian boundary), the Taghanic Event (mid-Devonian: late Givetian, about 385 mya; James J. Zambito IV et al., herein) and possibly the Cenomanian–Turonian Event (about 93.5 mya).

These ‘Second Order’ extinction events as well as the largest of all extinction events about the Permian–Triassic boundary (mentioned above; around 251 mya) were not instantaneous as one might expect had they been generated by an asteroid or comet impact. Rather, they were, ‘packages of sub-events’. For example, Lennart Jeppsson, from an enormous database of painstakingly and systematically accumulated conodonts (about a half million of them), from the island of Gotland, has discriminated eight discrete extinction episodes (sub-events) that together constitute the Ireviken Event at the base of the Middle Silurian. At least five of these sub-events can be identified elsewhere around the globe (cf. Peter D. Molloy and Andrew J. Simpson). Lennart and fellow workers have shown that a subsequent (mid-Late Silurian) global extinction event, the Lau Event, not only had a significant impact globally, but also can be shown from intensive sampling to have included sub-events defined by identifiable ‘data points’.

Popular science, as noted above, refers to five major extinction events punctuating the broad increase in biodiversity that occurred through Phanerozoic time (the last 550 million years of Earth history) and ignores the rest. Characteristics of the database on which this assertion is based smooth out all but the most dramatic events. But even then, the massive Late Devonian ‘extinction event’ is a composite of data from three significant events: the Lower Kellwasser (late Frasnian, early in the *linguiformis* Conodont Zone), Upper Kellwasser (at the base of the Famennian) and Hangenberg (latest Famennian) global extinction events.

James J. Zambito IV et al. believe that lesser studied and more frequent events that resulted in faunal restructuring and replacement at regional to global scales may have had a greater aggregate effect on the evolution of life than the ‘Big Eight’. This they exemplify by the late Middle Devonian (Givetian) Taghanic Biocrisis in the type area, northern Appalachian North America, where three main bioevents – a series of pulsed biotic transitions and extinctions – ultimately resulting in an end to previous faunal provinciality and appearance of a global cosmopolitan fauna.

Enzo Farabegoli and Cristina Perri, by meticulous observation, have demonstrated the ‘mother of all extinction events’ at the Permian–Triassic boundary consisted of at least three sub-events.

Gerta Keller insists that the massive Cretaceous–Cenozoic (K/T) Boundary Event (about 65.5 mya) could not have been connected with the Chicxulub bolide on the Yucatan Peninsula, the widely accepted ‘culprit’. She argues that it impacted about 300,000 years before the K/T global extinction event and points to the voluminous extrusion of the Deccan Traps volcanics as a more likely driving force behind the devastating K/T extinction event. Jeffrey D. Stilwell and Eckart Håkansson probe extinction/survivorship patterns of some of the biota through the K/T boundary interval, and Vivi Vajda neatly analyses the important role of fungi as a driving force in normalisation of the terrestrial carbon cycle following that massive extinction event.

Six contributions focus on past biogeography: a quantitative analysis of brachiopod biogeography in northern Asia through several time-slices of the Early and Middle Devonian (John A. Talent et al.); the biogeography of Pennsylvanian crinoids and blastoids (Johnny Waters and Gary D. Webster); the biogeography of Late Mesozoic ostracods of western Australia (Michelle Guzel); two contributions that, to a degree, complement one another: one on Mesozoic dinosaurs of the southern hemisphere (Federico Fanti), the other on Mesozoic mammals (Thomas H. Rich and Patricia Vickers-Rich); and extinction patterns in North American Miocene gastropods (Edward J. Petuch). The time is ripe for using large databases! Databases thus generated, coupled with increased knowledge of past climate, are important for modelling the biosphere and its history, specifically past patterns of biogeography and, from these patterns, information on the disposition of crustal blocks (major and minor) during at least the past 550 million years – and of the pattern of extinction events, exemplified earlier, that have affected life regionally and even globally since the appearance of the first metazoan life-forms.

