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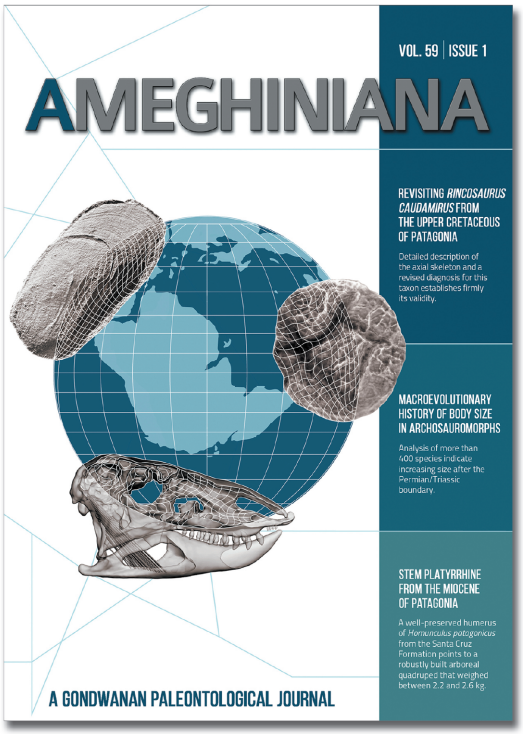

INTRODUCTION TO PALEOBIOLOGY AND THE FOSSIL RECORD (2ND EDITION)

Benton, Michael, J. and David A. T. Harper. 2020. 656 pp + supplemental online resources. Wiley-Blackwell. ISBN: 978-1-119-27288-5 (eBook). ISBN: 978-1-119-27285-4 (print).

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PLEASE SCROLL DOWN FOR ARTICLE

REVISITING *RINCOSAURUS CAUDAMIRUS* FROM THE UPPER CRETACEOUS OF PATAGONIA

Detailed description of the axial skeleton and a revised diagnosis for this taxon establishes firmly its validity.

MACROEVOLUTIONARY HISTORY OF BODY SIZE IN ARCHOSAUROMORPHS

Analysis of more than 400 species indicate increasing size after the Permian/Triassic boundary.

STEM PLATYRRHINE FROM THE MIOCENE OF PATAGONIA

A well-preserved humerus of *Homunculus patagonicus* from the Santa Cruz Formation points to a robustly built arboreal quadruped that weighed between 2.2 and 2.6 kg.

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How do you condense the current knowledge, methods, and concepts of a massive field as Paleobiology in a book updated with the latest findings and developments? That seems the question that M. J. Benton and D. A. T. Harper decided to answer when writing *Introduction to Paleobiology and the Fossil Record*. But that's only one part of the challenge they took on. The other part was making it clear and easy to understand for non-specialists and young students of related fields.

The second edition of *Introduction to Paleobiology and the Fossil Record* arrives more than ten years after the well-known first edition. Paleobiology is a dynamic discipline. Every year, new findings across the world increase our understanding of life that once inhabited the Earth, as well as the one that today dwells on the planet. Ordovician cryptospores that push back the origin of land plants, a giant Cretaceous mammal that challenges the view of "furry rat sized creatures living in the shadows of dinosaurs", new Cambrian invertebrate remains that suggest that the bizarre *Anomalocaris* was a filter-feeding creature, and so on. New methods and technologies develop and allow obtaining more information from new and old findings. As such, an updated new edition is totally justified. When compared with the first edition, visual updates have been introduced. Most of the figures stand out with colors that not only are cosmetic, but also improve their understandability. Several case studies and examples correspond to new findings and developments made in recent years. Additionally, many chapters were rewritten to incorporate new developments.

The book is aimed at Geology and Biology students taking courses of Paleontology and Biology and would serve as well to Paleontology students in the first years of their degrees. The text is concise, clear, and friendly, and even an occasional reader interested in paleontology would be able to understand and enjoy the text from the beginning to the end, maybe even encouraging Paleobiology as a career choice.

As the authors state in the prologue, the objective wasn't a new book focused exclusively on descriptions of major fossil groups, but a more general view of the discipline. And, in this sense, the first third of the book is not devoted to a particular group, but to concepts that are intimately related to Paleobiology, such as fossilization, paleoecology, evolution, and extinctions. Most of these concepts are often briefly discussed (or even not included) in textbooks, when in fact, it results critical to have a complete picture of the history of life on Earth.

