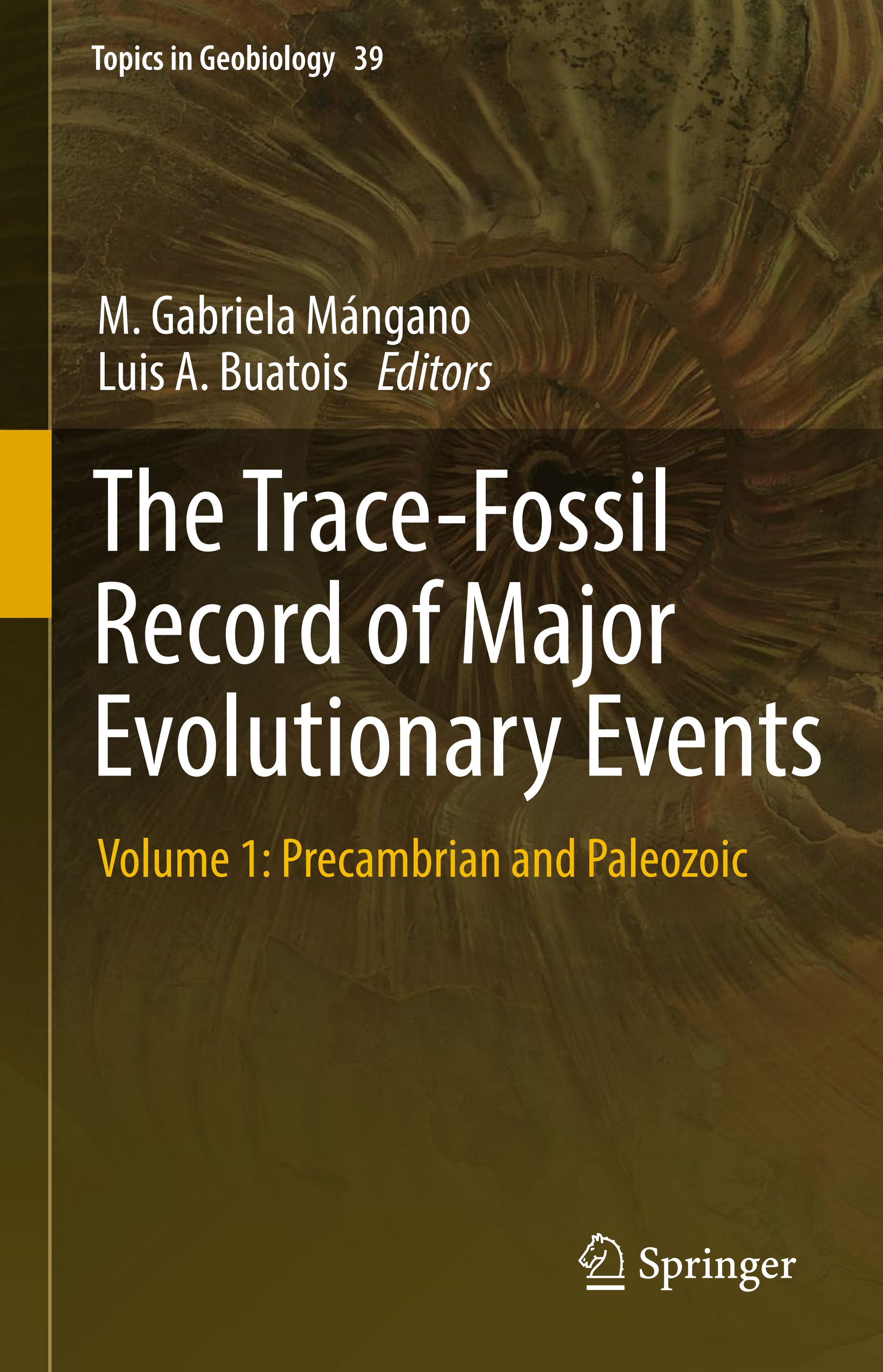

Topics in Geobiology 39

M. Gabriela Mángano
Luis A. Buatois *Editors*

# The Trace-Fossil Record of Major Evolutionary Events

## Volume 1: Precambrian and Paleozoic

Springer

# Topics in Geobiology

## Volume 39

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Editors

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ISSN 0275-0120
Topics in Geobiology
ISBN 978-94-017-9599-9 ISBN 978-94-017-9600-2 (eBook)
DOI 10.1007/978-94-017-9600-2

Library of Congress Control Number: 2016951934

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*To Dolf Seilacher, who, as usual, thought about these issues long before us.*

# Foreword

Imagine a world much like our own: an oxygen-rich atmosphere, dynamic tectonic activity, and a rich and diverse biota of plants, animals, and teeming associations of microbes. Indeed a world just like ours, with a similarly deep history of life, but with one slight difference: no body fossils. No shark teeth eroding from cliffs, no trilobites, no dinosaur bones cluttering up museums and the dreams of impressionable 5-year-olds (and Hollywood moguls). Worst of all, of course, we would be missing the remarkable schnozzle of *Opabinia*. Much of the rich morphological detail provided by body fossils would be irretrievably lost, but how much of the history and diversity of life could we recover? Would we be able to identify the explosive evolutionary dynamism of the Cambrian diversification? Would the paleontologists of this imaginary world be able to chart changing patterns of animal diversity and morphological disparity? Identify the invasion of land or the great mass extinctions? Chronicle advances in behavioral patterns? Would changing climate patterns be evident, or the rise of great plodding vertebrates?

If we stipulate that tracks, trails, and burrows were preserved in all the detail documented in the chapters of this volume and the richly informative photographs and diagrams, then a remarkable detailed view of animal diversity, morphological disparity, and behavior emerges. For those not intimately acquainted with the extensive strides made over the past couple of decades of research in ichnology, this volume illustrates the range of information which can be recovered from the primary record of organismal behavior to analysis of changing patterns of diversity and disparity.

As a graduate student during the early 1980s the focus of ichnology seemed to be on describing new structures and providing them (mystifyingly to those of us who did not study trace fossils) Latin binomials. Yet ichnology was already undergoing a conceptual shift in concert with changes within the broader field of paleobiology. As facies concepts spread through sedimentology, the concept of ichnofacies was adopted. The increased emphasis on taphonomy, preservation, and the quality of the fossil record beginning in the 1980s found a similar expression in ichnology in the recognition that the same animal could produce very different structures depending on the environment and the nature of the sediment, and that tracks can look very different depending on what level one examines within their stratigraphy. One result of such studies has been considerable revision in the diversity of ichnotaxa. As described in Chap. 2 of this volume, many fossils that we happily accepted as burrows in the mid-1990s have now been recognized as components of a diverse assemblage of latest Ediacaran tubes, and not trace fossils at all. Restudy of Ediacaran traces has drastically reduced the number of accepted ichnogenera.

To a non-ichnologist, what is particularly striking about this book is how faithfully the general outlines of evolutionary dynamics are visible with trace fossils alone. As illustrated by Chaps. 2 and 3, the integration of trace fossils has long been standard for studies of the Ediacaran and Cambrian diversification. It is not just that the base of the Cambrian is currently defined by the first occurrence of the ichnotaxon *Treptichnus pedum*, rather it is hard to imagine any survey of the Ediacaran–Cambrian diversification *not* including a discussion of the trace-fossil record. Data from ichnological studies has been essential to revealing patterns of morphological novelty and innovation, which is why several generations of workers, from Dolf Seilacher and Peter Crimes to Mary Droser, Soren Jensen and the editors of this volume, have played critical roles in expanding our integrated understanding of this interval. Indeed, Chap. 3 notes that in important ways the trace-fossil record may provide a more reliable picture of the diversity dynamics during the Fortunian, the first stage of the Cambrian, than do other fossils.

The pattern continues with later chapters. The Ordovician biodiversification event reveals breakthroughs in paleoecology including movement into infaunal habitats with increased tiering, increased bioturbation, and colonization of new environments (Chap. 4). Unlike the Cambrian, the Ordovician increase in the diversity of ichnotaxa was not accompanied by an increase in ichnodisparity. Indeed a thread throughout the chapters is the frequency of "early burst" patterns of diversification. The exploration and exploitation of new habitats is a consistent theme throughout this volume. The invasion of land, discussed in Chap. 5, reveals a pattern of colonization, a rapid exploration of new behaviors and architectural designs, followed by variation on the established themes. Other episodes that are addressed are the expansion of terrestrial ecosystems, the Mesozoic marine revolution, and lacustrine revolutions. Chapter 14, on the Cenozoic mammalian radiation, suggests that the tracks of this episode, like the traces of the Cambrian, may provide a richer record of evolutionary change than does skeletal elements, and in addition provides unique information on locomotion, body size, and ecology. I must confess that I had never considered the nature of trace fossils associated with soils, but Chap. 15 illuminates the unexpected complexity in the evolutionary exploitation of paleosols. Chapter 16 provides an insightful analysis of patterns of ecospace occupation through the Phanerozoic, advances in ecosystem engineering, and patterns of ichnodiversity and ichnodisparity. I was particularly struck by the proposal that a space of all possible "ichno-structures" that was explored relatively early by marine invertebrate clades, with similar architectures subsequently discovered independently by different clades. Not surprisingly, this pattern matches studies of ecospace by Bambach and colleagues, and of morphological disparity by many writers.

But of course the diversity and disparity of these structures varied with events in the history of life, as demonstrated by ichnological studies associated with the end-Permian, end-Triassic, and end-Cretaceous mass extinctions, as discussed in Chaps. 7, 8, and 12. The early Triassic aftermath of the end-Permian mass extinction reveals as complicated a pattern of ichnofaunal re-emergence as has been found looking just at body fossils. Returning to the counterfactual musings with which I began this foreword, the evidence presented in Chap. 7 makes it clear that we would be able to recover much of the complexity of the biotic recovery from the trace-fossil record alone. (I must confess to a certain pleasure in Chap. 7 as a proposal I made in 1993 which had been discarded by later workers is resurrected therein.)

Sadly of course, the trace-fossil record on my mythical, alternate Earth would be no more complete than the record we possess today. Trace fossils might hint at morphologies not found among extant animals, but phylogenetic analysis, to take one example, would be greatly hampered by a loss of character information from the early history of many clades: the origins of turtles might forever remain a mystery. There would be many questions accessible with our extant fossil record that would be unanswerable. But of course this is just the strength of the fossil record that we possess. The trace and body fossil records each have their strength, and their weaknesses. This volume wonderfully elucidates the power of the ichnofossil record, properly interpreted, to reveal much of the ecological and evolutionary dynamics of life on this Earth. As students read this volume (and I hope many do), the chapters here should provide a plethora of questions to pursue. While I am sure that this book will attract many students to ichnology, in some ways the most significant impact of the book would be to convince paleontologists to more fully integrate ichnological data and analyses into projects on evolutionary diversifications and radiations, mass extinctions, and paleoecological dynamics.

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# Prologue

> *"A beginning has been made and the discipline has been advanced to the point where some of the highlights in the history of life may be examined from a paleoecological perspective"*
>
> (Valentine 1973, Evolutionary Paleoecology
> of the Marine Biosphere)

In a remarkable book on the meaning of geologic time, Stephen Jay Gould explored the dichotomy between time's arrow and time's cycle (Gould 1987). According to this view, time's arrow encompasses history as an irreversible sequence of unrepeatable events, whereas time's cycle refers to a nondirectional time characterized by repetition according to a recurrent pattern. As we have emphasized elsewhere (e.g., Mángano and Buatois 2012, 2015), ichnology can be viewed as an expression of the tension between these two faces of geologic time.

The remarkable success of ichnology to solve problems in facies analysis, paleoenvironmental reconstruction, and sequence stratigraphy is clearly an expression of the emphasis on recurrence. In fact, the very same definition of archetypal ichnofacies, as trace-fossil suites that record responses of benthic organisms to a given set of environmental conditions and that recur through geologic time, epitomizes time's cycle. In this view, regardless of the age of the unit animals should respond to ecological parameters in a similar way, reflecting their adaptation to the environment they inhabit. This nomothetic program for ichnology, with its power as a predictive conceptual tool, is the reason that sedimentary geologists now typically include trace fossils in their toolkit to scrutinize the stratigraphic record.

However, this success when dealing with practical issues, often of economic importance, should not prevent us from the realization that ichnology has much to contribute to our understanding of the changing ecology of the past by recovering a time's arrow perspective. While working on a previous book (Buatois and Mángano 2011), it became increasingly obvious to us that this other face of ichnology has received far less attention. However, even a cursory review of the recent paleobiologic literature shows that there is an increased awareness of the importance of bioturbation and bioerosion as driving forces in the history of life, playing major roles as a connecting players between biotic and abiotic factors involved in complex feedback loops that result in evolutionary change (e.g., Erwin and Tweedt 2012).

In its essence, this book reflects the growing interest within the ichnologic community in expanding the potential of ichnology to contribute to evolutionary paleoecology. The authors of the different chapters are eclectic in their perspectives and methodologies. However, there are some common themes and conceptual tools, such as ichnodiversity and ichnodisparity, ecospace utilization, environmental expansion, innovation associated to major radiation events, and the re-organizations of ecological units, in particular communities and ecosystems, after mass extinctions. What emerges is a wealth of information and the idea that the history of life can be accurately reconstructed looking through the ichnologic glass.

There are two strategies to bring back the time's arrow perspective of ichnology. One would be to assess the trace-fossil record of the colonization of specific depositional settings, being the main focus on the reconstruction of major trends in global ichnodiversity. In fact, this approach has a relatively long history, starting with the colonization of the deep sea through geologic time due to pioneer papers by Seilacher (1974, 1977) and Crimes (1974), continuing with more recent studies on the same topic (Orr 2001; Uchman 2003, 2004), as well as on the colonization of continental environments (Buatois and Mángano 1993; Buatois et al. 1998), estuaries (Buatois et al. 2005), and tidal flats (Mángano and Buatois 2015). Another approach would be to evaluate how the interactions between animals and substrates were shaped by major macroevolutionary events, such as the Cambrian explosion and the Permian mass extinction. These changes are analyzed from an ecological perspective. For this book we have decided to follow this later approach.

The first volume opens with Chap. 1, where Minter et al. briefly revise the conceptual and methodological tools of ichnology, with the aim of providing the reader with the basic information necessary to explore the rest of the book. The approach is eclectic with brief summaries of the basic principles and concepts in the field, as well as revisions of the ichnofacies model and the ichnofabric approach. The chapter also introduces a number of concepts and methods that are used in subsequent chapters, including the notion of ichnodiversity and ichnodisparity as a novel approach to unlock the potential of ichnofaunas to provide insights into mode of life, ecospace colonization, and ecosystem engineering.

Chapter 2, by Buatois and Mángano, starts our journey through time by evaluating the highly controversial trace-fossil record of the Ediacaran. The chapter can be understood as an attempt to revisit from an ichnologic perspective the so-called Darwin's dilemma on the supposed absence of evidence of life in the Precambrian by critically searching for the roots of animal life in the Ediacaran. In addition, ichnologic information is used to reveal the nature of Ediacaran ecosystems and the complexities involved in the transition to the Phanerozoic world.

In Chap. 3, Mángano and Buatois look at the other side of the great divide, by exploring the trace-fossil record of the Cambrian explosion. The chapter emphasizes the importance of trace-fossil data to calibrate the Cambrian diversification event. Also, the profound changes that took place at ecosystem scale are analyzed in detail, emphasizing the role of bioturbation as an agent of evolutionary change. The chapter closes with an evaluation of the paleoenvironmental breadth of the Cambrian explosion, the significance of the ichnofaunas associated with Burgess shale-type deposits, and the dual nature of the Fortunian from an evolutionary standpoint.

Chapter 4, by Mángano et al., examines the following evolutionary radiation, the Great Ordovician Biodiversification Event. This chapter analyzes ichnodiversity and ichnodisparity trajectories through the Ordovician, comparing patterns in different depositional environments and paleocontinents. The contrasting nature of diversification in soft-bottom and hardground communities is emphasized by showing that innovation in macrobioerosion was significantly delayed when compared with bioturbation.

Minter et al. explore the initial steps of life on land in Chap. 5 focusing on the Ediacaran–Ordovician timespan. The chapter traces the early stages of animal expansion from fully marine settings into marginal-marine coastal environments and ultimately truly continental settings by the Late Ordovician. This prelude to terrestrialization involves the gradual colonization of new environments followed by rapid filling of ecospace, the establishment of new architectural designs, and diversification within the framework of these new behavioral programs. Links between these evolutionary innovations, and the incipient establishment of a land flora and changes in fluvial styles are discussed.

In Chap. 6, Minter et al. continue with the analysis of terrestrialization by examining the trace-fossil record of marginal-marine and continental environments during the remainder of the Paleozoic. Following the protracted prelude reviewed in the previous chapter, the Silurian to the Permian was characterized by an explosion of diversity and expansion into newly colonized environments, such as river channels, overbanks, deserts, and lakes, coupled with increasing exploitation of the infaunal ecospace. The chapter underscores how colonization of continental settings by benthic organisms parallels changes in vegetation and fluvial styles.

Hofmann closes the first volume with Chap. 7, addressing the trace-fossil record of the end-Permian mass extinction. By carefully evaluating ichnologic data, he provides insights into the extinction event and the subsequent recovery. The impact of burrowing organisms on geochemical conditions of the marine sediment is emphasized, providing a critical evaluation of previous ideas regarding the role of oxygen-depleted conditions as a cause of delayed recovery. It is argued that bioturbation was strongly reduced as a result of the end-Permian mass extinction, leading to the collapse of the mixed layer. The large-scale consequences of such collapse are evaluated in detail.

Volume 2 marks the passage to the post-Paleozoic world, opening with Chap. 8, where Barras and Twitchett analyze the end-Triassic mass extinction. The authors revised the ichnologic record of both terrestrial and marine environments through the Triassic-Jurassic transition, outlining how the benthic faunas responded to the mass extinction. Their review suggests that climatic and environmental change were main factors controlling benthic communities on land and in the sea.

In Chap. 9, Buatois et al. take the reader to the new world arisen from the Mesozoic Marine Revolution. The main group of bioturbators and bioeroders are reviewed, and the trace-fossil record of Mesozoic and Cenozoic marine environments is revised to track evolutionary innovations, discussing the timing of Mesozoic Marine Revolution. The environmental breadth of this major event is evaluated by summarizing evolutionary innovations not only in shallow-marine environments but also in marginal-marine and deep-marine settings. It is argued that infaunalization predated an increase of predation pressures by approximately 50 Myr, pointing towards a complex set of feedback mechanisms between the two.

In Chap. 10, Bernardi et al. explore the vertebrate radiation during the Mesozoic. By revising in detail available ichnologic data, they show how the trackway record yields insights into several issues, such as locomotor mechanics and behavior, therefore providing information that typically is not revealed by the body-fossil record. In turn, biases inherent to the trace-fossil record are discussed, arguing that the integration between the trackway and the skeletal record is essential to provide a more holistic picture of the evolutionary changes underwent by terrestrial vertebrates during the Mesozoic.

Chapter 11, by Buatois et al., discusses another series of evolutionary breakthroughs that took place in continental settings: those resulting from the Mesozoic lacustrine revolution. Lakes are evaluated from an ichnologic perspective, contrasting lacustrine ecosystems prior to this evolutionary event with those that arose after the Mesozoic lacustrine revolution. Aspects discussed in this chapter include ichnodiversity changes through time, the establishment of modern lacustrine food webs, and the role of behavioral convergence on both sides of the salinity divide.