Two contributions round out the volume: environmental shifts during the Cenozoic (Brian McGowran) and a comprehensive survey of the biostratigraphy, phylogenetic palaeoecology and palaeobiogeography of Australian marsupials (Karen H. Black et al.). The latter, serendipitously, draws attention to the impact of climate change on Australia’s marsupials over the past 55 million years. Their chapter ends with the words: ‘. . .it seems probable that the next time the history of these unique marsupials is reviewed there will be considerably less scepticism about the capacity of climate change to drive extinctions’.

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Sydney, NSW, Australia John A. Talent

Contents

Part I Articles of a General Nature

Phanerozoic Marine Biodiversity: A Fresh Look at Data, Methods, Patterns and Processes 3
Martin Aberhan and Wolfgang Kiessling

Coordinated Stasis Reconsidered: A Perspective at Fifteen Years 23
Carlton E. Brett

Whilst This Planet Has Gone Cycling On: What Role for Periodic Astronomical Phenomena in Large-Scale Patterns in the History of Life? 37
Bruce S. Lieberman and Adrian L. Melott

Climate Change Through Time 51
John Dodson

Development of Intertidal Biotas Through Phanerozoic Time 63
Markes E. Johnson and B. Gudveig Baarli

Marine Sclerobiofacies: Encrusting and Endolithic Communities on Shells Through Time and Space 129
Carlton E. Brett, Trisha Smrecak, Karla Parsons Hubbard, and Sally Walker

Brachiopods and Their Auloporid Epibionts in the Devonian of Boulonnais (France): Comparison with Other Associations Globally 159
Bruno Mistiaen, Denise Brice, Mikolaj K. Zapalski, and Christian Loones

Fossil Fish Taphonomy and the Contribution of Microfossils in Documenting Devonian Vertebrate History 189
Carole J. Burrow and Susan Turner

Messel Pit Fossil Site – The Legacy of the Environment and Life of the Eocene 225
Stephan Schaal

Part II Evolution Exemplified by Specific Phyla or Classes

Evolutionary Scenario of the Early History of the Animal Kingdom: Evidence from Precambrian (Ediacaran) Weng'an and Early Cambrian Maotianshan Biotas, China 239
Jun-Yuan Chen

The Ordovician Radiation: Macroevolutionary Crossroads of the Phanerozoic . . . 381
Arnold I. Miller

Phylogeny of Palaeozoic Gastropods Inferred from Their Ontogeny . . . 395
Jiří Frýda

Palaeozoic Innovations in the Micro- and Megafossil Plant Record: From the Earliest Plant Spores to the Earliest Seeds . . . 437
Philippe Steemans, Elodie Petus, Pierre Breuer, Paula Mauller-Mendlowicz, and Philippe Gerrienne

Tentaculitoids – An Enigmatic Group of Palaeozoic Fossils . . . 479
Eberhard Schindler

Palaeozoic Ammonoids – Diversity and Development of Conch Morphology . . . 491
Dieter Korn and Christian Klug

Quantitative Approach to Diversity and Decline in Late Palaeozoic Trilobites . . . 535
Rudy Lerosey-Aubril and Raimund Feist

Devonian Cladid Crinoid Evolution, Diversity, and First and Last Occurrences: Summary Observations . . . 557
Gary D. Webster

Palaeoecology, Aerodynamics, and the Origin of Avian Flight . . . 585
Sankar Chatterjee and R. Jack Templin

Part III Global Extinction Events and Biocrises

An Analysis of the Ireviken Event in the Boree Creek Formation, New South Wales, Australia . . . 615
Peter D. Molloy and Andrew J. Simpson

Isotope Geochemistry and Plankton Response to the Ireviken (Earliest Wenlock) and *Cyrtograptus lundgreni* Extinction Events, Cape Phillips Formation, Arctic Canada . . . 631
Paula J. Noble, Alfred C. Lenz, Chris Holmden, Monika Masiak, Matthew K. Zimmerman, Simon R. Poulson, and Anna Kozłowska

Late Ludfordian Correlations and the Lau Event . . . 653
Lennart Jeppsson, John A. Talent, Ruth Mawson, Anita Andrew, Carlo Corradini, Andrew J. Simpson, Jane Wigforss-Lange, and Hans Peter Schönlaub