Paleontology courses often group students from different disciplines that may lack knowledge of certain topics needed to understand paleontological concepts. Biology students may have scarce knowledge of stratigraphy. Geology students may struggle with concepts of species and how evolution works. These first chapters will help them level these differences.

The book is organized in a preface, twenty chapters and a finale (a small final chapter), followed by a glossary, two appendices and an index. An online instructor companion site is also available, with PowerPoint files containing the figures of each chapter, which is very useful for educational purposes.

Chapters follow a similar scheme. They start with a textbox containing Key Points of the chapter, where the most important topics discussed are presented as bullet points. Then, a brief introduction is given, followed by explanations and descriptions of the concepts and groups developed in that particular section. Interspersed between the chapters, five types of topic-boxes are presented (*i.e.*, Hot topics/debates, Paleobiological tool, Exceptional and new discoveries, Quantitative methods, and Cladogram/classification). These are used to expand concepts, present methodologies, and show the state of the art and debates of the field. The end of each chapter contains review questions, useful for self-evaluation or discussion with the course, recommended readings, and the cited bibliography. Chapters are illustrated

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with clear photographs, graphics, and drawings, including many "upgraded" colored versions of the black and white ones used in the first edition of the book. Below, I summarize and comment on the content of each chapter.

Chapter 1 ("Paleontology as a science"), presents Paleontology as a discipline, explaining why it is considered a science (and what *is* science), and how relevant is the study of fossil remains in the understanding of the past and present life on Earth. Fossils as a key tool for paleontological work are presented, with a historical perspective of how they received different interpretations across centuries. The last part of the chapter is devoted to explaining what it means to do paleontological research.

Chapter 2 ("Stratigraphy") begins with Nicolaus Steno's, but also with Leonardo da Vinci's and Giovanni Arduino's different observations regarding the superposition of rocks, used as an introduction to Stratigraphy. Then, the different types of units are presented, and Lithostratigraphy, Biostratigraphy, Chronostratigraphy, and Sequence Stratigraphy are explained in detail. Cyclostratigraphy and Astrochronology, Isotope Stratigraphy and Magnetostratigraphy are also presented. In the final part of the chapter, the Geological Time Scale (and the reason for the existence of different geological time scales) is explained. Perspectives for extraterrestrial stratigraphy close the chapter.

Chapter 3 ("Paleogeography and Paleoclimatology") begins with the concept of the biogeography of extant species, its counterpart in the past, and how the distribution of taxa with a certain degree of endemism contributed (and contributes) to reconstructing past geographies. The authors introduce concepts of dispersal and vicariance, and barriers and corridors, to explain biotic distributions and dispersals in the past. The second part of the chapter focuses on fluctuations of paleoclimates across Earth history and their possible effects in the evolutionary processes of the biotas, as well as stances where life affected the Earth climatic regime. The chapter closes with the concept of the Anthropocene and the effect of human species in the climate, as well as the problems of a formal definition as a chronostratigraphic unit of the Holocene.

Chapter 4 ("Paleoecology") introduces concepts used in ecology and paleoecology, such as niche and habitat, as well as different lifestyles found in living organisms, and the concept of trophic structures. Then, it focuses on paleocommunities and discusses how they are described, how they changed across time and the different interactions that can be recognized in the fossil record. The final part of the chapter is devoted to evolutionary paleoecology and the changes of the paleocommunities across the Phanerozoic.

Chapter 5 ("Taphonomy and the quality of the fossil record") begins with the concept of Taphonomy and the probabilities of different organisms becoming fossils, depending on the composition of their body parts, and the concept of *Lagerstätte*. The chapter also provides descriptions of the different ways in which plants and animals are preserved. The second part of the chapter discusses the fact of the incompleteness of the fossil record, and how this fact may or may not affect conclusions obtained from fossils.

Chapter 6 ("Fossil form and function") is the first chapter that introduces concepts of evolution. It starts by describing the concept of form and how it relates to adaptations. Thenm it focuses on variability in morphological features of organisms, and its causes. The relationship between developmental changes and phylogenetic changes (*e.g.*, heterochrony, homeobox genes) is discussed and the evo-devo research field is presented. The last part of the chapter is dedicated to answering the question: "How can the function be interpreted from fossils?".

Chapter 7 ("Macroevolution and the tree of life") continues exploring concepts of evolution and begins with Charles Darwin and his theory of evolution by natural selection. The concept of species (some *concepts* of species) is discussed, as well as different models of speciation and their correlation with the fossil record. Then, the authors introduce the concept of the tree of life and how phylogenetic trees are constructed, profusely describing the cladistic methodology, as well as molecular clocks and bayesian analysis using genomic data.