In Chap. 12, Labandeira et al. shift our attention to another extinction event: the end-Cretaceous mass extinction. These authors evaluate both the record of plant–arthropod interactions on land and that of invertebrate trace fossils in the sea, therefore providing a comprehensive picture of the extinction event and its aftermath. A number of methodological, empirical, and theoretical advances resulting from the use of ichnologic data are outlined, including application of innovative methods to quantify ichnologic information, access to novel ecologic data, and evaluation of catastrophic vs. gradualistic scenarios based on the analysis of bioturbated sediment, among many others.

Chapter 13, by Genise et al., represents a general departure to the overall structure of the book in that it does not address a specific evolutionary event, but instead traces a series of dramatic changes in paleosols covering most of, if not all, the Phanerozoic. In doing so, they provide an in-depth characterization of four revolutions in paleosol ichnofaunas. In addition, this chapter provides an interesting twist to the concept of ichnofacies by showing that their establishment in terrestrial settings is fully linked to a series of evolutionary innovations by soil-burrowing organisms.

In Chap. 14, Krapovickas and Vizcaino explore the evolution of mammals based on their footprint record. Although this chapter summarizes the Mesozoic and Cenozoic record of tracks attributed to mammals worldwide, emphasis is on changes in South American mammals during the Cenozoic. The authors show that Eocene-Oligocene trackway assemblages mostly consist of forms of uncertain affinity, whereas later assemblages consist of trackways of both native South American and North American mammals that arrived during the Great American Biotic Interchange. This chapter emphasizes the strong provincialism of mammal faunas, representing a starting point towards a more global examination of their ichnologic record.

Chapter 15, by Lockley et al., deals with the trackway record of hominin evolution. Starting with the famous 3.6 Ma tracks from Laetoli, the reader is taken through a journey that explores the expansion of our ancestors from Africa to Eurasia, the New World, and Australasia. References to footprints on the Moon and tracks of robotic vehicles on Mars add another dimension to the trip. Along the way, the authors discuss various controversies, including the alternative interpretations of the Laetoli trackways and the differences between early hominin footprints and those from modern humans.

The book closes with Chap. 16, where Buatois and Mángano take the challenge of trying to summarize possible recurrent trends revealed by the trace-fossil record that may provide insights into the underlying dynamics of animal–substrate interactions through geologic time. In particular, the chapter discusses organism–substrate interactions during evolutionary radiations, benthic fauna response to mass extinctions, patterns of ecospace colonization, and environmental shifts through time. In contrast to the other chapters, which by reviewing individual evolutionary events are anchored in an idiographic approach, this last chapter takes on a more nomothetic perspective by trying to find recurrent patterns and processes in evolutionary paleoecology.

In the process of planning this book, it became clear that, although there is an explicit attempt to bring a picture of the state of the art in the contributions of ichnology to the understanding of evolution at the macroevolutionary scale, our book does not offer a comprehensive treatment or a closure on the topic. In fact, during this process, we have identified numerous areas of interest where there is limited ichnologic information to the point that it was not possible to include chapters on these issues. For example, the end-Ordovician and Late Devonian mass extinctions have received significantly less treatment than any of the other so-called Big Five. Also, some of the chapters provide fresh approaches to our exploration of the colonization of infaunal ecospace and the impact of ecosystem engineers by using ichnologic data in an innovative fashion. This may serve as inspiration for applying new numerical and conceptual tools to a wider spectrum of paleobiologic issues. This book is a tangible testimony that ichnology counts with a solid theoretical framework and sufficient methodological tools to tackle evolutionary questions and offer crucial pieces in the reconstruction of the puzzle of the history of life. Our ambition with this book echoes the Gouldian aim, paraphrased in Chapter 10, of sitting Ichnology at the High Table of Macroevolution and Paleobiology.

We would like to thank the reviewers of the many chapters, who did a great job of providing valuable feedback. These are: Andrea Baucon, Zain Belaústegui, Angela Buscalioni, Karen Chin, Matthew Clapham, Darin Croft, Phillip Currie, Bill DiMichele, Tony Ekdale, Russell Garwood, Sören Jensen, Dirk Knaust, Conrad Labandeira, Spencer Lucas, Ken McNamara, Christian Meyer, Nic Minter, Guy

Narbonne, Eduardo Olivero, Paul Olsen, Roy Plotnick, Gustavo Politis, Charles Savrda, Thomas Servais, Alfred Uchman, Jean Vannier, Sally Walker, Mark Wilson, and Anna Żylińska. Also we thank Doug Erwin for writing the Foreword.

Finally, as with almost all things ichnologic, Dolf Seilacher has been there before. He should be recognized as the scientist who started to think along this line of evidence, putting forward the idea that trace fossils represent the "other" fossil record, underexplored and immensely valuable. Not necessarily an alternative archive for the history of life, but more of an essential companion that should be integrated to the other lines of evidence to decipher the complex evolutionary pathways in the history of life. Needless to say, Dolf's influence has been huge in the field of ichnology and the same can be said of his influence in our personal careers. It all started long time ago when we were Geology students and he planted some "seed ideas" during a Trace Fossil course that he taught at the Argentinean Paleontological Association (APA). Sadly, he passed away during the completion of this book. We would like to dedicate this book to his memory.

M. Gabriela Mángano
Luis A. Buatois

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# Chapter 1
# The Conceptual and Methodological Tools of Ichnology

**Nicholas J. Minter, Luis A. Buatois, and M. Gabriela Mángano**

## 1.1 Introduction

Ichnology is the multidisciplinary science that focuses on the study of traces produced by organisms (both animals and plants) on or within a substrate, including all issues related to bioturbation, bioerosion, and biodeposition (Pemberton et al. 1992; Bromley 1990, 1996; Buatois and Mángano 2011). Ichnology has undergone an explosive development since the 1960s, particularly after the publication in English of the seminal papers by Dolf Seilacher (e.g., Seilacher 1964, 1967). At that time somewhat off the radar of the English-speaking world were his earlier studies (e.g., Seilacher 1953a, b, 1955, 1958, 1963) and all the impressive corpus of work done by the German school, including the development of the so-called "actuopalaeontology" (e.g., Richter 1929; Abel 1935; Schäfer 1956, 1962, 1972), which delineates a tradition to which Seilacher's research program undoubtedly belongs (Mángano and Buatois 2012).

Before exploring the potential of trace fossils in macroevolution it is necessary to summarize the conceptual framework of ichnology, as well as to outline the various approaches adopted by its practitioners. The aim of this introductory chapter is to provide such an overview. Extensive coverage of these topics can be found in several textbooks (e.g., Ekdale et al. 1984; Bromley 1990, 1996; Buatois and Mángano 2011), whereas in-depth functional analysis of the most important groups

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M.G. Mángano, L.A. Buatois (eds.), *The Trace-Fossil Record of Major Evolutionary Events*, Topics in Geobiology 39,
DOI 10.1007/978-94-017-9600-2_1

of trace fossils was provided by Seilacher (2007). Because of this, our review in this introductory chapter is succinct, summarizing information in tables, rather than in an extensive text.

## 1.2 Basic Concepts

As with every science, ichnology is plagued by terminology that can be somewhat intimidating. Some of these terms (e.g., track, trail) refer to observable entities and are easier to grasp, whereas others deal with concepts of more abstract nature (e.g., ichnofacies, ichnoguild). The notion of "trace," an individual and distinctive structure of biogenic origin showing some sort of link to the morphology of its producer (Frey 1973), lies at the center of ichnology. The classification schemes for biogenic structures have been reviewed elsewhere (Frey and Wheatcroft 1989; Pemberton et al. 1992; Buatois and Mángano 2011), and there is no need for repetition here, so only some brief definitions are provided.

The broad category of biogenic structures includes a wide variety of structures of organic origin, some of which fall within the realm of ichnology, whereas others (e.g., stromatolites, a typical biostratification structure) are commonly regarded as outside the field. Of the structures included within the field of ichnology, bioturbation and bioerosion structures are the most important ones. Bioturbation structures are biogenic sedimentary structures reflecting the disruption of stratification features or sedimentary fabrics by the activity of an organism, whereas bioerosion structures comprise biogenic structures produced mechanically or biochemically by an organism into rigid substrates, such as hardgrounds, clasts, bones, invertebrate skeletons, wood, or rocks (Frey and Wheatcroft 1989). A third group of structures embraced by ichnology are biodeposition structures, which reflect production or concentration of sediment by the activities of an organism and include coprolites, fecal pellets, pseudofeces, regurgitation pellets, and fecal castings (Frey and Pemberton 1984; Frey and Wheatcroft 1989).

The vast majority of the biogenic structures discussed in this book are bioturbation structures. These include tracks, trails and burrows. Tracks are imprints left by an individual locomotion appendage (the related term "trackway" refers to a repeated pattern of tracks). Trails are continuous impressions or grooves produced during locomotion. Burrows are permanent to semipermanent structures excavated within the sediment. Bioerosion structures are also addressed in several chapters. These include macroborings (down to the millimeter scale) and microborings (smaller than a millimeter) (Bromley 1994). Bioerosion structures encompass a wide variety of morphologic types, including borings, embedment structures, rasps and scrapes, surface etching scars, durophagous damage, drill holes, and bite marks (Bromley 1992, 1994). This classification scheme is not without problems, as reflected by the uncertain placement within this framework of other structures that are prominent in some chapters of the book, such as biogenic structures preserved in wood, leaves, and seeds (e.g., Labandeira 2002).

## 1.3 The Peculiarities of Trace Fossils

Trace fossils differ in many ways from body fossils, regarding both their mode of formation and their taphonomic histories (Seilacher 1964; Frey 1975; Ekdale et al. 1984; Frey and Pemberton 1985; Pemberton et al. 1990, 2001; Bromley 1990, 1996; Buatois and Mángano 2011). As a result, ichnologists attempted to outline these peculiarities in terms of a list of characteristics (Seilacher 1964; Frey 1975) or

**Table 1.1** The ten main characteristics of trace fossils (based on Buatois and Mángano 2011)

| Characteristic | Comment |
|---|---|
| Trace fossils represent evidence of behavior | Analysis of the morphology and architecture of trace fossils provides evidence on the anatomy and ethology of their producers. Behavior may range from simple (e.g., trace of a worm-like animal moving through the substrate) to complex (e.g., the work of social insects). Releasing the behavioral signal unlocked in a biogenic sedimentary structure is central to any ichnologic analysis |
| The same organism may produce more than one ichnotaxon | A single organism may produce several ichnotaxa by changing its behavior. Intergradational forms that show the transition of one ichnotaxon into another are referred to as "compound ichnotaxa." In addition, the same organism may produce different traces during its different ontogenetic stages |
| The same ichnotaxon may be produced by more than one organism | The same ichnotaxon can be produced by many different organisms, as a result of behavioral convergence. Establishing a one-to-one relationship between producer and biogenic sedimentary structure is not possible in the vast majority of cases. In general, the simpler a trace fossil is, the weaker the link between the biogenic sedimentary structure and its producer. In any case, morphologic features commonly may supply enough information on burrowing technique and anatomy, so a link with a certain group of organisms can be established |
| Multiple architects may produce a single structure | A single biogenic sedimentary structure may reflect the activities of more than one producer. This may result from producers operating more or less at the same time or in successive bioturbation events. The first case is difficult to recognize in the fossil record and commonly results from the establishment of symbiotic or commensalist relationships. The second case is common in the fossil record and is represented by abandoned biogenic sedimentary structures that are reoccupied by a different animal. The term "composite ichnotaxa" has been proposed to name forms that superficially look like a single burrow system, but actually result from the interpenetration of individual discrete ichnofossils |
| Producers are commonly soft-bodied animals that are rarely preserved | The body-fossil record for the most part reflects those groups that have developed hard parts, whereas trace fossils commonly record the activities of soft-bodied animals. This is because the trace-fossil record is biased towards the activities of infaunal organisms, and the presence of skeletons is commonly detrimental for infaunal life. Exceptions to this principle are represented by the preservation of the producer directly associated with the biogenic sedimentary structure |

(continued)

**Table 1.1** (continued)

| Characteristic | Comment |
|---|---|
| Trace fossils are commonly preserved in rock units that are otherwise unfossiliferous | Conditions favoring the preservation of trace fossils are remarkably different from those of body fossils. Diagenetic processes conducive to destruction of body fossils may favor trace-fossil preservation by promoting mineral precipitation around burrow walls. Biogenic sedimentary structures commonly represent the only biotic evidence in many rock units |
| The same biogenic sedimentary structure may be differentially preserved in various substrates | Biogenic sedimentary structures reflecting identical burrowing technique by the producer may result in apparently disparate trace fossils if produced under contrasting substrate conditions. This is a serious complication for ichnotaxonomy, because underappreciating this issue may lead to oversplitting |
| Trace fossils commonly have long stratigraphic ranges | The vast majority of ichnotaxa display long stratigraphic ranges, commonly spanning most if not all the Paleozoic and a small number originating in the Ediacaran. This fact reveals behavioral convergence rather that a common producer through geologic time. Certain behaviors were established relatively early in the history of metazoan life and have remained essentially unchanged. However, there are many departures to this principle, as it will become evident to the reader of this book |
| Trace fossils commonly have narrow environmental ranges | In fairness, this characteristic applies more accurately to trace-fossil associations rather than to individual ichnotaxa. In any case, it reveals that biogenic sedimentary structures are strongly controlled by environmental factors and, therefore, the large majority of them occur preferentially in certain depositional environments |
| Trace fossils are rarely transported | Trace fossils represent the in situ record of biogenic activity, and therefore typically they have not suffered secondary displacement. Exceptions include borings transported together with the host medium (e.g., bioeroded logs, shells, clasts) and burrows with strongly reinforced walls that make them resistant to erosion and reworking |

ichnologic principles (Ekdale et al. 1984; Bromley 1990, 1996), which are here listed in Table 1.1, based on a recent synthesis by Buatois and Mángano (2011).

Preservational issues need to be assessed in any study involving trace fossils. In particular, toponomy, which comprises the description and classification of biogenic structures with respect to their mode of preservation and occurrence, has received most attention (Frey and Pemberton 1985; Rindsberg 2012). Mode of occurrence is usually defined according to the position of the structure on or within the stratum, or relative to the casting medium. Mechanical processes involved in the fabrication of the structure (stratinomy) and its alteration (taphonomy) are included within toponomy as well. A number of classification systems have been introduced to address stratinomy. Those of Seilacher (1964) and Martinsson (1970) are the ones that have met with most acceptance (Fig. 1.1).

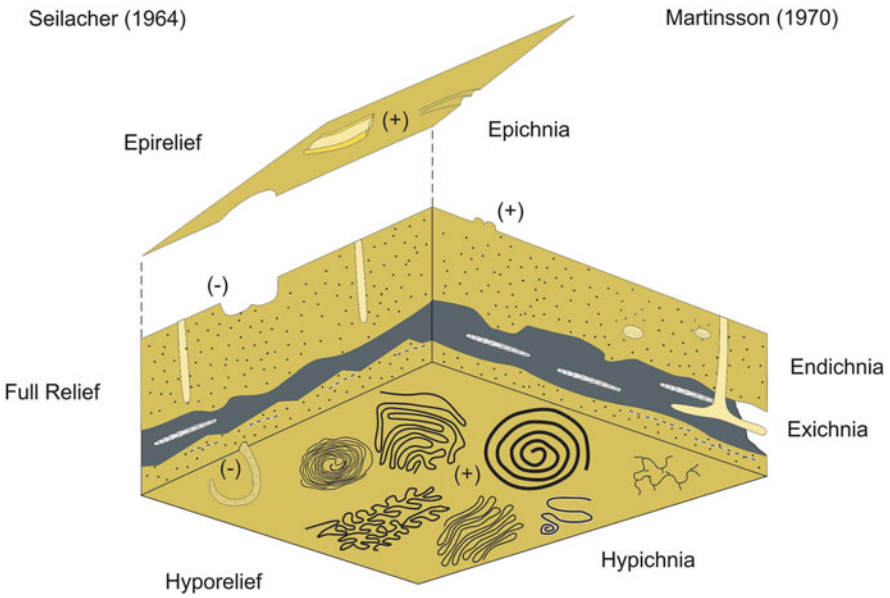

**Fig 1.1** Block diagram illustrating the terms used in the stratinomic classifications of Seilacher and Martinsson. In Seilacher's scheme, full-relief structures are preserved within the stratum, whereas semirelief structures are preserved at lithologic interfaces. Semirelief structures are in turn subdivided into epirelief (preserved at the *top*) or hyporelief (preserved at the *base*) of the sandstone bed. The terms "concave" (negative) and "convex" (positive) are employed to provide a picture of the trace-fossil relief. In Martinsson's classification, epichnial preservation refers to structures preserved at the upper surface of the casting strata, whereas hypichnial preservation includes those at the lower surface of the casting strata. The terms grooves and ridges are used to denote negative and positive reliefs, respectively. Endichnial preservation includes structures preserved within the casting medium, whereas exichnial preservation comprises those preserved outside the casting medium (after Buatois and Mángano 2011)

Because trace fossils are primarily evidence of animal behavior, evaluation of the ethologic significance of trace fossils is central to any application of ichnology. Therefore, the ethologic classification of trace fossils proposed originally by Seilacher (1953a) is now considered an essential component of the conceptual framework of ichnology. The original system consists of five categories: resting traces (Cubichnia), locomotion traces (Repichnia), grazing traces (Pascichnia), feeding traces (Fodinichnia), and dwelling traces (Domichnia), but many other categories have been added subsequently (Frey 1973; Ekdale et al. 1984; Ekdale 1985; Bromley 1990; Genise and Bown 1994; de Gibert et al. 2004; Tapanila 2005; Genise et al. 2007; Seilacher 2007; Lehane and Ekdale 2013; Vallon et al. 2015a, b). The validity and utility of the more recent categories continue to be evaluated (Vallon et al. 2015a), and only the more widely accepted ones are listed and illustrated in this chapter (Table 1.2 and Fig. 1.2). Although it has been argued that many com-

**Table 1.2** The ethologic categories (based on Seilacher 1953a; Frey 1973; Ekdale et al. 1984; Ekdale 1985; Bromley 1990; Genise and Bown 1994; de Gibert et al. 2004; Tapanila 2005; Genise et al. 2007; Seilacher 2007; Buatois and Mángano 2011 and Vallon et al. 2015a)

| Ethologic category | Description | Examples |
|---|---|---|
| Resting traces or Cubichnia | Produced by vagile organisms that temporarily dig down, forming shallow depressions, in order to find protection from predators or to stop their usual activities during quiescent moments. Subordinate behaviors are typically involved. Resting traces reflect the latero-ventral anatomy of their producers and, therefore, can be ascribed to their producers with a higher degree of certainty than other categories | *Lockeia*, *Tonganoxichnus*, *Tripartichnus*, *Selenichnites*, *Asteriacites*, *Rusophycus*, *Medousichnus*, *Raaschichnus*, and *Limulicubichnus* |
| Locomotion traces or Repichnia | Structures resulting from organisms moving from one place to another. Subordinate activities, such as feeding, might be involved, but they are not reflected by the biogenic structure. Locomotion traces may provide information on the type and number of appendages involved in locomotion and the role of muscles used for displacement | *Umfolozia*, *Kouphichnium*, *Diplichnites*, *Mirandaichnium*, *Octopodichnus*, *Paleohelcura*, *Cruziana*, *Gyrochorte*, *Diplopodichnus*, *Didymaulichnus*, and *Protovirgularia* |
| Death traces or Mortichnia | Structures reflecting the last movements of the producers that are preserved together with their trace fossils. In these cases, a trace fossil is attributed without any doubt to a producer (e.g., arthropod trackways ending in a body fossil) | *Telsonichnus* and *Vadichnites* |
| Grazing traces or Pascichnia | Structures reflecting a combination of locomotion and feeding due to the fact that the producer searches for food while traveling. Produced by mobile, infaunal deposit feeders or epifaunal detritus feeders. Structures tend to be more regular than trails that simply reflect locomotion. Typical structures are unbranched and horizontal, ranging from simple, straight trails to curved, circular, and meandering trails, including tight guided meanders that reveal sophisticated feeding patterns | *Gordia*, *Mermia*, *Helminthoidichnites*, *Archaeonassa*, *Psammichnites*, *Helminthopsis*, *Nereites*, *Bichordites*, and *Scolicia* |
| Feeding traces or Fodinichnia | Structures reflecting combined dwelling and feeding activities. Typically produced by infaunal deposit feeders, involving an "underground mining" strategy. Variable morphologies, ranging from simple to extremely complex. Intergradations with dwelling traces are common. Common patterns include simple burrows, branched burrow systems, spreiten burrows, radial structures, and U-shaped tubes. Evidence of active infill (e.g., backfill) is almost diagnostic | *Asterosoma*, *Arthrophycus*, *Rhizocorallium*, *Treptichnus*, *Dictyodora*, *Lophoctenium*, *Teichichnus*, *Daedalus*, *Syringomorpha*, *Gyrophyllites*, *Dactyloidites*, and *Phycodes* |