The Late Middle Devonian (Givetian) Global Taghanic Biocrisis in Its Type Area (Northern Appalachian Basin): Geologically Rapid Faunal Transitions Driven by Global and Local Environmental Changes . . . 677
James J. Zambito IV, Carlton E. Brett, and Gordon C. Baird

The Permian—A Time of Major Evolutions and Revolutions in the History of Life . . . 705
Monica J. Campi

Millennial Physical Events and the End-Permian Mass Mortality in the Western Palaeotethys: Timing and Primary Causes 719
Enzo Farabegoli and Maria Cristina Perri

The Cretaceous–Tertiary Mass Extinction, Chicxulub Impact, and Deccan Volcanism 759
Gerta Keller

Survival, but...! New Tales of 'Dead Clade Walking' from Austral and Boreal Post-K–T Assemblages 795
Jeffrey D. Stilwell and Eckart Håkansson

Fungi, a Driving Force in Normalization of the Terrestrial Carbon Cycle Following the End-Cretaceous Extinction 811
Vivi Vajda

Part IV Palaeobiogeography

Changes in the Pattern of Brachiopod Biogeography in Northern Asia Through Early and Middle Devonian Times 821
John A. Talent, Yevgeniy A. Yolkin, Valentina N. Yolkina, Tat'yana P. Kipriyanova, and Rimma T. Gratsianova

The Paleobiogeography of Pennsylvanian Crinoids and Blastoids 831
Johnny Waters and Gary D. Webster

Jurassic and Early Cretaceous Ostracods from Western Australia: What They Reveal About Evolution of the Indian Ocean . . . 849
Michelle Guzel

Cretaceous Continental Bridges, Insularity, and Vicariance in the Southern Hemisphere: Which Route Did Dinosaurs Take? 883
Federico Fanti

Palaeobiogeography of Mesozoic Mammals – Revisited 913
Thomas H. Rich and Patricia Vickers-Rich

Part V Cenozoic Era

Cenozoic Environmental Shifts and Foraminiferal Evolution 937
Brian McGowran

Miocene Asteroid Impacts: Proposed Effects on the Biogeography and Extinction Patterns of Eastern North American Gastropods 967
Edward J. Petuch

The Rise of Australian Marsupials: A Synopsis of Biostratigraphic, Phylogenetic, Palaeoecologic and Palaeobiogeographic Understanding 983
Karen H. Black, Michael Archer, Suzanne J. Hand, and Henk Godthelp

Epilogue – A Perspective 1079
John A. Talent

General Index 1085

Taxonomic Index (Genera and Species) 1097

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Part I

Articles of a General Nature

Phanerozoic Marine Biodiversity: A Fresh Look at Data, Methods, Patterns and Processes

Martin Aberhan and Wolfgang Kiessling

Abstract

Patterns of Phanerozoic global biodiversity continue to be a major focus of palaeobiological research. Recent advances have been fuelled by the establishment of the Paleobiology Database. This new type of data compilation, based on the actual occurrences of taxa in fossil collections, has entailed the development and application of a whole set of new analytical methods. These allow to account for large-scale biases that affect estimates of palaeodiversity, in particular uneven sampling and differential preservation of rocks and fossils. The new curve of global diversity of marine genera (Alroy et al. 2008) deviates in important aspects from traditional ones. Rather than an exponential post-Palaeozoic increase in diversity, it shows an only modest rise from the mid-Palaeozoic to the Neogene. This rise is paralleled by an increase in within-assemblage (alpha) diversity. Contrasting previous conceptions, between-assemblage (beta) diversity, here presented for the first time by a Phanerozoic beta curve, does not show a long-term trend. We approximate the new global Phanerozoic marine diversity trajectory by two consecutive logistic curves, one for the Palaeozoic and one for the Mesozoic to Cenozoic. This implies two thresholds for global diversity in the Phanerozoic, although these are not far apart. We discuss the concept of a biosphere-wide carrying capacity and argue that competition for limited resources and incumbency effects are constraining the diversity of marine life on macroevolutionary scales.