Chapter 8 ("Biodiversity, extinction, and mass extinction") explores different diversification models. Then, the authors embark on one of the most renowned concepts in paleontology: mass extinctions. How to define mass extinctions is one of the first topics discussed, as well as the difficulties in recognizing mass extinctions in the fossil record. The big five mass extinctions of the Phanerozoic are discussed, focusing on both the end-Permian and the K-Pg events. Other extinction events (*e.g.*, archaeocyathids at the end of the late Cambrian, the Carnian pluvial event) are

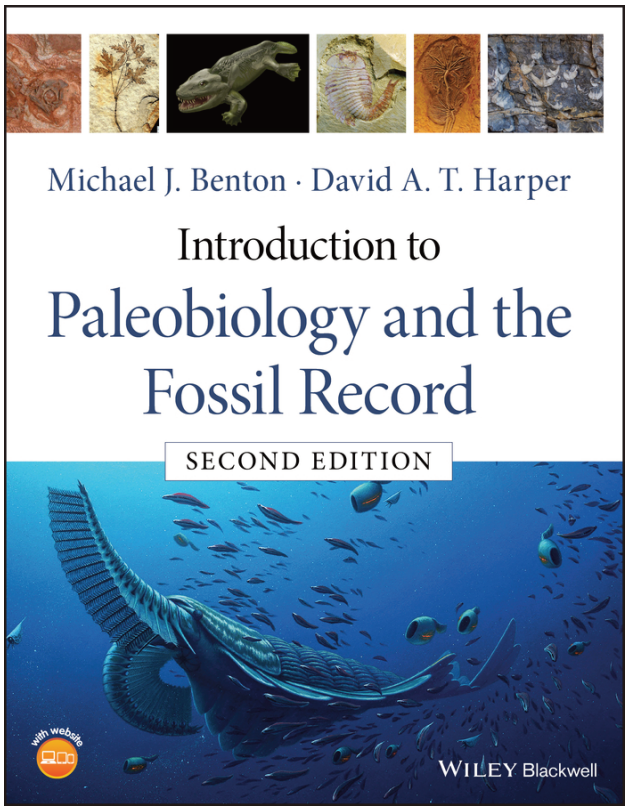

Figura 1. Cover of the book Introduction to Paleobiology and the fossil record, Second Edition, Wiley Blackwell.

briefly discussed too. The chapter closes with a discussion (which is appropriately left open) on the modern extinction.

Chapter 9 ("The origin of life") starts with the presentation of different models to explain the origin of life. The oldest accepted fossils (as well as some controversial ones) are introduced, including stromatolites and the famous Gunflint and Strelley Pool Formations microfossils. The process of changes in the metabolism of Proterozoic organisms and the resulting effect on the oxygenation of the atmosphere are discussed by the authors. The rest of the chapter focuses on the rise of eukaryotes, multicellularity and sex reproduction, and their fossil record.

Chapter 10 ("Protists") is focused on Micropaleontology and the groups studied by this discipline, the polyphyletic nature of its study objects and the utilities of microfossils. Then, selected fossil groups are presented, including foraminifera, radiolarians, acritarchs and chitinozoans, and taxa included in the phytoplankton as diatoms, dinoflagellates and coccoliths. Each one of these groups is characterized morphologically, most of them with an accompanying taxonomic (or parataxonomic) scheme, and with information about their fossil record and evolution.

Chapter 11 ("Origin and expansion of metazoans") recapitulates the oldest fossil records of multicellularity, including corporeal fossils, ichnofossils, the famous Doushantuo embryos, biomarkers, as well as estimates for its origin using molecular clocks. The link between the Snowball Earth and the origin of multicellularity is discussed before focusing on famous early metazoan assemblages. In this regard, the authors explore the characteristics of the Ediacaran biota and its changes across time, as well as the existence of biomineralization by Ediacaran times. The chapter ends by discussing three significant Paleozoic events: the Cambrian Explosion, the Great Ordovician Diversification, and the Devonian Nekton Revolution.