(continued)

**Table 1.2** (continued)

| Ethologic category | Description | Examples |
|---|---|---|
| Dwelling traces or Domichnia | Structures comprising permanent domiciles constructed by infaunal organisms, typically sessile suspension feeders and passive predators and, less commonly, active predators and deposit feeders Other activities may be involved. Both burrows and borings are included. Morphology varying from simple burrows to U-shaped tubes and branched burrow systems. Lined walls are typical | *Skolithos*, *Arenicolites*, *Ophiomorpha*, *Thalassinoides*, *Monocraterion*, *Camborygma*, *Lunulichnus*, and *Palaeophycus*. |
| Farming traces or Agrichnia | Structures representing combined dwelling and feeding activities that are interpreted to be produced for bacterial farming, or as traps to capture meiofauna or microorganisms. Complex and highly regular burrow patterns, also known as graphoglyptids. Morphologies include branched meanders, spirals, and nets | *Spirorhaphe*, *Belorhaphe*, *Helicolithus*, *Urohelminthoida*, *Paleomeandron*, *Desmograpton*, *Paleodictyon*, *Megagrapton*, and *Protopaleodictyon* |
| Escape traces or Fugichnia | Structures produced in response to rapid sedimentation, typically event deposition. Animals rapidly readjust their burrows to avoid burial. Typical escape structures are indicated by the vertical repetition of dwelling traces, commonly forming cone-in-cone structures | No formal ichnotaxonomic names are given |
| Equilibrium traces or Equilibrichnia | Structures formed in substrates affected by progressive aggradation and degradation, reflecting more gradual adjustments under background sedimentation. Infaunal organisms move up and down trying to maintain a certain depth with respect to the sediment–water interface. Typical morphologies include vertically oriented, spreiten U- or V-shaped burrows | *Diplocraterion yoyo*, *Rosselia socialis*, and *Scalichnus* |
| Predation traces or Praedichnia | Structures reflecting predatory activities, typically borings in hard substrates (e.g., shells, bones). Typical morphologies are round drill holes, gnawings, and the chipped margins observed in gastropod and bivalve shells | *Oichnus* and *Caedichnus* |
| Nesting traces or Calichnia | Nests constructed or excavated for breeding purposes. Insect larvae are confined to cells or chambers that are provisioned by the adults. Typical morphologies include cells and chambers | *Coprinisphaera*, *Quirogaichnus*, and *Celliforma* |
| Pupation chambers or Pupichnia | Structures produce by insects for their protection during pupation. The same individual that produces the structure subsequently emerges from it, although in a different developmental stage. Chambers represent the typical morphology | *Fictovichnus*, *Pallichnus*, and *Rebuffoichnus* |

(continued)

**Table 1.2** (continued)

| Ethologic category | Description | Examples |
|---|---|---|
| Fixation/ anchoring traces or Fixichnia | Structures formed on hard substrate by sessile epilithic organisms to provide attachment. Some are formed by the anchoring of an organism by means of soft parts, while others are produced by the fixation of its skeleton | *Centrichnus*, *Podichnus*, *Renichnus*, *Stellichnus*, and *Leptichnus* |
| Bioclaustration structures or Impedichnia | Structures recording two distinct behaviors during construction of a cavity in skeletal material. They result by the activity of the endosymbiont that inhibits skeletal accretion of the host and by the host, which alters skeletal growth to accommodate the infesting organism. Also known as embedment structures | *Helicosalpinx*, *Tremichnus*, *Chaetosalpinx*, *Hicetes*, *Klemmatoica*, and *Eodiorygma* |

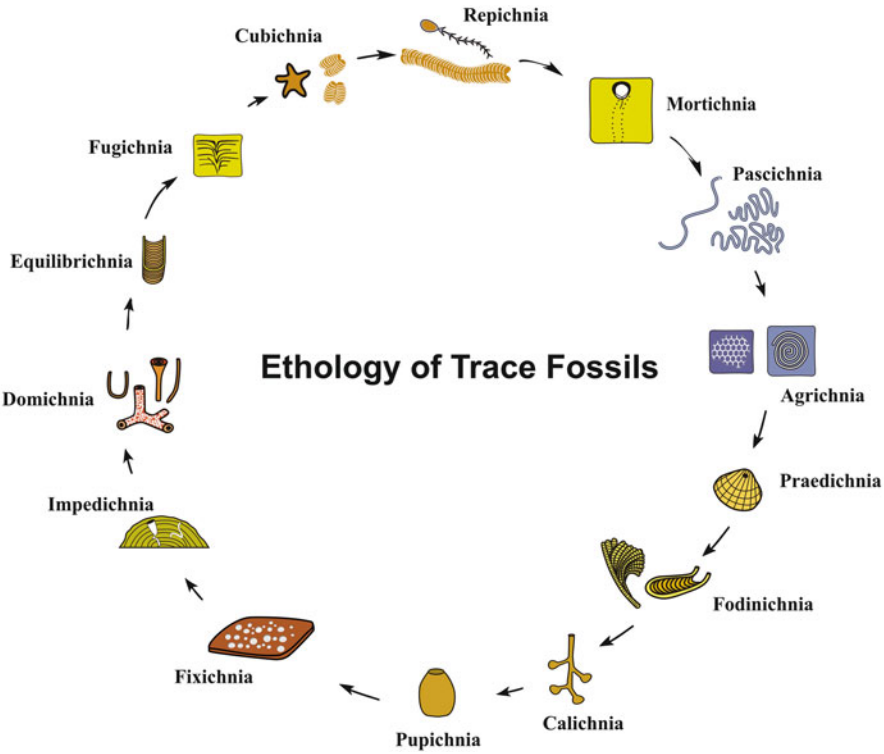

**Fig 1.2** Idealized reconstruction of ethologic categories (after Buatois and Mángano 2011)

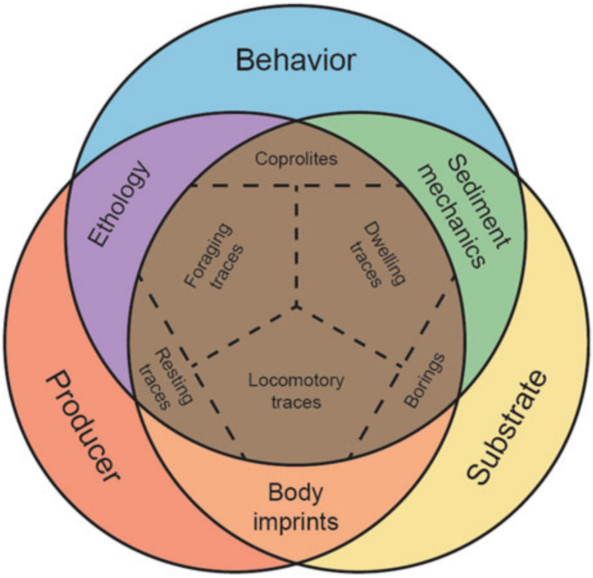

**Fig 1.3** Venn diagram highlighting that trace fossils are the product of three parameters: the producer, its behavior, and the substrate conditions; and also that these can have varying degrees of influence on the resultant morphology of the trace fossil (modified from Minter et al. 2007)

plex trace fossils cannot be accommodated in the traditional classification scheme (Miller 1998, 2003), the ethologic categories continue to be widely used in ichnologic studies.

In addition to the above classification schemes, trace fossils are classified into ichnogenera and ichnospecies on the basis of their morphology. The morphology of a trace fossil represents the result of a behavioral interaction between an organism and a substrate (Bertling et al. 2006). As such, the morphology is a result of three key factors: the anatomy of the producer, its behavior, and the substrate conditions (Baird 1957; Padian and Olsen 1984a, b; Minter et al. 2007) (Fig. 1.3). Diagnoses and descriptions of trace fossils should be limited to morphological features, but it is important to appreciate morphological variation and the processes of behavioral and substrate variation that can be responsible. The relative influences of the three factors (producer, behavior and substrate) vary depending on the type of trace fossil (Minter et al. 2007). For example, the morphologies of different trackways and resting traces are more strongly influenced by, and therefore reflective of, the anatomy of the producer and substrate conditions compared to the behavior. Conversely, grazing and feeding traces have their morphology more strongly influenced by the behavior of the producer.

## 1.4 A Plurality of Research Strategies: The Ichnofacies Model and the Ichnofabric Approach

Ichnologists tend to frame their work within two different research traditions: the ichnofacies model and the ichnofabric approach. The ichnofacies model was introduced in a series of papers by Seilacher (1954, 1955, 1958, 1963, 1967), having been refined and expanded in subsequent papers (e.g., Frey and Seilacher 1980; Bromley et al. 1984; Frey and Pemberton 1984, 1985, 1987; Buatois and Mángano 1995; de Gibert et al. 2007; Genise et al. 2000, 2010; Ekdale et al. 2007; Hunt and Lucas 2007; Krapovickas et al. 2016). Although there are several definitions of ichnofacies, there is general agreement that Seilacherian or archetypal ichnofacies are conceptual constructs based on the identification of key features shared by different ichnocoenoses of a wide range of ages formed under a similar set of environmental conditions (e.g., MacEachern et al. 2007; Buatois and Mángano 2011). It has been suggested that the elaboration of an ichnofacies involves two steps: (1) the distillation process or selection of key features within a representative sample (i.e., carefully selected ichnocoenoses covering a long stratigraphic range) and (2) the articulation of key features, linking concepts and organizing them in a coherent structure (Buatois and Mángano 2011). Table 1.3 summarizes the main characteristics of invertebrate ichnofacies in both marine and continental environments (see also Fig. 1.4). An updated evaluation of the ichnofacies model can be found in Buatois and Mángano (2011).

The ichnofabric approach was introduced by Ekdale and Bromley (1983). An ichnofabric refers to any aspect of the texture and internal structure of a substrate resulting from bioturbation and bioerosion at any scale (Bromley and Ekdale 1986; Ekdale et al. 2012). There are other concepts that acquired their full meaning within the framework of the ichnofabric approach. In particular, for the scope of this book, the concepts of tiering and ichnoguild are key. Tiering consists of the vertical partitioning of the habitat (Bottjer and Ausich 1982; Bromley and Ekdale 1986). The tiering concept in ichnology refers to the vertical partitioning of infaunal communities, which is essentially controlled by the consolidation of the substrate, the type and amount of organic matter, and the oxygen level (Bromley 1990, 1996). Analysis of infaunal tiering structure shows that organisms tend to group together within the same tier to exploit the same resources in similar ways, which resulted in the proposal of the ichnoguild concept (Bromley 1990, 1996). An ichnoguild reflects three parameters: (1) bauplan, (2) food source, and (3) use of space. With respect to bauplan, biogenic structures are categorized as permanent to semipermanent burrows produced by stationary organisms, or transitory structures made by vagile animals. Food source includes categories, such as detritus feeding, deposit feeding, suspension feeding, gardening, and chemosymbiosis. Use of space is essentially equivalent to the vertical position within the substrate recorded by the tiering structure.

**Table 1.3** Characteristics and implications of Seilacherian ichnofacies (based on Seilacher 1954, 1955, 1958, 1963, 1967; Frey and Seilacher 1980; Bromley et al. 1984; Frey and Pemberton 1984, 1985, 1987; Buatois and Mángano 1995, 2011; de Gibert et al. 2007; Genise et al. 2000, 2010; Ekdale et al. 2007; and Hunt and Lucas 2007; Krapovickas et al. 2016)

| Ichnofacies | | Characteristics | Representative ichnogenera | Implications |
|---|---|---|---|---|
| Softground marine | *Psilonichnus* | Dominance of vertical J-, Y-, or U-shaped dwelling burrows produced by ghost crabs; presence of small, unlined vertical dwelling burrows with bulbous basal cells produced by arachnids and insects; local presence of vertebrate trackways and invertebrate trails and trackways; root traces; coprolites; low ichnodiversity, and low abundance | *Cellicalichnus*, *Coenobichnus*, *Cylindricum*, *Psilonichnus*, and *Skolithos* | Extreme variations in energy, grain size, and salinity, as well as subaerial exposure, periodic influx of freshwater due to precipitation, and storm surges. Transitional conditions between marine and continental settings. Coastal environments, such as barrier islands, strand plains, delta plains, estuaries, lagoons, and bays. Within these settings it may be present in backshore areas, washover fans, coastal dunes and supratidal flats |
| | *Skolithos* | Dominance of vertical, cylindrical, simple or U-shaped dwelling burrows of suspension feeders and passive predators; presence of spreiten U-shaped equilibrium burrows and escape traces; abundance of three dimensional burrow systems dominated by vertical components; scarcity of horizontal traces produced by a mobile fauna; low ichnodiversity, and variable abundance | *Arenicolites*, *Bergaueria*, *Conichnus*, *Diplocraterion*, *Ophiomorpha*, and *Skolithos* | High abundance of organic particles that are kept in suspension in the well-oxygenated water column by waves and currents. Relatively high energy and intense erosion. Shifting and soft sandy substrates. Foreshore to upper- and middle-shoreface environments in wave-dominated shorelines. Tempestites emplaced in deeper-water positions, typically lower shoreface to lower offshore. Subtidal sandbodies to lower-intertidal sand flats. Various marginal-marine environments, such as delta fronts, sandy bars and spits, tidal inlets, flood and ebb tidal deltas, sandy bay margins, estuary-mouth complexes, and bay-head deltas. High-energy zones of deep-marine turbidite systems |

(continued)

**Table 1.3** (continued)

| Ichnofacies | | Characteristics | Representative ichnogenera | Implications |
|---|---|---|---|---|
| | *Cruziana* | Dominance of horizontal traces and subordinate presence of vertical and inclined structures; wide variety of ethologic categories, including locomotion, feeding, resting, dwelling, and grazing traces; dominance of deposit and detritus feeding traces, although suspension feeding and predation are involved also; dominance of traces produced by a mobile fauna and subordinate presence of permanent domiciles; high ichnodiversity, and high abundance | *Archaeonassa*, *Arthrophycus*, *Asteriacites*, *Asterosoma*, *Cruziana*, *Curvolithus*, *Cylindrichnus*, *Didymaulichnus*, *Dimorphichnus*, *Diplichnites*, *Gordia*, *Gyrochorte*, *Heimdallia*, *Helminthoidichnites*, *Helminthopsis*, *Lockeia*, *Monomorphichnus*, *Ophiomorpha*, *Palaeophycus*, *Phoebichnus*, *Phycodes*, *Phycosiphon*, *Protovirgularia*, *Rhizocorallium*, *Rosselia*, *Rusophycus*, *Schaubcylindrichnus*, *Teichichnus*, and *Thalassinoides* | Accumulation of organic detritus in the sediment under moderate- to low-energy conditions. Overall environmental stability and low to moderate sedimentation rates, although episodic sedimentation (i.e., storms) may punctuate fair-weather conditions. Lower shoreface to the lower offshore. Tidal flats. Marginal-marine, brackish-water environments, such as estuarine basins, bays, and lagoons (depauperate *Cruziana* Ichnofacies) |
| | *Zoophycos* | Dominance of relatively simple to complex feeding structures having spreite; subordinate occurrence of grazing traces; dominance of deep-tier structures of deposit feeders or farmers; low ichnodiversity, and high abundance | *Chondrites*, *Nereites*, *Phycosiphon*, and *Zoophycos* | Poor oxygenation in interstitial waters. Typically slow and continuous sedimentation due to suspension fallout in quiet-water settings. Possibly organic-rich substrates under conditions of abundant food supply. Settings below storm-wave base, particularly in shelfal to slope areas |

| | | | | |
|---|---|---|---|---|
| | *Nereites* | Dominance of complex graphoglyptids produced by animals that farm bacteria and trap microorganisms; presence of sophisticated grazing trails and feeding traces of detritus and deposit feeders; dominance of shallow-tier trace fossils; very high ichnodiversity, and high abundance, but low density of individual ichnotaxa | *Acanthorhaphe*, *Belorhaphe*, *Cardioichnus*, *Capodistria*, *Circulichnis*, *Cosmorhaphe*, *Desmograpton*, *Fustiglyphus*, *Glockerichnus*, *Halopoa*, *Helicolithus*, *Helminthorhaphe*, *Lorenzinia*, *Megagrapton*, *Nereites*, *Paleodictyon*, *Paleomeandron*, *Polykampton*, *Protopaleodictyon*, *Scolicia*, *Spirocosmorhaphe*, *Spirorhaphe*, and *Urohelminthoida* | Very stable environmental conditions in an overall low-energy, well-oxygenated setting with scarce food resources. Base-of-slope turbidity systems, being particularly common in the fringe of terminal splays, crevasse splays and levees |
| Substrate-controlled | *Glossifungites* | Presence of sharp-walled, unlined, passively filled, dwelling burrows of suspension feeders or passive predators; dominance of robust, vertical to subvertical, simple and spreiten U-shaped burrows; presence of branched burrow systems; presence of burrows with ornamented walls; low ichnodiversity, and high abundance | *Arenicolites*, *Diplocraterion*, *Gastrochaenolites*, *Rhizocorallium*, *Skolithos*, *Spongeliomorpha*, and *Thalassinoides* | Stable and cohesive substrates, referred to as firmgrounds. Commonly dewatered muds and, more rarely, highly compacted sands. Erosional exhumation of previously buried sediments in siliciclastic deposits, either relative sea level changes or autogenic erosional processes. Regressive surfaces of erosion formed during forced regressions, lowstand erosion surfaces due to relative sea level fall (incised canyons), ravinement surfaces formed during transgressions, and co-planar surfaces or amalgamated surfaces of lowstand and transgressive erosion (incised valleys). erosion due to migrating tidal channels and tidal creeks. Omission surfaces in carbonates |

(continued)