Keywords

Palaeobiodiversity • Sampling • Biases • Analytical methods • Carrying capacity • Diversity thresholds

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Introduction

The entire diversity of life – from the diversity of genes to the diversity of species and ecosystems up to the diversity of biomes – is currently shrinking at unprecedented rates and affects all hierarchical levels.

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In the midst of this biodiversity crisis, we increasingly recognize that diversity matters. Apart from ethical arguments, there are strong practical and economical reasons to conserve biological diversity. As the consequences of biodiversity loss are unclear, a thorough understanding of diversity patterns and controlling factors is not just an academical exercise.

Although not strictly comparable to modern biodiversity, the historical perspective of the fossil record offers the unique opportunity to study the temporal and spatial dynamics of diversity over long intervals of time, in particular the 542 million years of the Phanerozoic eon. In spite of its obvious biases, the fossil record documents how the diversity of life has evolved; it promotes an understanding of how past diversity has shaped present diversity; it highlights the evolutionary consequences of mass extinctions; and it enables us to assess the evolutionary dynamics of the biotic recovery following these major extinctions. Thus, the study of diversity of the geological past can yield valuable insights of relevance and urgency to our society.

At the global scale, diversity is the result of the interplay between the origination and extinction of taxa. At the regional and local scale, the immigration and emigration of taxa play an additional role. Most commonly, diversity is calculated as taxonomic (or taxic) diversity, which measures the number of taxa, for palaeontologists often genera. Another way of expressing diversity is phylogenetic diversity, which refers to the evolutionary history of clades and is a metric for the gain and loss of evolutionary distinctiveness. Morphological diversity (disparity) analyses the occupation of morphospace through time, and functional diversity characterizes the impact of different ecological groups (Erwin 2008). Further measures include architectural and developmental diversity as well as behavioural complexity.

In this chapter we focus on the well-studied taxonomic dimension of Phanerozoic diversity history. We confine ourselves to the marine realm because its record is richest and exhibits high levels of preservational completeness and palaeoecological reliability (e.g. Kidwell 2001, 2005). We evaluate the two main biases affecting palaeodiversity analyses – uneven sampling and differential preservation – and summarize the state-of-the-art methods to overcome these deficiencies. We review diversity patterns at various geographical scales, ranging from the diversity of local assemblages (alpha diversity) to global diversity (gamma diversity). We investigate between-assemblage diversity (beta diversity) and present the first Phanerozoic curve on beta diversity based on the Paleobiology Database (PaleoDB). We evaluate two principal classes of models that have been applied to understand the processes controlling global biodiversity. In the equilibrium model, diversity increase is described as a logistic curve with initial exponential growth that slows down as saturation begins and finally stops (Sepkoski 1978). In contrast, the expansion model allows global diversity to rise without a predictable limit (Benton 2009). Finally, we assess the role of the potential drivers of diversity dynamics: extrinsic abiotic factors stress changes in the physico-chemical environment; extrinsic biotic forcing mechanisms comprise biological interactions such as competition and predation; and intrinsic biological controls revolve around key adaptive innovations and clade-specific rates of origination and extinction.

We conclude that global, marine genus diversity has twice reached an upper limit in the Phanerozoic, one in the Devonian and one in the Late Cretaceous. Logistic growth models driven by intrinsic diversification rates are suitable to capture the rough pattern but global environmental perturbations and large-scale climatic fluctuations need to be evoked to model the second-order pattern.