Chapter 12 ("The basal metazoans: sponges and corals") begins with a morphological characterization of sponges, along with a classification of the group in four classes. Stromatoporoids and archaeocyathids are also described in detail. The role of sponges in reef communities is discussed across the Phanerozoic. Then, the cnidarians are presented, following a similar scheme: a morphological characterization of the group, a classification scheme, and detailed descriptions of the most abundant fossil cnidarians (Scleractinia, Tabulata and Rugosa), and their participation in reef associations across time. The chapter ends by presenting the threatening situation of modern coral reefs.

Chapter 13 ("Lophophorates 1: brachiopods and bryozoans") focuses on the two most important lophophore bearing clades among Lophotrochozoans. First, the morphological features of brachiopods are described in detail, and this is accompanied by a classification scheme with particular features of each order. Additionally, paleoecological aspects are approached, discussing lifestyles inferred from morphological aspects. Other topics discussed include provincialism and the role of brachiopods across the Phanerozoic. The second part of the chapter has bryozoans as protagonists. The general morphology of the group is described using the modern genus *Amathia*, and then a classification scheme and characterization of each recognized class is provided. Their ecology, patterns across the Phanerozoic, and a detailed characterization of the different types of colonies produced by the group close the chapter.

Chapter 14 ("Lophotrochozoans 2: mollusks and annelids") is mostly focused on the Phylum Mollusca, certainly due to its diversity and abundance in the fossil record. The authors begin the chapter characterizing the mollusks as a whole, presenting their shared anatomical structures and using the hypothetical archaic mollusk as a pedagogical tool to explain the evolution of the group. A classification scheme of the group, that includes general features of each class, is provided, as well as a phylogenetic tree for the group. Putative early molluscan fossils, as *Kimberella* and *Halkiera*, are illustrated and their current knowledge is discussed. Several classes are then selected for exhaustive characterization. The Bivalvia receive a lot of attention here, with a detailed general characterization of the basic body plan, and then comments on both protobranchs and autobranchs. The authors chose not to dive in detail into the different orders of bivalves, preferring to focus on the different morphologies of their shells and how they relate to their modes of life and their relationship with the substrate. Then gastropods are characterized in detail, and comments on the main groups and their ecology are given. A major part of the chapter goes to the Cephalopoda, starting with *Nautilus* as a model for understanding the group. This section focuses on the morphology, ecology, and evolution of ammonoids and, in minor proportion, on belemnites. Perhaps the inclusion of orthocerids or endocerids would have been beneficial to discuss different adaptations to buoyancy. Other mollusks treated in this chapter, although less exhaustively, are scaphopods and rostroconchs. A summary of the evolutionary trends in mollusks across the Phanerozoic is presented before approaching the second phylum of the chapter. Given their scarce fossil record, annelids are briefly discussed. It includes a general characterization of the group and a recapitulation of its fossil record, including the mention of scolecodonts.

Chapter 15 ("Ecdysozoa: arthropods") begins with a general characterization of arthropods and their general classification at subphyla level. Then, a review of early arthropod faunas is presented, with examples from the well-known Burgess Shale, Sirius Passet, and Chengjiang biotas. It follows a large section focused on trilobites, where the authors describe their general morphology, ontogenetic changes, diversity and their paleoecology. Paleogeography and evolution of the group are also described, including their use for macroevolutionary studies. The chapter continues with the subphylum Chelicerata, with a brief characterization of the group, and then it focuses on eurypterids, their fossil record and their different ecological strategies and colonized environments. The subphylum Crustacea is also included in this chapter, where ostracods are described in detail, and their evolutionary trends are discussed. Miriapoda and Hexapoda are briefly characterized and discussed, as their fossil record is sparser among the arthropods. The chapter ends with comments on exceptionally preserved faunas and the striking representation of Arthropoda, as in extant assemblages.

Chapter 16 ("Deuterostomes: echinoderms and hemichordates") is the last chapter focusing on invertebrates. It begins with the distinctive features of Echinoderms and their classification (class level). Major groups of echinoderms are described in detail, with crinoids and echinoids standing out. Evolutionary aspects of the evolution of echinoderms are included, with a detailed analysis of the regular to irregular transition of echinoids. The second part of the chapter is devoted to the Hemichordata, with a brief introduction of extant forms, and then a detailed account of graptolites, with focus on Graptoloidea and Dendroidea, and it ends with a brief discussion about their evolutionary patterns, their biogeography, and uses as biostratigraphic markers.