**Table 1.3** (continued)

| Ichnofacies | | Characteristics | Representative ichnogenera | Implications |
|---|---|---|---|---|
| | *Trypanites* | Dominance of deep-tier borings; dominance of sharp-walled, unlined, passively filled, vertical to subvertical, cylindrical, simple, tear-, vase-, or U-shaped dwelling borings of suspension feeders or passive predators; presence of branched and multi-chambered borings produced by suspension feeders; low to moderate ichnodiversity, and high abundance | *Caulostrepsis*, *Conchotrema*, *Entobia*, *Gastrochaenolites*, *Maeandropolydora*, *Trypanites*, and *Ubiglobites* | Cemented, fully lithified substrates. Long-term colonization windows. Sediment-starved hardgrounds, cliffs, beachrock, and reefs. Marine bone beds or coquinas. Different types of unconformities forming either omission or erosive surfaces |
| | *Gnathichnus* | Dominance of shallow to very shallow-tier grazing structures; presence of other ethological categories, such as domichnia, fixichnia and praedichnia; subordinate occurrence of deeper structures; dominance of radulation and gnawing traces produced by algal grazers; presence of etched attachment scars; occurrence of sock-shaped borings; low to moderate ichnodiversity, and high abundance | *Centrichnus*, *Gnathichnus*, *Maeandropolydora*, *Podichnus*, *Radulichnus*, and *Renichnus* | Cemented, fully lithified substrates. Short-term colonization windows. Spatially restricted, mobile shellgrounds formed under moderate energy conditions |
| | *Teredolites* | Dominance of clavate borings; boring walls ornamented with the texture of the host substrate; very low ichnodiversity, most commonly monospecific suites, and high density of borings, albeit with rare interpenetration | *Teredolites* and *Thalassinoides* | Resistant xylic (woody and coaly) substrates, including drifted log pavements and peat deposits that may be preserved as coal or lignite in the stratigraphic record. Omission surfaces formed in shallow-marine and marginal-marine environments, such as bays, estuaries, lagoons, and deltas |

| | | | | |
|---|---|---|---|---|
| Continental invertebrate | *Scoyenia* | Abundance of horizontal meniscate backfilled traces; abundance of locomotion traces, including both trackways and bilobate trails; presence of vertical domiciles; a mixture of invertebrate (mostly arthropod), vertebrate and plant traces; low to moderate ichnodiversity, and localized high abundance | *Acripes*, *Beaconites*, *Cochlichnus*, *Cruziana*, *Cylindricum*, *Diplichnites*, *Fuersichnus*, *Hexapodichnus*, *Merostomichnites*, *Palaeophycus*, *Permichnium*, *Planolites*, *Rusophycus*, *Scoyenia*, *Skolithos*, *Taenidium*, and *Umfolozia* | Sediments periodically exposed to air or periodically inundated, and intermediate between aquatic freshwater and terrestrial environments. Low-energy. Silty-sandy, soft to firm substrates. Fluvial overbank settings, such ponds, levees, and crevasse splays. Lake-margin areas in both open and closed lacustrine basins, and in both ephemeral and perennial lakes. Wet interdunes |
| | *Mermia* | Dominance of horizontal to subhorizontal grazing and feeding traces produced by mobile deposit feeders; subordinate occurrence of locomotion traces; relatively high to moderate ichnodiversity; high abundance, and low degree of specialization of grazing and feeding patterns | *Circulichnis*, *Cochlichnus*, *Diplopodichnus*, *Gordia*, *Helminthoidichnites*, *Helminthopsis*, *Mermia*, *Treptichnus*, and *Undichna* | Permanent subaqueous freshwater environments. Low-energy. Silty-sandy, soft substrates. Well-oxygenated settings. Abundant food supply. Open perennial lacustrine basins, typically hydrologically open. Floodplain water bodies under subaqueous conditions. Fjord settings under freshwater conditions due to glacial melting |
| | *Coprinisphaera* | Dominance of trace fossils of bees, wasps, ants, and beetles; subordinate presence of termite ichnofossils; dominance of nesting traces or calichnia; tiering structures that result from variable depths of emplacement of hymenopterous, termite, and dung-beetle nests; moderate to relatively high ichnodiversity, and high abundance | *Attaichnus*, *Celliforma*, *Chubutolithes*, *Coprinisphaera*, *Eatonichnus*, *Ellipsoideichnus*, *Fontanai*, *Monesichnus*, *Pallichnus*, *Palmiraichnus*, *Parowanichnus*, *Rosellichnus*, *Teisseirei*, and *Uruguay* | Paleosols associated with herbaceous plant communities, mostly savannas, grasslands, prairies, and steppes. Climatically ranging from dry and cold to humid and warm conditions. Various depositional systems subject to subaerial exposure and soil development, such as alluvial plains, overbank, and eolian environments |

(continued)

**Table 1.3** (continued)

| Ichnofacies | | Characteristics | Representative ichnogenera | Implications |
|---|---|---|---|---|
| | *Termitichnus* | Dominance of trace fossils of termites; low ichnodiversity, and high abundance | *Fleaglellius*, *Krausichnus*, *Masrichnus*, *Termitichnus*, and *Vondrichnus* | Paleosols formed in closed forests with plant growth under warm and humid conditions. Abandoned channels and overbank areas |
| | *Celliforma* | Dominance of halictid bee nests; association with hackberry endocarps, and freshwater and terrestrial snail shells; dominance of callichnia; presence of pupichnia; moderate ichnodiversity, and high abundance | *Celliforma*, *Pallichnus*, *Palmiraichnus*, *Rebuffoichnus*, *Rosselichnus*, *Taenidium*, and *Teisseirei* | Carbonate-rich paleosols associated with scrubs and woodlands. Palustrine environments and calcretes |
| | *Camborygma* | Dominance of burrows produced by crayfish and earthworms; common cross-cuttings relationships; low ichnodiversity; and high abundance | *Camborygma*, *Cellicalichnus meniscatus*, *Dagnichnus*, *Edaphichnium*, and *Loloichnus* | Paleosols formed in forests, scrubs, and open herbaceous communities, particularly in marshes, bogs, swamps, or wetlands. High and fluctuating water table, mostly under warm climates. Various depositional systems subject to subaerial exposure and soil development, such as abandoned channels, floodplains, levees, crevasse splays, and loessic, ponds |
| | *Octopodichnus–Entradichnus* | Low- to more rarely moderate ichnodiversity; dominance of simple sub-superficial dwelling traces produced mostly by members of Coleoptera, Orthoptera, and Arachnida, with horizontal and/or vertical orientation; superficial locomotion traces produced by arthropods, especially arachnids; and subordinate feeding simple and meniscate traces | *Arenicolites*, *Digitichnus*, *Entradichnus*, *Octopodichnus*, *Palaeophycus*, *Paleohelcura*, *Planolites*, *Skolithos*, and *Taenidium* | Mobile and temporary stabilized sandy substrates, subject to frequent erosion and deposition, and to strong seasonality. Environments with reduced humidity and low nutrient availability. Sand dune, dry interdune, and sand sheet deposits of wet eolian systems typically associated with arid deserts and/or in arid intervals of hyper-arid deserts |

For a refinement of the *Octopodichnus–Entradichnus* Ichnofacies, see Krapovickas et al. (2016) and for definition of the *Camborygma* Ichnofacies, see Chap. 13

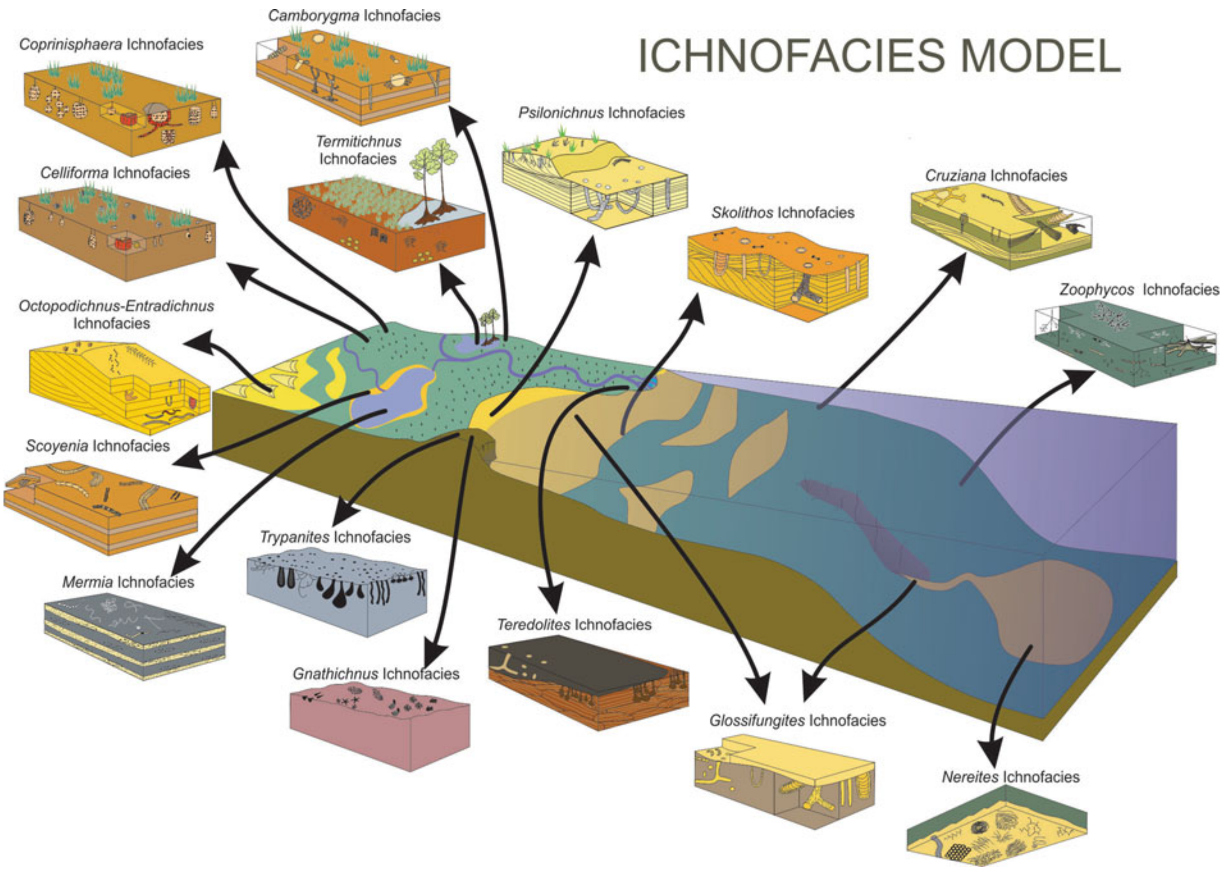

**Fig 1.4** The ichnofacies model (modified from Buatois and Mángano 2011)

Another concept that is used extensively in this book is degree of bioturbation. Degree of bioturbation can be assessed following Taylor and Goldring (1993), based on a previous scale proposed by Reineck (1963). A sedimentary unit characterized by no bioturbation (0 %) corresponds to a bioturbation index (BI) of 0. Sediments that display sparse bioturbation with few discrete traces equal BI 1 (1–4 %). Low bioturbation in deposits that still have preserved sedimentary structures equals BI 2 (5–30 %). BI 3 (31–60 %) refers to sediment with discrete trace fossils, moderate bioturbation, and still distinguishable bedding boundaries. A BI of 4 (61–90 %) is characterized by intense bioturbation, high trace-fossil density, and common overlap of trace fossils, with primary sedimentary structures mostly erased. Deposits with completely disturbed bedding and showing intense bioturbation equals a BI of 5 (91–99 %), and completely bioturbated and reworked sediment, owing to repeated overprinting of trace fossils would be BI 6 (100 %).

Although some authors have put forward the idea that one approach should replace the other one (e.g., Goldring 1993, 1995), we have advocated for a pluralistic methodological approach in ichnology (Buatois and Mángano 2011). In fact, we have the impression that the whole debate viewing the ichnofacies model and the ichnofabrics approach as competing strategies is somewhat dated and not supported by recent developments in the field. Both research strategies may be employed in conjunction, resulting in a more holistic view of the trace-fossil record. The strength of the ichnofacies model relies on its archetypal nature, whereas the strength of the ichnofabric approach resides in the evaluation of the taphonomic controls that filter the biogenic signal through the fossilization barrier (Buatois and Mángano 2011).

## 1.5 Assessing Changes in Types of Animal–Substrate Interactions Through Time

### *1.5.1 Ichnodiversity and Ichnodisparity*

The concepts of ichnodiversity and ichnodisparity are used in various chapters of this book to evaluate changes in the types of animal–substrate interactions through time. The concept of ichnodiversity has a long history in ichnology, having been used to address general trends in ichnotaxonomic richness along a depositional profile, within specific sedimentary environments and through geologic time (e.g., Seilacher 1974; Ekdale 1985; Crimes 1994; Bromley 1996; Buatois et al. 1998, 2005; Orr 2001; Uchman 2004). Surprisingly, there has been relatively little discussion about its meaning and significance (Buatois and Mángano 2011, 2013; Wisshak et al. 2011; Knaust et al. 2014; Buatois et al. 2016a). Recently, the three components of global diversity (alpha, beta, and gamma) commonly used in the body-fossil literature have been also discriminated to summarize ichnologic data (Buatois and Mángano 2011, 2013). These authors indicated that an analogue to alpha diversity (i.e., alpha ichnodiversity) is the one commonly used to assess trace-fossil diversity for individual facies or environmental zones. An analogue to beta diversity (i.e., beta ichnodiversity) may provide information about the degree of similarity between ichnofaunas formed along an environmental gradient, but has been overlooked in trace-fossil studies. Finally, application of the notion of gamma diversity to ichnologic studies (i.e., gamma ichnodiversity) may yield insights into potential paleobiogeographic patterns that may emerge from the trace-fossil record (e.g., Seilacher 1992, 1994; Orr 1996; Systra and Jensen 2006; Jensen et al. 2013). In contrast to ichnodiversity, the concept of ichnodisparity has been proposed recently (Buatois and Mángano 2011, 2013; Buatois et al. 2016a) and, therefore, its potential has not been used extensively yet, although some studies are showing its significance to understand evolutionary radiations (Mángano and Buatois 2014; Buatois et al. 2016b). Whereas ichnodiversity refers to ichnotaxonomic richness, ichnodisparity provides a measure of the variability of trace-fossil morphologic plans. The categories of architectural designs used to assess ichnodisparity are listed in Chap. 16. Within each of these architectural designs there may be variation upon a theme represented by different ichnogenera. Analysis of the relationship between ichnodiversity and ichnodisparity provides potential insights into the mechanisms of ecospace colonization. For example, during the colonization of a new habitat, do ichnodiversity and ichnodisparity track one another? Or are they decoupled with new architectural designs and behavioral paradigms appearing relatively quickly, followed by a proliferation of ichnotaxa through variations upon established themes?

### *1.5.2 Analysis of Modes of Life and Characterization of Ecospace Occupation*

Analysis of modes of life and characterization of ecospace occupation is common practice with body fossils. Bambach et al. (2007) and Bush et al. (2007) refined a framework for identifying modes of life based upon categorization within three parameters: tiering, motility and mode of feeding. Categories across these parameters define total possible ecospace, and the modes of life of individual taxa may be identified within this to determine occupied ecospace at any one point in time. Trace fossils provide an excellent model system to analyze benthic ecospace occupation using such principles, and this may also be partnered to include ecosystem engineering through time (see Sect. 1.5.3). Trace fossils provide precise information on the tiering position of animals within the sediment, and the motility and mode of feeding of the trace fossil producer is either directly evidenced by, or may be inferred from, the form of the trace fossil.

Occupied ecospace is analyzed herein on the basis of three parameters: tiering, motility, and feeding mode (Fig. 1.5a). This differs from ichnoguilds, which consider the bauplan of the biogenic structure instead of just the motility of the organism. Tiering refers to the life position of an animal. For a trace fossil to form, an animal must interact with a substrate. Therefore, unlike the categories of Bambach et al. (2007) and Bush et al. (2007) that include positions both above and below the sediment surface, the realm of trace fossil analysis is largely restricted to being at or

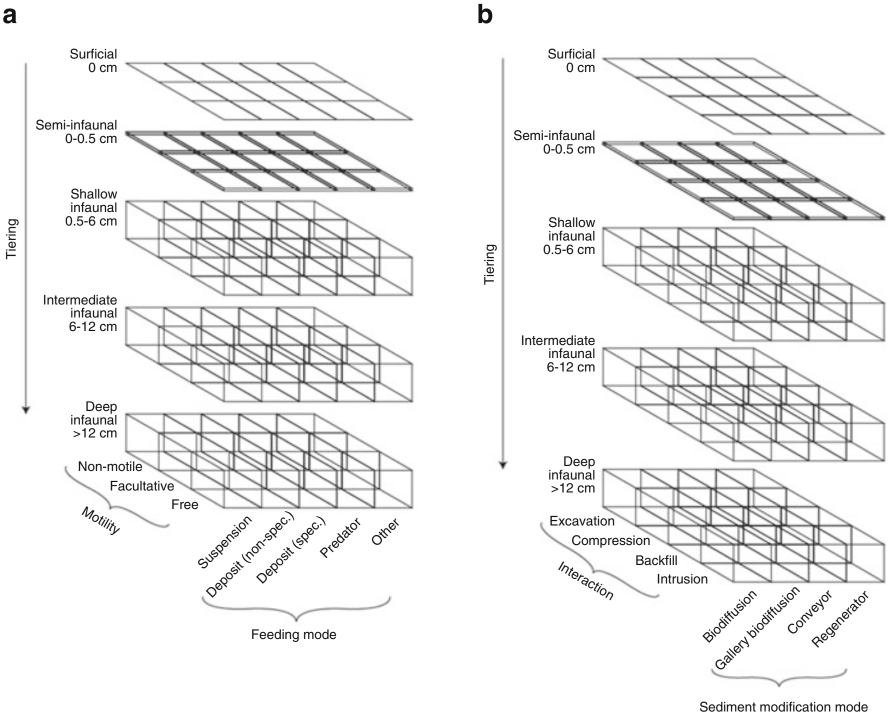

**Fig 1.5** Framework for analysis of ecospace occupation and ecosystem engineering. (**a**) Ecospace occupation; (**b**) ecosystem engineering

below the sediment surface. There are exceptions in that terrestrial animals such as termites may construct a structure above ground and animals may interact with substrates that are above the ground, such as plants, or with mobile substrates such as logs. For the purposes of this discussion on subaqueous to subaerial habitats, tiering categories are limited to being at or below the sediment surface.

Bambach et al. (2007) and Bush et al. (2007) categorized a surficial tier for animals living on the sediment surface and not extending significantly upward, and a semi-infaunal tier for animals that are partly infaunal and exposed to the overlying water column. These categories can be readily adopted here, and they can be expanded to subaerial environments where animals living in the semi-infaunal tier are exposed to the overlying air. Bambach et al. (2007) and Bush et al. (2007) also identified shallow and deep tier infaunal categories for animals living within the top 5 cm of the sediment or at depths greater than 5 cm, respectively. Trace fossils provide direct information on the life positions of animals and it is possible to be more precise on infaunal tiering levels. The system of Ausich and Bottjer (1982), Bottjer and Ausich (1986), and Mángano and Buatois (2014) is adopted here, with a shallow infaunal tier for depths of 6 cm, an intermediate infaunal tier for depths of

6–12 cm, and a deep infaunal tier for depths of greater than 12 cm. This allows for the differentiation of intermediate tier and truly deep tier infaunal animals.

By their very nature, trace-producing animals generally have some degree of motility, the exception being nonmobile animals that leave attachment structures. Bambach et al. (2007) and Bush et al. (2007) defined three major levels of motility: mobile, facultatively mobile, and nonmobile, each with two sublevels. In this analysis, we prefer to restrict categorization of motility to these three higher levels. Specifying whether an animal is slow or fast when it is freely mobile is somewhat arbitrary. Also, animals that are fast and freely mobile will tend to live at or above the sediment–water interface whereas ones that maintain intimate contact and burrow within the substrate will tend to be slower moving. Such a distinction in motility therefore introduces a spatial bias in terms of tiering whereas our framework of ecospace occupation is intended to be inclusive, with all modes of life being theoretically possible. Dwelling burrows of suspension feeders or predators or escape trace fossils can be assigned to facultatively mobile animals that are generally stationary but are capable of movement.