Estimating Diversity from an Incomplete Record of Rocks and Fossils

For a long time, researchers of palaeobiodiversity took the Phanerozoic fossil record at face value to characterize the dynamics of diversifications, major extinctions and the recovery thereof. This has led to the perception that the diversity of species, genera and families has increased considerably through time (Fig. 1a). More recently, variations in the availability of sedimentary rocks and the intensity with which fossils are collected were recognized as important sources of systematic biases (Raup 1976, 1979; Smith 2001; Peters and Foote 2001). A proper understanding of the trajectory of past diversity in time and space requires identifying and correcting for such biases. Such modified diversity curves look quite different from the previous ones (Fig. 1b and see below), and it appears that much of the

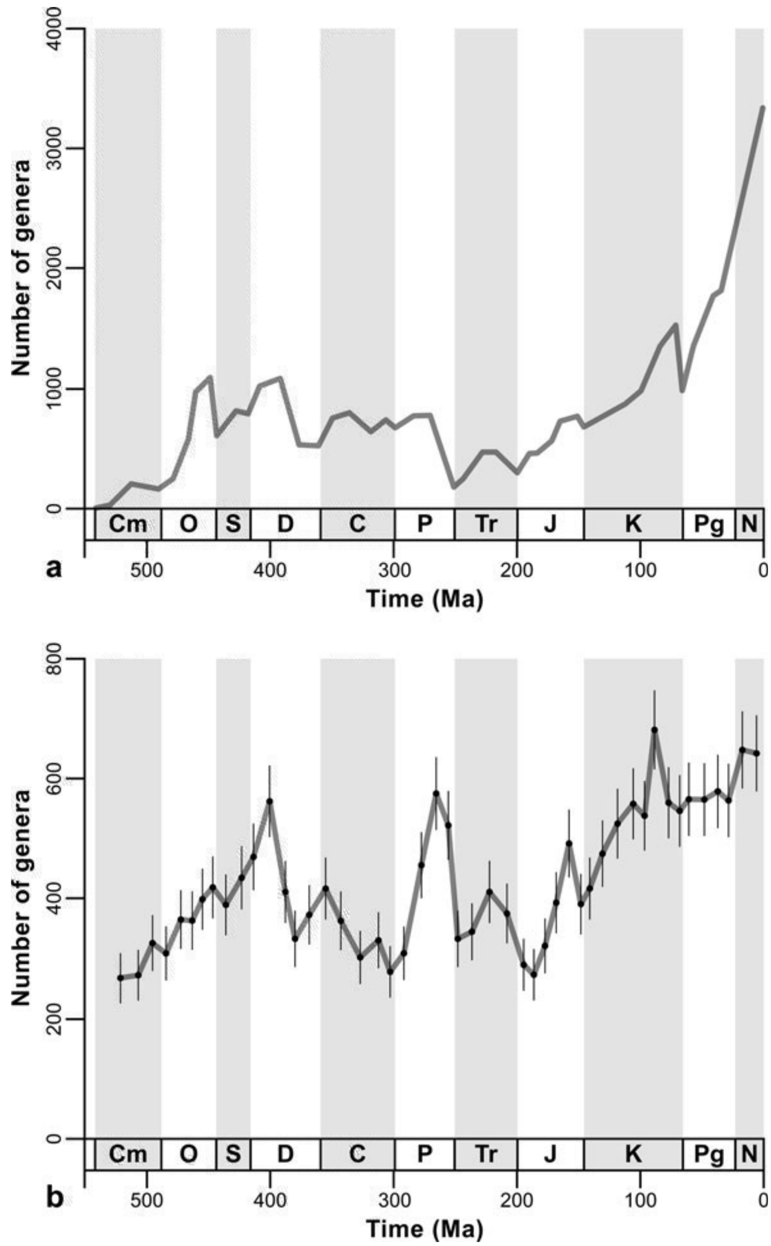

Fig. 1 Global diversity of marine genera (metazoans less tetrapods) during the Phanerozoic. (**a**) Traditional diversity curve utilizing Sepkoski's (2002) compendium of fossil marine animals resolved to the same time intervals as b. The curve is based on the record of a genus' first and last occurrence; each genus is counted at all interval boundaries lying between the times of its first and last occurrence (boundary crossers). It is increasingly recognized that these kinds of curves are severely biased and suffer from the Pull of the Recent effect (see text). (**b**) Diversity curve based on an analysis of the Paleobiology Database. Diversity values rest on the actually recorded occurrence of genera for altogether 48 time intervals of roughly equal duration (ca. 11 Ma). Data are standardized to account for bin-to-bin variations in geographic coverage of samples and sampling intensity. *Vertical lines* denote 95% confidence intervals. For detailed methodology see text and Alroy et al. (2008). Ma, million years ago. Cm, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; Pg, Paleogene; N, Neogene. Redrawn from Alroy et al. (2008)

steep diversity increase of the past 100 Ma evident in previous curves is an artefact of uneven sampling effort and variation in the rock record. The potential biases arise from systematic variations in the rock record, in the quality of fossil preservation and in the effort raised to sample collections.