Chapter 17 ("Fishes and basal tetrapods") is the first part of the vertebrate's coverage in the book. It begins with a characterization of vertebrates, and the origin of the bone and the oldest vertebrates. Then, follows a section where agnathan fishes are briefly described, and a detailed characterization of conodonts, including characteristics of the denticulate elements, the conodont animal, and their uses. Jaw-bearing fishes are covered next, with comments on the pulses of radiation of actinopterygians and sharks. Then, the process of terrestrialization is introduced, with mention of classic transitional forms (*Ichthyostega* and *Acanthostega*), and a characterization of amphibians, mostly focused on temnospondyls. The development of the cleidoic egg and the origin of amniotes is discussed next, with a characterization of the three main patterns of skull temporal fenestration. The chapter ends with the synapsid lineage and the transition to true mammals.

Chapter 18 ("Dinosaurs and mammals") is the second

and last part of the vertebrate coverage in the book. Beginning with the rise of the Diapsida, the authors characterize the Archosauria and discuss the lineages of diapsids that radiate during the Triassic (pterosaurs, crocodilians, lepidosaurs and turtles), and then focus on dinosaurs, with characterizations of saurischians and ornithischians, and a discussion about their gigantism. *Archaeopteryx* and its kin are briefly commented on, as well as Mesozoic marine reptiles. In the following part of the chapter, the authors pick up again the synapsid lineage but it starts with true mammals and their unique synapomorphies. After some comments on early Mesozoic mammals, the Mammalia crown group is introduced, with features of marsupials and major clades of placentals, finishing with the history of our kin, from early Primates to modern humans.

Chapter 19 ("Fossil plants and fungi") begins with fossil fungi and their scarcity in the fossil record, with a similar scheme used for mosses and liverworts. Then, the classification of tracheophytes is presented, along with adaptations to life on land and an introduction to the life cycles of plants. The next part presents early vascular plant records of the Silurian and Devonian. Lycopsids, horsetails and ferns are described next, with general comments of some of their characteristics and their fossil record. I particularly disagree with the inclusion of the statement that fern leaves are technically branches with leaves (pinnules). Homologies among leaves of euphyllophytes (and even among ferns) are far from solved. Most authors consider the whole structure as the leaf. In a book intended as introductory, I believe incorporating such controversial topics (and not clarifying them as controversial/unanswered) may not be constructive or pedagogic. The origin of seed is covered next, with a brief characterization of some Paleozoic pteridosperm groups before the introduction of conifers. Other groups of gymnosperms, such as ginkgoaleans, bennettitaleans, cycadaleans, and gnetaleans are also described. Angiosperms are covered in detail, starting with their characteristics and their classification, following with their oldest fossil records and pulses of radiation, and then ending with their uses as paleoclimatic proxies.

Chapter 20 ("Trace fossils") is the final of the book and it covers concepts used in ichnology, parataxonomy, types of trace fossils and how they preserve, the behavioral classification, their use as environmental indicators and the ichnofacies model (although continental ichnofacies are only represented by the mention of the *Scoyenia* ichnofacies), ichnofabrics and their use in the oil industry.

Closing the book, the authors included a section called Finale, where they chose ten major evolutionary adaptations that happened during the history of life on Earth, and that reflect modern diversity. The volume ends with a Glossary of terms used in the text, and two appendices (a stratigraphic chart and paleogeographic models for six moments of the Phanerozoic).

The amount of information contained in the book is massive, in its attempt to cover all aspects of paleobiology and also to give all the tools to understand every concept. The magnitude of topics covered obviously results in a selection made by the authors and editor that may or may not cover the expectations of all readers, in particular the ones with a background in paleontology. As such, it is clear that opinions of what should be included or not are subjective. Despite this, I am including below some opinions and comments that may be considered for future editions of the book.

I cannot stress how important I believe the inclusion of chapters 1 to 8 is in an introductory Paleobiology book. As stated above, these topics are often minimally treated in the literature to focus on the fossil taxonomic groups. Having a solid base in concepts as stratigraphy, evolution, and paleoecology allows interpreting the rest of the book from a more complete perspective. The major drawback I can see is the imbalance in the coverage of some of the analyzed groups in Chapters 12 to 19. This is particularly noticeable when invertebrate groups are compared with vertebrates and plants. Invertebrates, in my opinion, are covered in detail and at a very good level to allow a comprehensive picture of the several clades, following a recurrent format of introducing the group with its generalities, then the important representatives of each clade, and it finishes with evolution, ecology and applications, or other relevant topics. Trace fossils are also covered in detail. In contrast, vertebrate groups are very briefly characterized, and the text follows a mixture of systematic and stratigraphic treatment, with Paleozoic events covered in Chapter 17 and Mesozoic and Cenozoic events in Chapter 18. This results in some strange situations, such as having the first part of the synapsid lineage in the last parts of the former chapter, and