Mode of feeding is constrained to five categories. Suspension feeders are those that obtain and capture food particles from the water column. Deposit feeders are those that actively ingest particles of food from a substrate. Again, to avoid spatial segregation, this category is used in a broad sense to include those that obtain their food from the surface, buried within the substrate, or by grazing (the categories of surface deposit feeding, mining, and grazing of Bambach et al. 2007 and Bush et al. 2007). However, deposit feeders are categorized on the basis of trace fossil morphology into non-specialized deposit feeders with non-patterned and overcrossing trails, and specialized systematic deposit feeders with patch exploration and non-overcrossing motifs. Predators are those tracemakers inferred to have been able to capture prey. The final category of “other” includes farming activities as exemplified by complex, regular, patterned, meandering, spiral, radiating, and network trace fossils known as graphoglyptids.

### *1.5.3 Analysis of Ecosystem Engineering*

The technique used to categorize ecospace occupation may be modified to provide a complementary parallel analysis of ecosystem engineering. Together with tiering, trace fossils may be designated by the ways in which the animal interacted with and modified the sediment (Fig. 1.5b). Animals may interact with a substrate by four principal means: intrusion, compression, backfilling, and excavation (Bromley 1996; Buatois and Mángano 2011). Intrusion involves displacement of sediment as the animal moves through but the sediment closes up behind it; compression involves the movement and compaction of sediment around the animal as it passes through; backfilling involves the active backward passage of sediment either around or through the animal; and excavation comprises the active loosening and transport of sediment from one location to another (Bromley 1996; Buatois and Mángano 2011).

Our categorization of the ways in which animals modify and rework sediments are borrowed and adapted from concepts developed by the marine benthic ecology community (François et al. 1997; Solan and Wigham 2005). As well as being well suited for this purpose, this approach fosters a commonality of language between ichnologists and benthic ecologists. In our analysis, we limit considerations of modes of sediment reworking to biodiffusion, gallery biodiffusion, conveyors, and regenerators (François et al. 1997; Solan and Wigham 2005). Biodiffusion is the movement of sediment particles over short distances, whereas gallery biodiffusion involves the rapid redistribution of sediment particles from one part of the sediment profile to another (François et al. 1997, 2002; Solan and Wigham 2005). Upward and downward conveyors (François et al. 1997; Solan and Wigham 2005) are subsumed within the simpler concept of conveyors, with animals also being able to convey sediment laterally. This category refers to animals that actively transport sediment particles across and within tiers. Regenerators are animals that actively move sediment to the surface from below, where it may be transported away by currents (François et al. 1997; Solan and Wigham 2005). We omit the categories of epifaunal bioturbators and surficial modifiers (Solan and Wigham 2005) because of their spatial constraints, being covered potentially by any of the other four means of sediment reworking in the epifaunal and semi-infaunal tier. Sediment reworking categories relate to movement of particles within fluids, and so are applicable to scenarios where that medium is either water or air.

## 1.6 Conclusions

The study of trace fossils and their applications have long been within the domain of paleoenvironmental analysis. The value of trace fossils in terms of elucidating major evolutionary events, and as a complementary record to that of body fossils that can provide independent tests, is increasingly being recognized. Together with a firm basis on the fundamentals of ichnology, development of new conceptual frameworks and adoption and refinement of methods of analysis from macroevolutionary paleobiology and ecology are opening up the opportunity for many fruitful avenues of research; not just in terms of analyzing patterns and processes at work across long-term "experiments" in the geological record but also being able to provide insights into future impacts of environmental and biotic change on ecosystems and society.

**Acknowledgments** Financial support for this study was provided by Natural Sciences and Engineering Research Council (NSERC) Discovery Grants 311727-08/15 and 311726-13 awarded to Mángano and Buatois; and a Government of Canada Postdoctoral Research Fellowship awarded to Minter under the Canadian Commonwealth Scholarship Programme. Zain Belaústegui reviewed this chapter providing valuable comments. It also benefitted from feedback on some of the methodologies presented from Russell Garwood, Ken McNamara, Bill DiMichele, and Godfrey Nowlan.

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# Chapter 2
# Ediacaran Ecosystems and the Dawn of Animals

**Luis A. Buatois and M. Gabriela Mángano**

## 2.1 Introduction

Tracking Precambrian evidence of life has been a conflicting issue at least since Darwin's times. In fact, as it is widely known, the supposed absence of signs of life before the Cambrian was explicitly noted as a serious problem by Darwin himself: "There is another … difficulty, which is much more serious. I allude to the manner in which species belonging to several of the main divisions of the animal kingdom suddenly appear in the lowest known [Cambrian-age] fossiliferous rocks … If the theory be true, it is indisputable that before the lowest Cambrian stratum was deposited, long periods elapsed … and that during these vast periods, the world swarmed with living creatures… [But] to the question why we do not find rich fossiliferous deposits belonging to these assumed earliest periods before the Cambrian system, I can give no satisfactory answer. The case at present must remain inexplicable; and may be truly urged as a valid argument against the views here entertained" (Darwin 1859).

Our view on this topic has considerably broadened, particularly since the discovery of Neoproterozoic body fossils. In fact, the first report of Ediacaran fossils was produced shortly after Darwin's publication of "On the Origin of Species" due to the publication by Billings (1872) of *Aspidella terranovica*, discoid impressions present in eastern Newfoundland (Fig. 2.1) (Gehling et al. 2000). However, it was the discovery of the so-called Ediacara biota in disparate places, such as Namibia (Gürich 1933), Australia (Sprigg 1947, 1949), England (Ford 1958), and Canada (Anderson and Misra 1968; Misra 1969), that fueled research and interest on Precambrian life.

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M.G. Mángano, L.A. Buatois (eds.), *The Trace-Fossil Record of Major Evolutionary Events*, Topics in Geobiology 39,
DOI 10.1007/978-94-017-9600-2_2

**Fig. 2.1** The first Ediacaran fossil named, *Aspidella terranovica*, Fermeuse Formation, Ferryland, Avalon Peninsula, Newfoundland, Canada. Field photo. Scale bar is 1 cm

Ichnologic evidence has been commonly invoked to track back in time the origin of bilaterians, and the potential of trace fossils to shed light on this evolutionary event has been noted at least since the seminal paper by Seilacher (1956). Some of the first attempts of analyzing the Neoproterozoic trace-fossil record focused on documentation of the stratigraphic distribution of ichnotaxa, with an emphasis on biostratigraphic zonations (Alpert 1977; Crimes 1987, 1992, 1994). Subsequently, the relevance of trace fossils to decipher macroevolutionary events and, in particular, the origin of bilaterians started to move to the center of the stage (e.g., Budd and Jensen 2000, 2004; Jensen et al. 2006). In fact, given the controversial nature of most of the Ediacaran body fossils, ichnologic evidence has been commonly considered to represent the clearest evidence of bilaterians in the Ediacaran (Seilacher 1989; Budd and Jensen 2000).

The aim of this chapter is to provide a review of the Ediacaran trace-fossil record to show how ichnologic evidence can illuminate our view on the dawn of animal life and the nature of Ediacaran ecosystems. This review is based on a systematic reevaluation of the Ediacaran trace-fossil record trough field work, study of collection material, and a critical examination of the available literature.

## 2.2 The Early Ichnologic Evidence of Animal Life: Hunting Ghostly Ancestors

Reconstructing the anatomy of the early animals and tracking the deepest divergence of the Metazoa is a challenging task. A growing number of molecular-clock studies show a clear trend towards increased consistency with the body-fossil record (e.g., Peterson et al. 2004, 2008), but divergence times are still placed deeper back in time than strictly indicated by the fossil record. In fact, more recent estimates placed the origin of the Metazoa by the Cryogenian (Erwin et al. 2011; Erwin and Valentine 2013; Erwin 2015; dos Reis et al. 2015; Pisani and Liu 2015). The present gap between molecular clock estimates and the fossil record suggests a missing 150–200 Myr of metazoan evolutionary history (Erwin 2015). Tracking these missing links or ghostly ancestors is a difficult enterprise (Erwin and Valentine 2013; dos Reis et al. 2015). Once and again, claims of incompleteness of the fossil record are revitalized in the literature. According to this view, these evolutionary ghosts did not leave a record as body fossils, and in many cases molecular clocks and developmental toolkits are placed at the center of the stage (Erwin 2015). Another well-established line of evidence, however, has been regarded as substantial: scrutinizing the Proterozoic record in the search for trace fossils. Also, trace-fossil evidence is of utmost relevance even in younger Ediacaran rocks given the absence of consensus on the affinities of many Ediacaran body fossils (Glaessner 1984; Seilacher 1989; Narbonne 2005; Budd 2015). In short, in our view this is one of the fields in which ichnology may provide its most outstanding contributions to our understanding of the history of life.

It is unsurprising that the question about the earliest ichnologic evidence of animal life is one of the most controversial in the science of organism–sediment interactions. History of research is plagued with frequent misinterpretations, resulting from both the continuous scrutiny of structures of controversial origin and the specific complexities of Precambrian paleobiology. As summarized by Bergström (1990) and Crimes (1994) already long time ago, structures originally interpreted as some of the earliest trace fossils invariably ended up either being not trace fossils, being present in rocks younger than originally thought, or being biogenic but younger than the host rock.

The list is long, with continuous additions until the time of this book going to press. An early example of these problems is illustrated by structures from Paleoproterozoic rocks (2.0 Ga) in Canada that were interpreted as trace fossils and regarded as new ichnotaxa, *Rhysonetron lahtii* and *R. byei* (Hofmann 1967). A few years later, they were reinterpreted by the same author as inorganic (Hofmann 1971). Structures in Mesoproterozoic (1.0 Ga) rocks of Zambia were originally interpreted as fossilized burrow systems (Clemmey 1976), but subsequently were reinterpreted as traces of modern termites (Cloud et al. 1980).

A more recent candidate for the earliest evidence of animal activity is represented by the Chorhat trace fossils documented by Seilacher et al. (1998) from India in rocks that were at the time considered as Mesoproterozoic in age (1.1 Ga). Subsequently, the rocks were dated as 1.6 Ga old (Rasmussen et al. 2002a; Ray et al. 2002). The structures were regarded as sinusoidal and branched burrows produced by vermiform triploblastic animals below a microbial mat. Later the structures were reinterpreted as inorganic in origin (Hofmann 2005; Seilacher 2007). Based on experimental studies, Seilacher (2007) has argued that the structures may have been formed by large shrinking bubbles forming strings.

Another candidate is the 2.0–1.8 Ga old Stirling biota of western Australia (Rasmussen et al. 2002b; Bengtson et al. 2007). In a first study (Rasmussen et al. 2002b), Ediacaran-like discoidal impressions and trace-like fossils were documented. The structures were subsequently reinterpreted as pseudofossils by other authors (Conway Morris 2002; Jensen 2003; Budd and Jensen 2004). However, Bengtson et al.

(2007) provided a detailed description of the structures interpreted as trace fossils, which were placed in a new ichnotaxon, *Myxomitodes stirlingensis*. This form consists of pairs of ridges preserved in positive hyporelief and the ridges were regarded as casts of sediment-laden mucus strings. These structures were assigned to multicellular organisms, but an animal origin was explicitly ruled out (Bengtson et al. 2007). While agreeing with Bengtson et al. (2007, p. 352) that failure to accept pre-Ediacaran fossils is strongly influenced by age and rarity, the fundamental ground for skepticism relies on fine morphology and taphonomy. The morphology of these structures poses multiple challenges to their constructional analysis. Although modern twisted and modified mucus strands are offered as analogs for irregularities and lack of continuity along the Stirling structures, these morphologic features are virtually unknown in fossil material and essentially impossible to be preserved on a surface. For example, bifurcations (their Fig. 12) seem closer to gallery branching than typically simple trail overcrossing (their Fig. 12) and irregular expansions (their Fig. 12, lower right) are difficult to interpret (although they could result from physical, post-construction modification). In some specimens, the double ridges of *Mixomytoides* that are interpreted as connected (representing pushed aside mucus) overcross each other (see their Fig. 14). A second significant caveat is the taphonomic pathway. The trace-like structures are preserved at the base of an erosive channel filled with upper-flow regime parallel laminated, medium- to coarse-grained sandstone. Mucus strands are envisioned to have been produced in the underlying mudstone drapes and later casted by the channel-fill sandstone. However, the sedimentologic context and hydrodynamic conditions that govern the deposition of the sandy casting medium suggest this is an implausible scenario. Although burrows have been occasionally described from the base of gutter casts and small intertidal channels (e.g., Mángano et al. 2002), preservation of epigenic (i.e., superficial) mucus trails is virtually unknown. Epigenic trackways and trails have been documented in Burgess Shale-type deposits where environmental constrains, such as low oxygen and energy, in association with microbial mat stabilization and/or early diagenetic cementation provided an exceptional preservational window for shallow-tier and even surficial structures (Mángano 2011). However, microbial structures that could have embedded and promoted preservation of superficial trails are unknown from the Sterling deposits (Bengtson et al. 2007, p. 365).

Based on the available evidence, we agree with Crimes (1994) in considering unlikely the possibility of animal trace fossils in pre-Ediacaran rocks. However, it is clear that a careful search should continue given the importance of the topic. In the last decade the target of ichnologic research has moved to Ediacaran strata that postdate the Gaskiers glaciation (ca 580 Ma). However, even this switch in focus is not without problems. Recently, bilaterian trails have been reported from supposed Ediacaran shallow-water strata (585 Ma) overlying glacial diamictites in Uruguay (Pecoits et al. 2012). The trace-fossil nature of these structures is undisputable, but the age of the trace fossil-bearing strata is highly contended, being a late Paleozoic age favored (Gaucher et al. 2013; Verde and Netto 2015). Pecoits et al. (2012) interpreted the structures as produced by worms. Interestingly, some of the photographs (see their Fig. 2) may hint to appendage imprints, as suggested by the possible presence of undertracks, which would indicate arthropod producers. Recent work in these outcrops has indeed confirmed the presence of arthropod trackways (Verde and Netto 2015). Furthermore, the same ichnospecies present in the supposed Ediacaran outcrops are widespread in later Paleozoic freshwater deposits in Gondwana, including the nearby Parana Basin and the Karoo Basin (see Buatois et al. 2010 for a review). Similarities between Ediacaran-lowermost Cambrian marine ichnofaunas and late Paleozoic freshwater ichnofaunas have been explained as a result of similar strategies in the initial exploitation of underutilized or empty ecospace, suggesting that the debate surrounding the Uruguay trace fossils may be viewed in the light of the so-called "the Déjà vu effect" (Buatois and Mángano 2011a; see Chap. 16).

Possible trails have been reported from 565 My-old deep-water deposits in the Mistaken Point Formation of Newfoundland, Canada (Liu et al. 2010, 2014). In particular, Liu et al. (2014) distinguished four morphotypes: specimens with transverse ridges, specimens lacking transverse ridges, complex clustering?, and isolated pits. Specimens with transverse ridges consist of horizontal structures having regular crescentic internal divisions and flanked by lateral ridges (Fig. 2.2a–c). Several specimens end in a negative circular impression (Fig. 2.2a). Liu et al. (2014) indicated that these structures could be assigned to *Archaeonassa*. Although this ichnogenus is known in younger Ediacaran rocks, specimens with possible transverse ridges have never been documented in any of the Ediacaran representatives of *Archaeonassa*. Specimens lacking transverse ridges comprise horizontal structures that may or may not be flanked by lateral ridges (Fig. 2.2b). Liu et al. (2014) indicated that these structures could be assigned to *Helminthoidichnites*. The complex clustering? refers to nine individual structures without transverse ridges and loosely concentrated around four central depressions. Given the fact that only one cluster has been found, the most parsimonious interpretation is one of a coincidental assemblage of discrete simple horizontal structures. Isolated pits consist of ovate to circular depressions, similar to those connected with some of the horizontal structures. The Mistaken Point structures were not ascribed to bilaterians, considering a possible affinity with cnidarians instead (Liu et al. 2010). However, the abrupt changes in width, the parallel orientation of some of the specimens, and the sharp marginal ridges, which do not resemble levees generated by a transient superficial organism, provide cautionary notes on the interpretation of these structures as trace fossils. The connection of some of these structures to pits raises the possibility that the dragging or uprooting of fronds through a microbially stabilized surface may have been involved, in an analog fashion to structures documented by Tarhan et al. (2010) from the Flinders Ranges. The fact that the Mistaken Point Formation represents deep-marine deposits should not be invoked to argue against such a possibility (cf. discussions by Retallack 2010 and Liu et al. 2014). In addition, the presence of these structures in a single, laterally restricted bedding plane prevents a definite interpretation at this point. Further examination of the Mistaken Point Formation in the search for uncontroversial evidence of animal mobility represents a highly relevant enterprise.

Crescentic structures have been found in association with *Aspidella*-disks on bedding tops and possible equilibrium structures are seen in cross section in the younger (approximately 560 Ma) and shallower-water Fermeuse Formation of Newfoundland (Menon

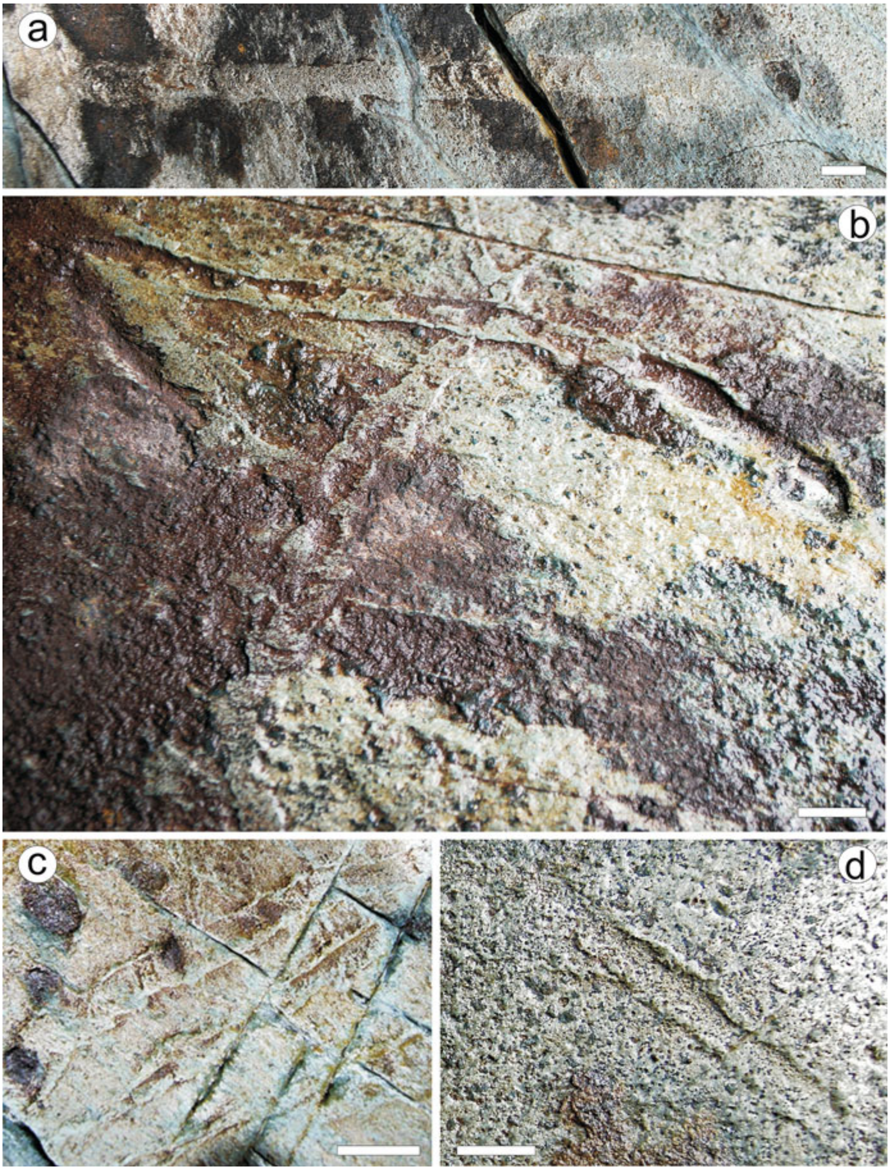

**Fig. 2.2** Possible trails from 565 My-old deep-water deposits, Mistaken Point Formation, Avalon Peninsula, Newfoundland, Canada. (**a**) Close-up of horizontal structures displaying regular crescentic internal divisions and lateral ridges; (**b**) General view of specimens cross-cutting each other; (**c**) General view of parallel-oriented specimens; (**d**) Close-up of specimen with well-developed lateral ridges. All are field photos. All scale bars are 1 cm. For detailed descriptions and interpretations, see Liu et al. (2010, 2014)

et al. 2013). The disks have been analyzed in detail by Gehling et al. (2000), who established a number of morphologic and taphonomic variants. The associated crescentic structures have been interpreted as evidence of horizontal displacement, where the structures seen in cross section are thought to record vertical movement in response to sediment aggradation, suggesting some degree of mobility in an organism probably of Cnidarian grade (Menon et al. 2013). We note here that, if the interpretation suggested is correct, then the Fermeuse structures may actually belong in *Bergaueria sucta*, an ichnospecies recorded in Ediacaran strata (Seilacher 1990; Seilacher et al. 2005; see Sect. 2.5). Although Menon et al. (2013) regarded the Fermeuse Formation horizontal structures as similar to those from the Mistaken Point Formation, both structures seem to be quite different in terms of overall morphology and size.