Variation in the Availability and Provenance of Fossiliferous Rocks

Of major concern is the observation that the amount of sedimentary rocks fluctuated considerably over Phanerozoic time and that it is correlated with sampled diversity. More numerous outcrops tend to yield more collections, which in turn provide more specimens and finally more species. The close link holds true for several proxies of rock quantity, namely geological map area covered by sedimentary rock (Raup 1976; Smith 2001; Smith and McGowan 2005, 2007; McGowan and Smith 2008), estimated volume of sedimentary rock (Raup 1976), number of rock sections (Peters 2005), and the number of named formations (Peters and Foote 2001, 2002). In regional studies of the New Zealand record, Crampton et al. (2003, 2006) concluded that outcrop area of sedimentary rock is the more reliable predictor of sampling bias. In contrast, the number of formations might be a better indicator of habitat heterogeneity. In the marine realm, habitat heterogeneity is expressed, for example, by the number of environments along an onshore-offshore gradient or the distribution of environments with siliciclastic substrates versus those with carbonate substrates. Changes in the spectrum and the proportions of preserved habitats are an important source of rock record bias. Everything else being equal, collecting from a new, so far unsampled environment is likely to raise sampled diversity at a higher rate than continued sampling of the same environment. Ultimately, the preserved volume and outcrop area of rock as well as the nature of represented environments are a function of tectonically mediated sea-level change (see Smith 2007b and references therein). The flooding of continents increases both the amount of habitable shelf area and the depositional area of shallow marine sediments that becomes part of the rock record. In contrast, regression reduces the area of shallow marine shelf and erosion leads to less marine sediments entering the rock record. Therefore, the correlation between the amount of rock and marine biodiversity can be the result of the species-area effect, the amount of rock that is preserved or a combination of both processes (Smith 2007a).

A further complication arises by the uneven geographical distribution of fossiliferous deposits in the geological record. It is well established that diversity declines with increasing latitude in both modern and ancient marine environments (e.g. Allison and Briggs 1993; Alroy et al. 2008). Changes through time in the preservation of tropical environments versus those from mid and high palaeolatitudes are thus a critical factor. A palaeolatitudinal sampling bias becomes particularly relevant by the strong focus of palaeontological research on Europe and North America. As these major continents migrated northward across the palaeoequator during the Phanerozoic, the representation of high-diversity, tropical shelf area (and the area of shallow-water carbonate accumulation) decreased over the same time interval (Allison and Briggs 1993; Walker et al. 2002). These trends are well reflected by the environmental distribution of marine collections in the PaleoDB (Fig. 2). The major drop of collections from tropical sites and carbonate environments occurred across the Triassic-Jurassic transition.

Variation in the Preservation of Fossils

Usually, only a very small fraction of the members of life assemblages become fossilized, even if they posses mineralized hard parts such as shells and skeletons (Kidwell and Flessa 1996). As long as this taphonomic bias remains constant through time, it does not pose a problem to palaeodiversity trajectories. However, the environmental circumstances under which organisms become part of a death assemblage are embedded in the sediment and finally turn into fossils during diagenesis can vary considerably. An extreme example is conservation Lagerstätten, which exhibit extraordinary completeness including the preservation of soft parts under anoxic conditions. Although they offer a highly complete record of ancient biodiversity at a particular locality, their erratic distribution in time and space introduces a bias. As palaeodiversity studies rely heavily on skeletal organisms, a temporal heterogeneity in the proportions of skeletal versus non-skeletal organisms can also introduce a major bias. Although the current contention is that there was little variation after the Cambro-Ordovician increase of skeletal