then the return of the lineage in the second part of the latter chapter; or marine reptiles described after archosaurian (pseudosuchians and most ornithodirans) and non-archosaurian diapsids, and before birds. While I am not against a stratigraphic perspective, I believe this may be confusing for the intended readers. Furthermore, descriptions of groups tend to be very brief, and general characterizations of the clades are scarce. Both issues would obviously be non-existent if the reader had a general background on vertebrate morphology and diversity, but that seems contradictory with the target public of the book, as reflected in the invertebrate chapters. Chapter 19 returns to the pure systematic scheme, but plant groups are very briefly described, and this often leads to a scarce focus on general morphology and anatomy (again, contrasting for example with the detailed descriptions of invertebrates, as brachiopods or bivalves). The text focuses on several major plant groups but leaves out others that are clearly important. Progymnosperms are only named in a phylogenetic tree (strangely, they were presented in the classification scheme of the first edition of the book). Seed ferns mentioned are Late Paleozoic taxa, Medullosales and Glossopteridales, being the latter not included in the systematic scheme nor the phylogenetic trees presented. Given the importance of Glossopteridales not only for the proposal of plate tectonics, but also as related to angiosperm origins in some studies, I believe this group should be added (at least tentatively) in the phylogenetic trees. Bennettitales and Gnetales have different positions in both phylogenetic trees presented. Regarding the origin of angiosperms inferred using phylogenomic data, it is stated that no gymnosperm group is more related to angiosperms than others. But this is only true for modern gymnosperms. Recent studies that incorporate fossils recover angiosperms as related to some seed fern groups, such as Caytoniales, Umkomasiales or Glossopteridales (and even bennettitaleans), but phylogenetic trees included in the chapter show angiosperm as a branch completely separated from the rest of the gymnosperm groups mentioned in the text. And, even if this can be true (excluding *Glossopteris* and maybe Bennettitales), the lack of basal non-angiosperm taxa in the angiosperm branch gives the idea of a ghost lineage originated in the Devonian without known representatives until the Cretaceous. This is more confusing with the inclusion of the Figure 19.21 legend, "evolution of the angiosperm flower", presenting a true angiosperm flower and flowerlike structures of both a bennettialean and a gnetalean. The main text states some gymnosperm clades had angiosperms like flowers but avoids mentioning they are not closely related to angiosperms under the scheme the authors are presenting, which totally separates gnetaleans and bennetittales (and their similar flower-like structures and nectar-like pollination drops to attract insects) from angiosperms (and their flowers and nectar). I recommend putting more emphasis in clearly stating that, if angiosperms are a clade separate from all extant gymnosperms, all these features are not shared features due to common ancestry.

I started this review by picturing the book as two different challenges taken by the authors: 1) writing an updated book covering the Paleobiology discipline as a whole and 2) making it easy to understand to non-specialists, given the target audience of the volume. Most of the book flawlessly succeeds in both challenges. I already mentioned what I think of the first two-thirds of the book (and Chapter 20), which certainly may become the bibliographic reference for a Paleontology course for first-years' students when dealing with fossil invertebrates, or searching information regarding methodologies or concepts of biology, geology, and paleontology.

As stated above, three chapters have, in my opinion, some flaws: Chapters 17 and 18 (vertebrates), and Chapter 19 (plants and fungi). While the coverage of the three classic major areas of systematic paleontology (paleobotany, fossil invertebrates and fossil vertebrates) and how useful would be in a particular course would depend on each particular teacher, I believe these three chapters would not be enough to cover the needs of picturing the fossil record of vertebrates and plants. And, while Chapters 17 and 18 may prove very informative once the change in format and the basis of general vertebrate anatomy and diversity are provided, the paleobotany section would most certainly need from another bibliographic source to complement several topics in the course (*e.g.*, plant morphology, fossil plant diversity and evolution, and, in particular, evolution of angiosperms).

Given that Paleobiology is a dynamic discipline, continuing to review, update and expands these contents is a task that this second edition of the book fulfills

programmatically and that must continue in the future due to the intrinsic dynamism of the discipline. I hope my comments become a small contribution to help the authors and editor in the development of a future third edition.

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