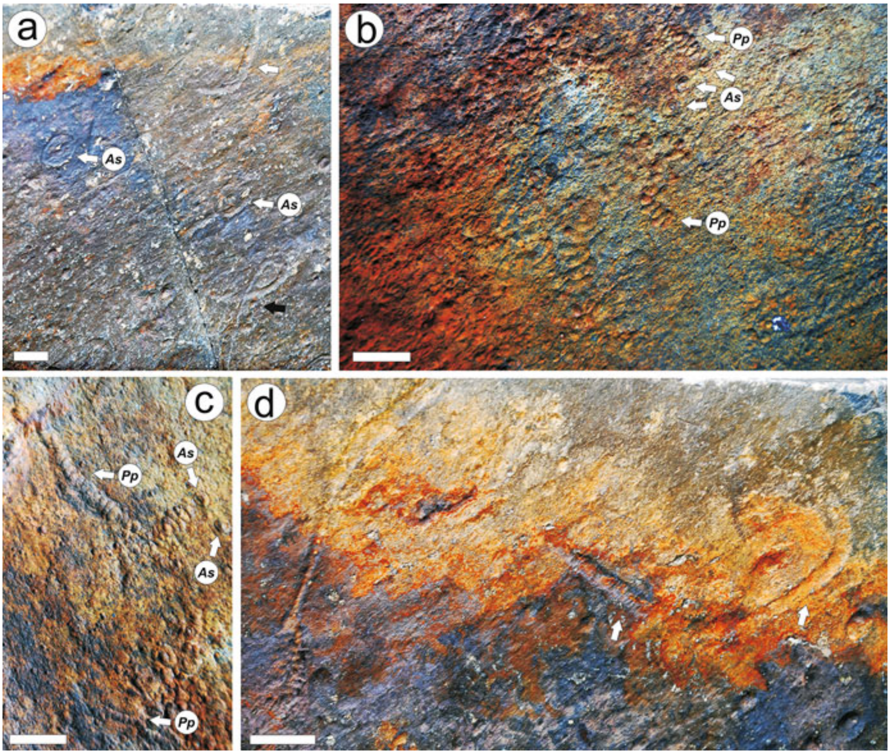

**Fig. 2.3** Problematic structures, Fermeuse Formation, Ferryland, Avalon Peninsula, Newfoundland, Canada. (**a**) Structure showing overcrossing resembling the ichnogenus *Gordia* (*black arrow*) and another problematic horizontal structure (*white arrow*). Note sharp variations in width in both specimens. Several *Aspidella* disks (*As*) are present on the surface; (**b**) General view of a surface containing several specimens of *Aspidella* (*As*) and *Palaeopascichnus* (*Pp*); (**c**) Close-up of *Aspidella* (*As*) and *Palaeopascichnus* (*Pp*). Note that the latter may be confused with a constricted burrow; (**d**) Poorly preserved specimens of *Palaeopascichnus*. Note that one of them seems to grade into a structure mimicking a trace fossil (*arrows*). All are field photos. All scale bars are 1 cm. For detailed descriptions and interpretations, see Liu and McIlroy (2015)

Other structures have been reported recently in the Fermeuse Formation (Liu and McIlroy 2015). These authors documented horizontal grooves preserved on top of beds, some of them showing transverse segments and very rarely self-overcrossing. The Fermeuse structures deserve further exploration and detailed analysis. However, the close association and apparent intergradations with the body fossil *Palaeopascichnus* preserved on the same bedding planes provide a cautionary note (Fig. 2.3a–d). The possibility that the Fermeuse structures represent a continuum of taphonomic variants of *Palaeopascichnus* is the most likely interpretation.

## 2.3 Shrinking the Number of Ediacaran Ichnotaxa

Approximately 15 years ago, the prevailing view was that Ediacaran ichnofaunas were relatively diverse, with studies listing a large number of ichnotaxa (e.g., Runnegar 1992a; Crimes 1992, 1994). For example, systematic compilations listed 35 ichnogenera, including complex trace fossils (e.g., *Chondrites*), and scratch marks produced by arthropods (*Monomorphichnus*), among many other examples (Crimes 1987, 1992, 1994). Implicit in this view was the fact that the trace-fossil record allowed to visualize a more gradual diversity increase across the Ediacaran–Cambrian transition, significantly diminishing the abrupt nature of the Cambrian explosion (Fig. 2.4). However, since the beginning of this century a number of studies started to build up a consensus of much more reduced global ichnodiversity levels during the Ediacaran (Haines 2000; Jensen 2003; Seilacher et al. 2003, 2005; Jensen et al. 2005, 2006; Droser et al. 2005; Mángano and Buatois 2007; Shen et al. 2007). In particular, Seilacher et al. (2005), Jensen et al. (2006), and Mángano and Buatois (2014) provided comprehensive reviews, leading to a dramatic reinterpretation of the trace-fossil nature of a large number of supposed Ediacaran ichnogenera.

In one of the first syntheses on the topic, Alpert (1977) established a group of trace fossils (Group 1) that were thought to be restricted to the Proterozoic. This group was interpreted as reflecting a failed evolutionary experiment (Crimes 1994). The list of supposed ichnogenera restricted to the Proterozoic includes *Annulicichnus*, *Archaeichnium*, *Beltanelliformis*, *Bucerusichnus*, *Bunyerichnus*, *Codonichnus*, *Dengyingella*, *Eilscaptichnus*, *Funisichnus*, *Gaojiashania*, *Harlaniella*, *Helanoichnus*, *Intrites*, *Linbotulichnus*, *Mawsonites*, *Medvezhichnus*, *Microspirolithus*, *Nenoxites*, *Nimbia*, *Ningxiaichnus*, *Palaeopascichnus*, *Planispiralichnus*, *Protospiralichnus*, *Shaanxilithes*, *Shipaitubulus*, *Suzmites*, *Taenioichnus*, *Vendichnus*, *Vermiforma*, *Vimenites*, and *Yelovichnus*. The vast majority of these supposed ichnotaxa are known from single localities, and there is no evidence indicating that they represent any type of recurrent morphology as an expression of behavior (i.e., they are not trace fossils). Of those known from more than one occurrence, only *Nenoxites* has provisionally survived critical scrutiny (Seilacher et al. 2005), and is currently one of the most controversial forms, therefore a body fossil origin is not completely ruled out. Dense aggregates of structures attributed to *Nenoxites* in the Khatyspyt Formation have been offered as the earliest example of bioturbation (Rogov et al. 2012), but doubts have

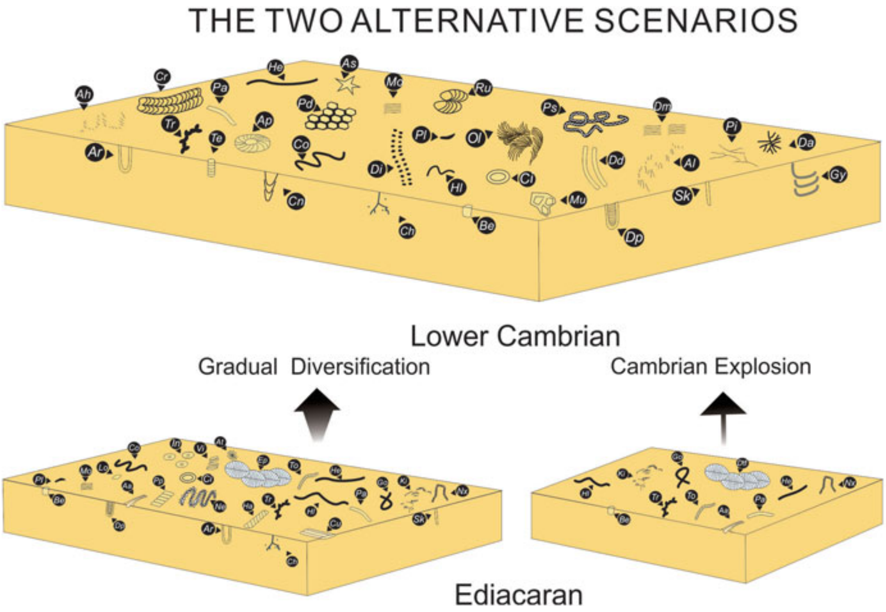

**Fig. 2.4** Contrasting diversification trajectories through the Ediacaran–Cambrian transition based on ichnologic information. The gradual diversification model is based mostly on Crimes (1992, 1994). According to this view, the Ediacaran was characterized by a wide variety of trace fossils, whereas the Cambrian only shows a slight increase in ichnodiversity. Ediacaran ichnofaunas include ichnotaxa that were restricted to this period, such as *Epibaion* (*Ep*), *Harlaniella* (*Ha*), *Intrites* (*In*), *Kimberichnus* (*Ki*), *Nenoxites* (*Nx*), *Palaeopascichnus* (*Pp*), and *Vimenites* (*Vi*), as well as others that continue into the Phanerozoic, including *Arenicolites* (*Ar*), *Archaeonassa* (*Aa*), *Asterichnus* (*At*), *Bergaueria* (*Be*), *Chondrites* (*Ch*), *Circulichnis* (*Ci*), *Cochlichnus* (*Co*), *Curvolithus* (*Cu*), *Diplocraterion* (*Di*), *Gordia* (*Go*), *Helminthoidichnites* (*He*), *Helminthopsis* (*Hl*), *Lockeia* (*Lo*), *Monomorphichnus* (*Mo*), *Palaeophycus* (*Pa*), *Planolites* (*Pl*), *Skolithos* (*Sk*) *Torrowangea* (*To*), and *Treptichnus* (*Tr*). The Cambrian explosion model is supported in this chapter. In this scenario Ediacaran ichnodiversity levels are considerably lower, being the Cambrian the time of diversification. Cambrian ichnofaunas include a wide variety of ichnogenera, including *Allocotichnus* (*Al*), *Asaphoidichnus* (*Ah*), *Asteriacites* (*As*), *Astropolichnus* (*Ap*), *Conichnus* (*Cn*), *Cruziana* (*Cr*), *Dactyloidites* (*Da*), *Dimorphichnus* (*Dm*), *Diplichnites* (*Dp*), *Diplopodichnus* (*Dd*), *Gyrolithes* (*Gy*), *Oldhamia* (*Ol*), *Multina* (*Mu*), *Paleodictyon* (*Pd*), *Pilichnus* (*Pi*), *Psammichnites* (*Ps*), and *Rusophycus* (*Ru*)

been raised on the trace-fossil interpretation of these forms mainly on the basis of peculiarities in the supposed meniscate back-fill (Brasier et al. 2013). Based on how these structures are packed and compacted showing some sort of rigidity (Rogov et al. 2012, their Fig. 2A), it is likely that these dense aggregates may represent some of the earliest examples of body fossil concentrations.

A body fossil origin has been proposed for almost all the structures that have shown some recurrence. *Yelovichnus* and *Palaeopascichnus* (Fig. 2.5a–d) were originally thought to be guided meandering trails, but have been reinterpreted as algal remains (Haines 2000), xenophyophorean protozoans (Seilacher et al. 2003, 2005),

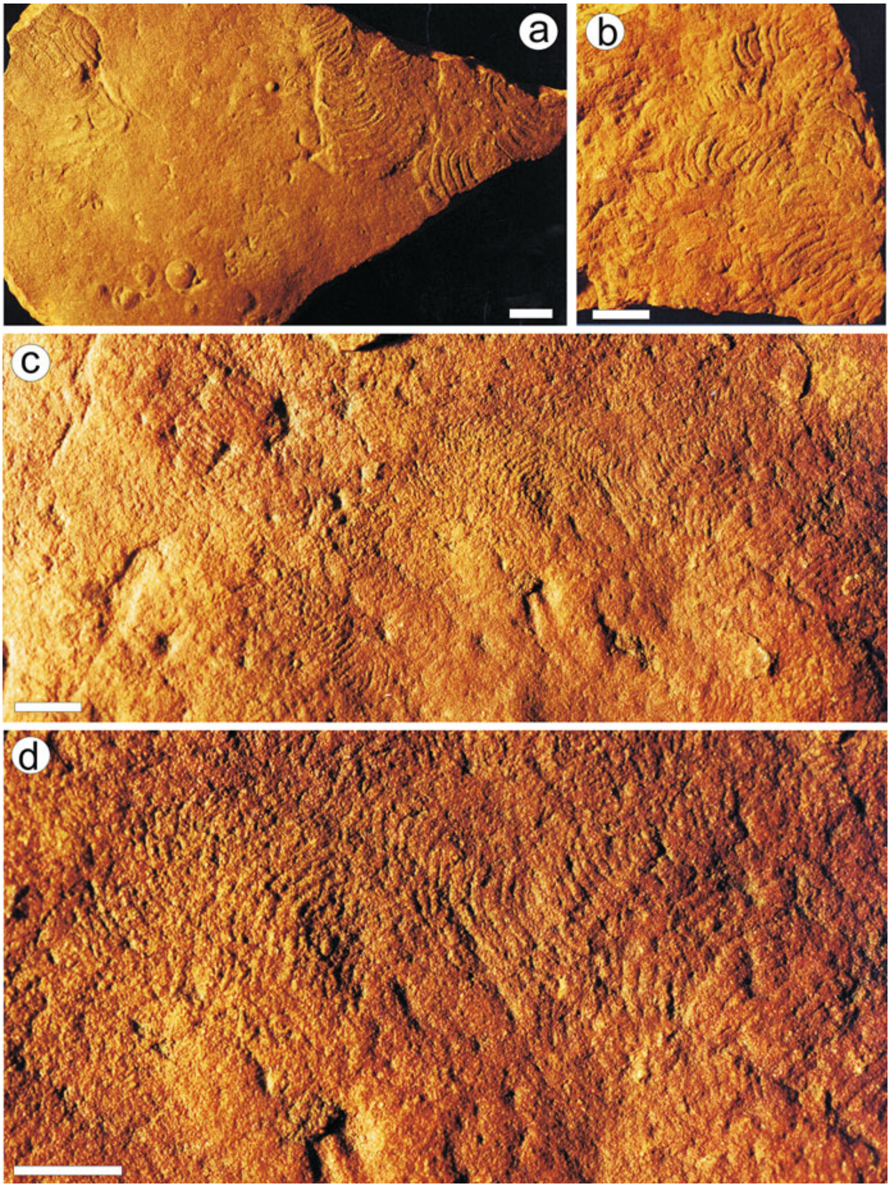

**Fig. 2.5** *Palaeopascichnus*, a body fossil originally regarded as a highly specialized meandering trail, Ediacara Member, Rawnsley Quartzite, Flinders Ranges, South Australia. (**a**) Patchly distributed specimens of *Palaeopascichnus*; (**b**) Close-up. Note that the supposed meandering trail cannot be traced along its course (i.e., these are transversal segments rather than continuous meanders); (**c**) General view of a surface with high density of specimens; (**d**) Close-up. All specimens are housed at the South Australia Museum and preserved as positive hyporeliefs in sandstones with combined-flow ripples. All scale bars are 1 cm

tubicolous animals (Shen et al. 2007), or unidentified protozoans (Antcliffe et al. 2011). *Shaanxilithes* and *Helanoichnus*, both consisting of serially repeated elements and originally thought to be grazing trails, are now regarded as tubular body fossils (Shen et al. 2007; Meyer et al. 2012). Another form consisting of serially repeated elements, more precisely closely spaced circular rings, is *Gaojiashania* (Zhang 1986; Ding et al. 1992; Zhuravlev et al. 2009; Cai et al. 2013). This form has been regarded as a trace fossil by Zhuravlev et al. (2009), who suggested affinities with locomotion by slime molds. However, recent reanalysis of the Chinese specimens suggests these are tubular body fossils, therefore underscoring similarities with *Shaanxilithes* and *Helanoichnus* (Cai et al. 2013). *Harlaniella*, a rope-like structure of uncertain behavioral significance, is now considered a body fossil showing affinities with *Palaeopascichnus* (Jensen 2003; Jensen et al. 2006), or to casts and impressions of tubes similar to vendotaenids (Ivantsov 2013). *Intrites*, a subcircular blob, has been reinterpreted as a body fossil of uncertain affinities (Gehling et al. 2000). The origin of the radial structure *Mawsonites* has been historically controversial, but there is present consensus that is not a trace fossil (Runnegar 1992b; Seilacher et al. 2005; Jensen et al. 2006). *Vermiforma*, which for some authors was regarded as a meandering backfilled structure, is now known to be a tectograph (Seilacher et al. 2000). *Protospiralichnus* is now regarded as a concentric microfault system producing by degassing below a mat (Seilacher 2007). *Aulozoon*, a large fossil resembling a flattened sand-filled sausage (Fig. 2.6), was originally interpreted as a trace fossil (Glaessner 1969), a view that was endorsed by Seilacher et al. (2003). In a later study, Seilacher et al. (2005) noted that *Aulozoon* departs from the typical style of Ediacaran trace fossils and considered this form as problematic, most likely a body fossil. However, the trace fossil interpretation has been reinstated recently by Seilacher and Gishlick (2014), who regarded *Aulozoon* as a burrow produced by flatworms. Overall morphologic features and preservational considerations suggest that *Aulozoon* is most likely a body fossil and not a trace fossil.

In addition to the problematic nature of those structures that were considered trace fossils exclusive of the Ediacaran, significant issues are evident as well with typical Phanerozoic ichnotaxa that were supposedly present in the Neoproterozoic (e.g., Becker 2010, 2013; but see Kolesnikov et al. 2015). *Chondrites* has been mentioned in Ediacaran strata from Australia (e.g., Jenkins 1995) and Russia (Becker 2010, 2013). However, the specimens from Australia are irregular, root-like structures preserved as negative epireliefs that lack the diagnostic bifurcation pattern and contrasting burrow fill of *Chondrites* (Fig. 2.7a). Accordingly, they have been reinterpreted as poorly preserved specimens of body fossils, such as *Hiemalora*, or as overlap of unbranched trace fossils (Seilacher et al. 2005; Jensen et al. 2006), and more recently as formed during growth of a sessile sediment-dweller (Droser et al. 2014). Similarly, the specimens from Russia do not display the diagnostic features of *Chondrites* and are now regarded as pseudofossils or, in one case, as possible paleopascichnids (Kolesnikov et al. 2015). Horizontal scratch marks (e.g., *Monomorphichnus*) attributed to arthropods rasping the sedimentary surface have been mentioned in Ediacaran rocks as well, but some of these are most likely inorganic tool marks (Fig. 2.7b), whereas others are true scratch marks, but produced not by arthropods, but by *Kimberella*, a metazoan of debatable affinities (Budd 2015), including priapulids or stem-group mollusks (Seilacher et al. 2005;

**Fig. 2.6** *Aulozoon*, a problematic fossil, Ediacara Member, Rawnsley Quartzite, Flinders Ranges, South Australia. Scale bar is 5 cm

Gehling et al. 2005, 2014; Ivantsov 2013). The arthropod trackway *Diplichnites* was mentioned for the Ediacaran of Russia (Becker 2013), but this has been more recently reinterpreted as paleopascichnids (Kolesnikov et al. 2015). Tracks have also been mentioned intergrading with other structures (Chen et al. 2013), but the morphologic evidence is unconvincing (see below).

The bivalve resting trace *Lockeia* has also been mentioned in the Ediacaran (e.g., Zhang 1986; Narbonne and Aitken 1990; Jenkins 1995; McMenamin 1996; Becker 2010, 2013). However, the diagnostic almond-shape of this ichnogenus does not seem to be present, neither any of the common morphologic details of this ichnogenus and, therefore, no convincing examples are known in the Ediacaran (Jensen et al. 2006; Kolesnikov et al. 2015). The bilobate trail *Didymaulichnus* is another typical Phanerozoic ichnotaxa that has been occasionally mentioned in Ediacaran rocks. However, as noted by Jensen et al. (2006), most of these recordings are dubious, and even in some cases the structures have been reinterpreted as microbially induced sedimentary structures (Porada and Bouougri 2008) (Fig. 2.7c). In addition, the type material of *Didymaulichnus miettensis* from western Canada, supposedly of Ediacaran age, is now thought to come from a loose float block of Cambrian age (personal communication of Jim Aitken to Guy Narbonne). The presence of the complex backfilled ichnogenus *Nereites* (and its preservational variant *Neonereites*) in the Ediacaran has been indicated many times (e.g., Fedonkin 1990; Crimes 1994; Brasier and McIlroy 1998). However, the complex internal structure of this ichnogenus has never been demonstrated for Ediacaran specimens. In fact, it has been argued that specimens that superficially resemble the *Neonereites* preservational variant may be body fossils of chambered xenophyophorans (Seilacher et al. 2003, 2005; Seilacher 2007). The body fossil *Pleuxus ricei* recently described by Joel et al. (2014) also may be confused with *Nereites*- or *Neonereites*-like trace fossils. Some wrinkle marks and cracks commonly present in Ediacaran microbial mats may display a network-like appearance superficially resembling graphoglyptid networks, such as *Paleodictyon* or *Protopaleodictyon* (Fig. 2.7d). Structures interpreted as guided meandering trails and assigned to the ichnogenera *Helminthoida* or *Palaeohelminthoida* (e.g., Jenkins 1995) belong in *Palaeopascichnus* (Fig. 2.5a and b).

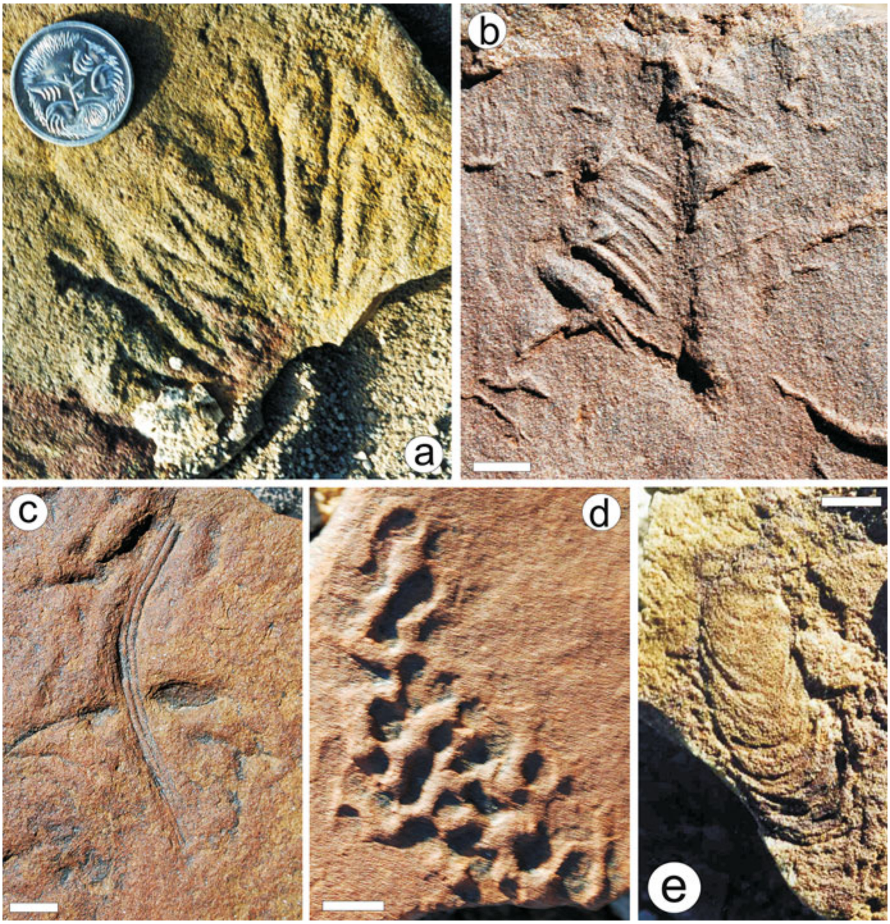

**Fig. 2.7** A variety of Ediacaran structures (pseudotraces) resembling Phanerozoic ichnotaxa. (**a**) Branched structure mimicking *Chondrites* preserved as a negative epirelief. In all probability, it is a poorly preserved body fossil similar to *Hiemalora*. Ediacara Member, Rawnsley Quartzite, Flinders Ranges, South Australia. Coin is 1.9 cm; (**b**) Tool marks resembling the arthropod scratch trace *Monomorphichnus*, preserved as positive hyporelief. Huns Member, Urusis Formation, Nama Group, Arimas Farm, Namibia; (**c**) Partially preserved microbially induced crack resembling the bilobate trace fossil *Didymaulichnus*, preserved as positive hyporelief. Huns Member, Urusis Formation, Nama Group, Arimas Farm, Namibia; (**d**) microbially induced crack resembling network graphoglyptids, such as *Protopaleodictyon* or *Paleodictyon*, preserved as positive hyporelief. Huns Member, Urusis Formation, Nama Group, Arimas Farm, Namibia; (**e**) Problematic structure resembling the spreiten burrow *Rhizocorallium*. Note its presence in a highly corrugated surface suggestive of a microbial mat. Ediacara Member, Rawnsley Quartzite, Flinders Ranges, South Australia. All are field photos. All scale bars are 1 cm

Supposed spreiten structures have been recently described from the Zaris Formation of the Nama Group in Namibia (MacDonald et al. 2014). However, the material is problematic and deserves further analysis. The authors compared these structures with Paleozoic *Zoophycos* (see their Fig. 5.1-3), although the material seems superficially closer to *Rhizocorallium*. It should be noted that the figured specimen from the Cambrian Wood Canyon Formation that serves for comparison (their Fig. 5.3) has been questioned recently (Mángano and Buatois 2014). The illustrated specimen from the Nama Group (their Fig. 5.4) does not display enough detailed morphologic features (e.g., regularly spaced secondary lamellae) to support affinity with *Zoophycos* (cf. Olivero 2003). The marginal tube, although mentioned in the description and traced on one of the illustrations (their Fig. 4), is not clearly visible in the photos (their Fig. 2A–C), making these arcuate structures highly controversial. Similar structures resembling spreiten burrows are present in Ediacaran rocks elsewhere (Fig. 2.7e), but after close examination a trace-fossil origin is unlikely. Finally, the sole occurrence of these structures also calls for caution because, with the exception of the smaller partial structures illustrated in their Fig. 3.2, all the other figures are different views of the same specimen, which seems to be confined to a single surface.

Vertical burrows, such as *Skolithos* or *Diplocraterion*, have been occasionally mentioned in Ediacaran strata, but unquestionable specimens have never been documented (Seilacher et al. 2005; Jensen et al. 2006). With the single exception of *Skolithos declinatus* from the White Sea (Fedonkin 1985), which requires further documentation, all recordings consist of short knobs preserved on bedding planes (e.g., Sokolov 1997; Grazhdankin 2014). Basal attachments or vertical portions of inclined *Palaeophycus* are the most likely interpretations for such structures (Jensen et al. 2006; Carbone and Narbonne 2014). In some cases, these short knobs are surrounded by concentric ridges formed by the rotation of the anchored organism, resembling the scratch circle *Kullingia* (Jensen et al. 2002).

## 2.4 Ediacaran Ichnodiversity and Ichnodisparity: A Case for Limited Morphologic Variability

After critical reevaluation, a convincing case can be made that global Ediacaran ichnodiversity and ichnodisparity (sensu Buatois and Mángano 2013; see Chap. 1) were remarkably low. A review of the main trace-fossil morphologies present in the Ediacaran indicates the existence of seven categories of architectural designs: simple horizontal trails, passively filled horizontal burrows, actively filled (massive) horizontal burrows, plug-shaped burrows, oval-shaped impressions, rasping traces, and horizontal burrows with horizontal to vertical branches (Mángano and Buatois 2014). If bioerosion structures are considered, circular holes and pits should be added to the list.

Ediacaran simple horizontal trails include four ichnogenera, namely *Helminthoidichnites* (Fig. 2.8a and b), *Helminthopsis* (Fig. 2.8c and d), *Gordia* (Fig. 2.8e and f), and *Archaeonassa* (Fig. 2.8g and h). *Helminthoidichnites* consists of simple

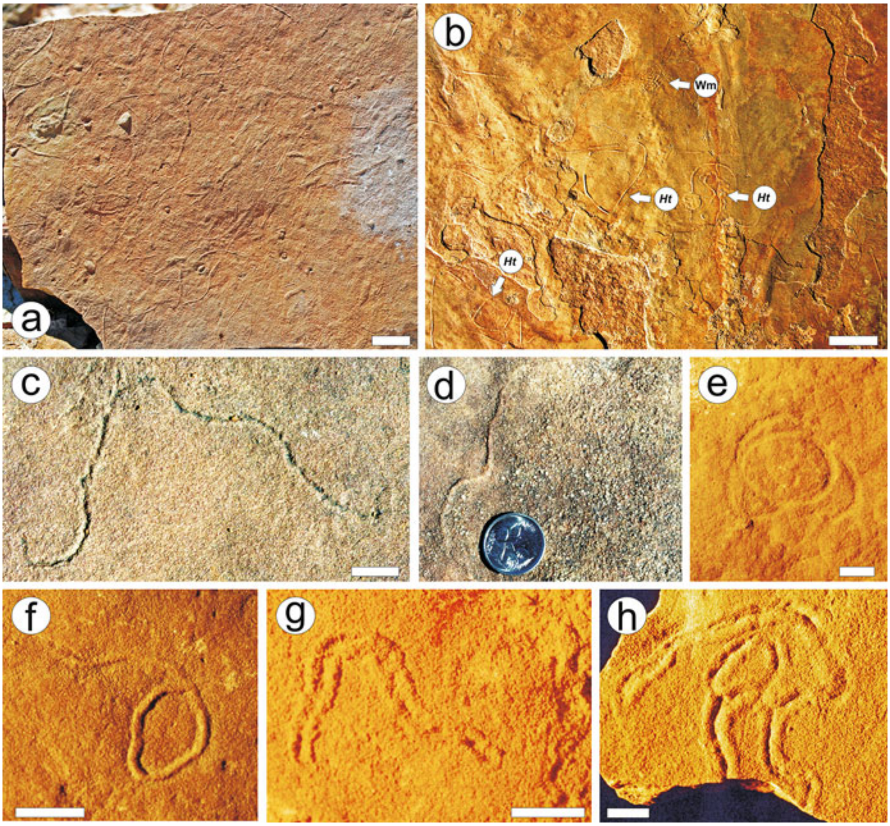

**Fig. 2.8** Simple horizontal trails. (**a**) Surface covered with *Helminthoidichnites tenuis* preserved as positive hyporelief. Spitskop Member, Urusis Formation, Nama Group, Swarpunt Farm, Namibia; (**b**) *Helminthoidichnites tenuis* (*Ht*) associated with wrinkle marks (Wm) suggestive of microbial mats, preserved as positive hyporelief. Arondegas Formation, Vanrhynsdorp Group, Arondegas Farm, South Africa; (**c**) *Helminthopsis tenuis* preserved as positive hyporelief. Ediacara Member, Rawnsley Quartzite, Flinders Ranges, South Australia; (**d**) *Helminthopsis tenuis* in unusually coarse-grained sandstone, preserved as positive hyporelief. Ediacara Member, Rawnsley Quartzite, Flinders Ranges, South Australia. Coin is 1.9 cm; (**e**) *Gordia marina* preserved as negative epirelief. Ediacara Member, Rawnsley Quartzite, Flinders Ranges, South Australia; (**f**) *Gordia marina* preserved as positive hyporelief. Ediacara Member, Rawnsley Quartzite, Flinders Ranges, South Australia; (**g**) *Archaeonassa fossulata* preserved as negative epirelief. Ediacara Member, Rawnsley Quartzite, Flinders Ranges, South Australia; (**h**) *Archaeonassa fossulata* preserved as negative epirelief. Ediacara Member, Rawnsley Quartzite, Flinders Ranges, South Australia. (**a**), (**b**), (**c**), and (**d**) are field photos; (**e**), (**f**), (**g**), and (**h**) are housed at the South Australia Museum. All scale bars are 1 cm

straight to curved trails, *Helminthopsis* displays a tendency to meander, *Gordia* shows self-overcrossing, and *Archaeonassa* is typified by marginal levees (Buatois et al. 1998; Buatois and Mángano 2002). This architectural category comprises the simplest types of animal–substrate interactions, and the four ichnogenera in fact represent very minor behavioral variants of a basic, non-specialized grazing pattern. Although apparent

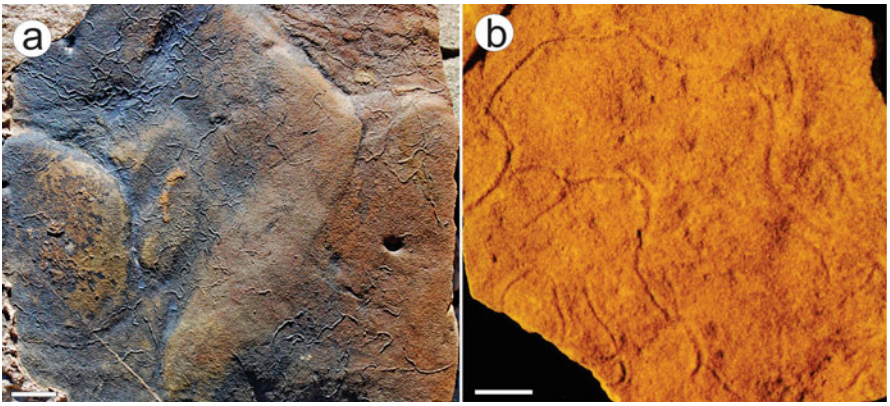

**Fig. 2.9** Simple trail overcrossing resembling more complex networks. (**a**) Field photo. Huns Member, Urusis Formation, Nama Group, Arimas Farm, Namibia; (**b**) Slab housed at the South Australia Museum. Ediacara Member, Rawnsley Quartzite, Flinders Ranges, South Australia. All scale bars are 1 cm

branching and irregular mesh-patterns have been mentioned (e.g., Gehling and Droser 2009), true branching has never been properly documented and trail overcrossing may mimic networks (Fig. 2.9a and b). Unsurprisingly, these ichnotaxa are by far the most abundant in the Ediacaran, being present in western Canada (Narbonne and Hofmann 1987; Narbonne and Aitken 1990; MacNaughton et al. 2000; Hofmann and Mountjoy 2010; Carbone and Narbonne 2014), eastern Canada (Crimes and Anderson 1985; Narbonne et al. 1987; Gehling et al. 2001), Spain (Vidal et al. 1994; Jensen et al. 2007), Namibia (Jensen and Runnegar 2005), South Africa (Buatois et al. 2007; Almond et al 2008), Bhutan (Tangri et al. 2003), and South Australia (Glaessner 1969; Jenkins 1995; Gehling 1999; Jensen 2003; Jensen et al. 2006), among other places. Similar trails in Phanerozoic strata have been attributed to worm-like bilaterians and identical structures are common in modern environments, produced by a wide variety of animals (Buatois and Mángano 2011b).

In any case, caution should be exercised because alternative interpretations have been put forward. For example, compressed carbonaceous filaments may be confused with simple grazing trails, as demonstrated by Jensen et al. (2006, 2007). In this regard, the presence of levees on both sides of the structure is a good evidence of sediment displacement, reinforcing a trace-fossil origin (Droser et al. 2005). Also, the giant protist *Gromia sphaerica* is known to produce simple trails on the modern sea bottom (Matz et al. 2008). However, these structures are commonly quite straight and variable in morphologic features (e.g., presence or absence of levees, presence or absence of axial ridge) both within a single specimen and considering the whole population of structures than most grazing trails attributed to bilaterians. In addition, it has been noted that protist trails tend to be quite short and that, because of protist very slow locomotion, their trails most likely are smothered or eroded almost as fast as they are produced (Gehling and Droser 2009). Retallack (2013b) put forward the idea that similar simple structures can be produced by mycetozooans (slime molds) rather than bilaterians. An additional problem for the recognition of Ediacaran trails is the fact that the widespread microbial activity resulted in a wide variety of microbially induced structures, some of them still poorly understood due to the paucity of modern analogs, which can easily resemble trace fossils (Seilacher 2007). Crack propagation in microbial mats affected by wave oscillation may result in sinusoidal cracks following ripple troughs, referred to as Manchuriophycus, which superficially resemble grazing trails (Seilacher 2007). Structures resembling grazing trails have also experimentally produced from interactions between oscillatory flows and centimetric microbial aggregates (Mariotti et al. 2016). However, grazing trails have been described from settings well below (storm) wave base, where oscillation at the sea bottom is extremely unlikely (e.g., MacNaughton et al. 2000; Carbone and Narbonne 2014). In short, the origin of these simple horizontal structures should be evaluated on a case-by-case basis and on a large collection of specimens.

Passively filled horizontal burrows are represented by the ichnogenus *Palaeophycus* (Fig. 2.10). This ichnotaxon consists of simple horizontal to subhorizontal lined burrows having an infill similar to the host rock (Pemberton and Frey 1982). In Ediacaran rocks, *Palaeophycus* is present in western Canada (Young 1972; Fritz and Crimes 1985; Narbonne and Hofmann 1987; Narbonne and Aitken 1990; MacNaughton and Narbonne 1999; MacNaughton et al. 2000; Hofmann and Mountjoy 2010; Carbone and Narbonne 2014), Mexico (Sour-Tovar et al. 2007), Norway (Banks 1970, 1973), Poland (Pacześna 1985, 1986, 1996), Russia (Fedonkin 1985), Namibia (Geyer and Uchman 1995), Bhutan (Tangri et al. 2003), China (Weber et al. 2007), eastern Australia (Webby 1970, 1984), and central Australia (Walter et al. 1989). Similar burrows in younger rocks have been considered as produced by the activity of worm-like bilaterians, most likely suspension feeders or active predators. As in the case of the simple grazing trails, evaluation should be done on a case-by-case basis because some body fossils may resemble *Palaeophycus*-like burrows (Sappenfield et al. 2011).

**Fig. 2.10** Simple horizontal burrow *Palaeophycus tubularis*. Note *Mawsonites*-like structure in the *upper right corner*. Slab housed at the South Australia Museum. Ediacara Member, Rawnsley Quartzite, Flinders Ranges, South Australia. Scale bar is 1 cm

Ediacaran simple actively filled (massive) horizontal burrows include *Torrowangea* and *Nenoxites*. *Torrowangea* is a horizontal trace fossil with regularly spaced constrictions. Although the Ediacaran age of its type material from eastern Australia (Webby 1970) is disputed, definite Ediacaran representatives are known from western (Narbonne and Aitken 1990; Carbone and Narbonne 2014) and eastern (Gehling et al. 2001) Canada, Namibia (Geyer and Uchman 1995), China (Weber et al 2007), and Poland (Pacześna 1996). The segmented nature of *Torrowangea* suggests burrowing by a worm-like deposit feeder using peristalsis (Narbonne and Aitken 1990), recording incipient exploitation of the infaunal ecospace.

As noted by Jensen et al. (2006), each individual case needs to be assessed in order to rule out the possibility of a body-fossil origin. Tubular body fossils may display a ropy appearance, as in the case of *Funisia dorothea* (Droser and Gehling 2008), resembling backfilled burrows (Fig. 2.11). *Nenoxites* has been commonly depicted as a segmented angular meander (e.g., Crimes 1987). Subsequent analysis suggests that the turns are not as sharp and that the segmentation reflects a wall lining made of elongate fecal pellets oriented perpendicularly to the burrow axis (Seilacher et al. 2005). If this interpretation is correct, *Nenoxites* most likely records the activity of a worm-like deposit feeder. However, many doubts remain concerning this structure (see also Brasier et al. 2013), and its trace-fossil nature may be regarded as uncertain. This ichnogenus is only known from the White Sea and the Olenek Uplift in Russia (e.g., Fedonkin 1985).

Plug-shaped burrows are represented in the Ediacaran by the ichnogenus *Bergaueria*, a structure which is typically regarded as resting or dwelling traces of cerianthid or actinarian anemones (Pemberton et al. 1988). As noted by Seilacher et al. (2005) and Jensen et al. (2006), the main problem is that the distinction of this ichnotaxon from body fossils, such as *Intrites*, *Beltanellifomis* and *Beltanelloides*, is not straightforward to say the least. The list of Ediacaran occurrences of plug-shaped burrows has significantly shrunk to the point of almost disappearance. However, Grazhdankin (2014)

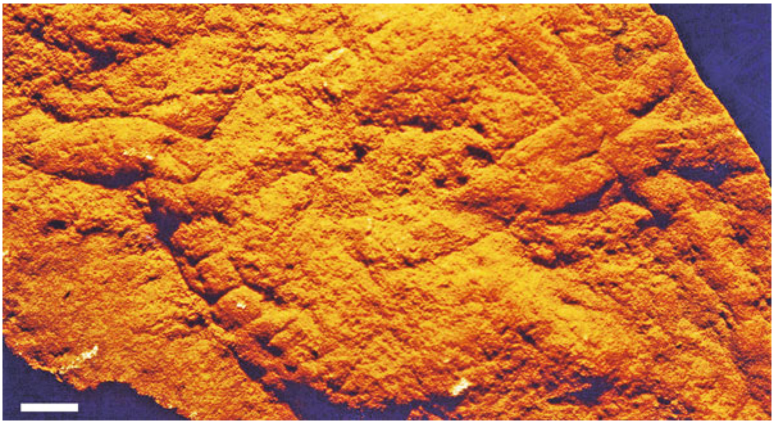

**Fig. 2.11** Tubular body fossil resembling a meniscate backfilled trace fossil. Slab housed at the South Australia Museum. Ediacara Member, Rawnsley Quartzite, Flinders Ranges, South Australia. Scale bar is 1 cm

recently illustrated a notable potential addition from the Ediacaran of the White Sea area. In addition, specimens from western Canada (Narbonne and Hofmann 1987) seem to show the morphology of plug-shaped burrows with a series of overlapping disks, favoring comparison with *Bergaueria sucta* (Seilacher 1990; Seilacher et al. 2005). In this interpretation, the structures reveal the lateral displacement of an anemone-like animal. Alternatively, the signs of lateral movement may be understood as a structural part of a globular structure, favoring instead comparisons with complex tubular fossils, such as *Gaojiashania* (Jensen et al. 2006). Subsequently, *Bergaueria sucta* has been also found in middle Cambrian deposits (Hofmann et al. 2012; Mángano et al. 2013) and possibly Middle Ordovician strata (de Gibert et al. 2011).

Oval-shaped impressions are represented by the ichnogenus *Epibaion* (Fig. 2.12a–f), which is regarded as a resting trace of *Dickinsonia* and *Yorgia*, whose body fossils have been found in direct association with the trace fossils in both the White Sea of Russia and the Flinders Ranges of Australia (Ivantsov and Malakhovskaya 2002; Gehling et al. 2005; Sperling and Vinther 2010; Ivantsov 2011, 2013). Passive transport has been suggested as an alternative (McIlroy et al. 2009), but the fact that many of these structures are arranged following a curved trajectory argues against mobilization of organisms by currents (Sperling and Vinther 2010). In addition, the orientation of the associated body fossil invariably indicates that they were formed in the direction of the anterior of the body axis (Gehling et al. 2005; Droser and Gehling 2015), which militates against passive transport. Clearly, there is no agreement on the affinities of *Dickinsonia* with interpretations encompassing a wide variety of candidates, such as cnidarians (Harrington and Moore 1956), polychaetes (Glaessner and Wade 1966); fungi (Retallack 2007), placozoans (Sperling and Vinther 2010), Proarticulata (Fedonkin 1983; Ivantsov 2011, 2013), some sort of bilaterians (Gold et al. 2015), and vendobionts (Seilacher 1984, 1989, 1992). In any case, regardless of the phylogenetic affinities of dickinsonids, ichnologic evidence suggests that these organisms were capable to move, probably feeding from direct external digestion of the mat (Sperling and Vinther 2010; Ivantsov 2011, 2013).

Rasping traces are represented by the ichnogenus *Kimberichnus*, which has been recorded in direct association with *Kimberella* in both the White Sea of Russia and the Flinders Ranges of Australia (Fedonkin 2003; Gehling et al. 2005, 2014; Ivantsov 2009, 2013) (Fig. 2.13a–d). Impressive examples of rasping traces, displaying apron-like arrangements in direct connection with *Kimberella* have been recorded from these localities (e.g., Fedonkin 2003, Fig. 16; Fedonkin et al. 2007, Fig. 22; Seilacher 2008, Plate 15). In particular, Fedonkin (2003, Fig. 16) illustrates an example of *Kimberella* with the scratch marks (*Kimberichnus*) forming an apron coming out from the front of the body fossil. This is hard to reconcile with Retallack's (2013a) claim that these structures represent ice needles (see also Xiao et al. 2013). The phylogenetic affinities of *Kimberella* are still matter of considerable debate, with stem-group mollusks (Fedonkin and Waggoner 1997) and priapulids (Gehling et al. 2014) being some of the proposed candidates. Based on morphologic and behavioral traits, Budd and Jensen (in press) suggested that *Kimberella* may be a stem-group bilaterian rather than representing the stem-group of any particular Phyllum. In any case, *Kimberella* was able to feed by systematically scratching microbial mats, a behavior that, from an ichnologic perspective, defines it as an animal.

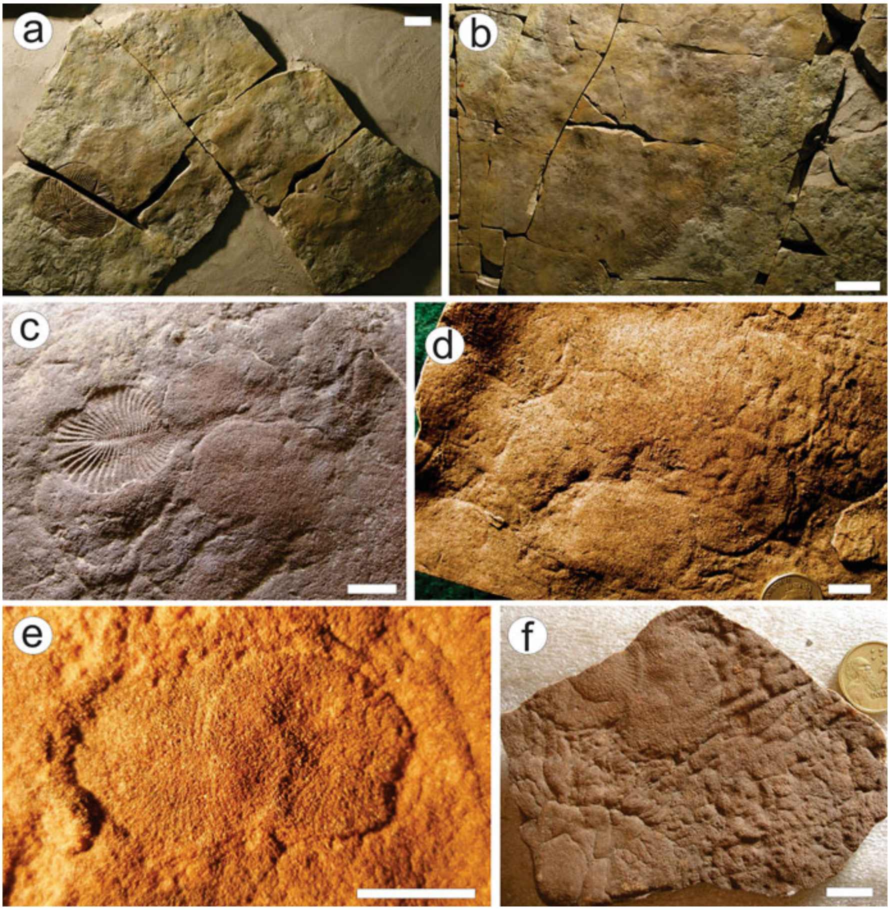

**Fig. 2.12** Dickinsonid resting trace fossils. (**a**) *Yorgia waggoneri* (*lower left*) with associated, poorly preserved resting traces of the ichnospecies *Epibaion waggoneri*, White Sea coast, Russia. Scale bar is 2 cm; (**b**) General view of overlapping "trace platforms," White Sea coast, Russia. Scale bar is 2 cm; (**c**) *Dickinsonia costata* (*left*) preserved at the end of a series of four overlapping resting traces assigned to the ichnospecies *Epibaion costatus*. Ediacara Member, Rawnsley Quartzite, Flinders Ranges, South Australia. Scale bar is 1 cm; (**d**) Three overlapping resting traces. Ediacara Member, Rawnsley Quartzite, Flinders Ranges, South Australia. Scale bar is 1 cm; (**e**) Close-up of a *Dickinsonia* on top of the resting trace. Ediacara Member, Rawnsley Quartzite, Flinders Ranges, South Australia. Scale bar is 1 cm; (**f**) Partially preserved resting trace associated with a textured organic surface. Scale bar is 1 cm. All photographs provided by Jakob Vinther; specimens from Russia housed at the Paleontological Institute of the Russian Academy of Sciences, specimens from Australia housed at the South Australia Museum. For detailed descriptions and interpretations of the White Sea specimens, see Ivantsov and Malakhovskaya (2002) and Ivantsov (2011, 2013); for detailed analysis of the Australia material, see Gehling et al. (2005) and Sperling and Vinther (2010)

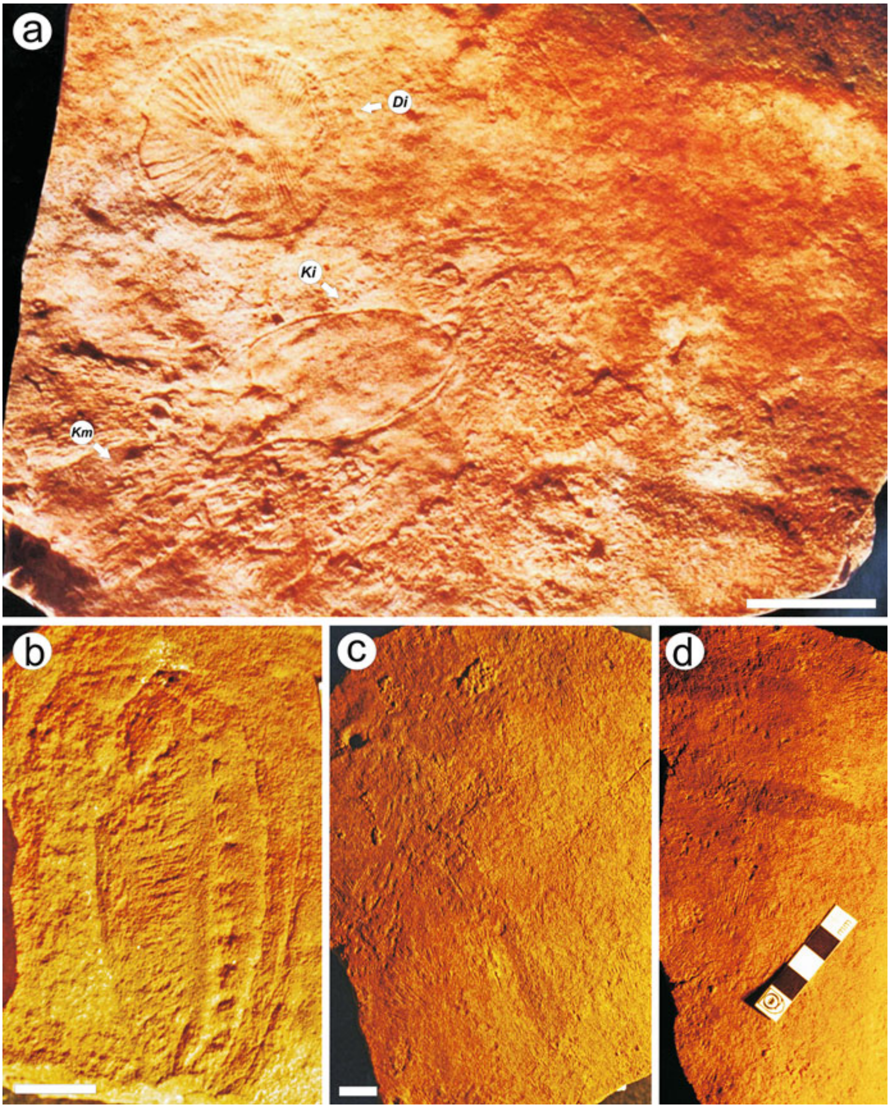

**Fig. 2.13** The body fossil *Kimberella* and associated rasping traces (*Kimberichnus*). (**a**) Radular marks attributed to the ichnogenus *Kimberichnus* (*Km*) in direct association with the producer, *Kimberella quadrata* (*Ki*). Note also the presence of *Dickinsonia* (*Di*). Scale bar is 5 cm; (**b**) The body fossil *Kimberella*. Scale bar is 1 cm; (**c**) Set of scratch marks. Scale bar is 1 cm; (**d**) Set of scratch marks. Ediacara Member, Rawnsley Quartzite, Flinders Ranges, South Australia. (**a**) is a photo from a cast at the exhibition Fossil Art (see Seilacher 2008); (**b**), (**c**) and (**d**) are photographs from slabs housed at the South Australia Museum. For detailed descriptions and interpretations, see Fedonkin (2003); Gehling et al. (2005, 2014), and Ivantsov (2009, 2013)

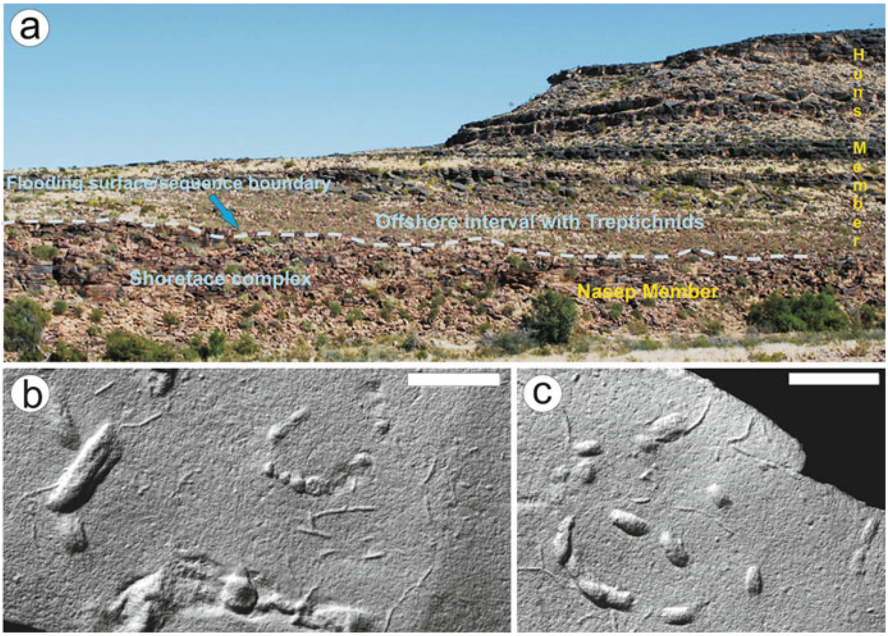

**Fig. 2.14** Horizontal burrows with horizontal to vertical branches (treptichnids) in the terminal Ediacaran. Huns Member, Urusis Formation, Nama Group, Arimas Farm, Namibia. (**a**) General view of the outcrop showing distribution of the main sedimentary facies and associated sequence-stratigraphic surfaces, including information on the precise stratigraphic occurrence of the treptichnids; (**b**) Close-up of specimen of treptichnids. Note associated tiny structures, one of them showing branching reminiscent of *Treptichnus bifurcus*. Scale bar is 1 cm; (**c**) Close-up of specimen of treptichnids and possible tiny grazing trails. Scale bar is 1 cm; (**b**, **c**) provided by Sören Jensen; specimens housed at South African Museum. For details on this treptichnid occurrence, see Jensen et al. (2000)

Horizontal burrows with horizontal to vertical branches, as recorded by the ichnogenus *Treptichnus*, are a very late addition to Ediacaran ichnodiversity and ichnodisparity, having been recorded only in the terminal Ediacaran of Namibia (Jensen et al. 2000). Forms with less defined morphology, but apparently reflecting three-dimensional burrow systems, are referred to as treptichnids (Fig. 2.14a–c), and, in addition to the Nama Group, are known from terminal Ediacaran strata in Finmark (Högström et al. 2013). The more complex branching burrow *Streptichnus* (Fig. 2.15a–f) originally documented from Ediacaran strata also in Namibia (Jensen and Runnegar 2005) is now within error of the Ediacaran–Cambrian transition based on recalibration of radiometric data (Schmitz 2012). The appearance of treptichnids by the terminal Ediacaran adds significant novelty into the incipient exploitation of the infaunal ecospace, signaling an increase in trace fossil complexity. Whereas treptichnids are known from the terminal Ediacaran, the first appearance datum of the much more regularly branching *Treptichnus pedum* indicates the base of the Cambrian (Brasier et al. 1994; Buatois et al. 2013; Landing et al. 2013). The recording of *T. pedum* 4.41 m below the GSSP in Fortune Head (Gehling et al. 2001) is unsurprising, simply reflecting the problem of confidence intervals (Landing et al. 2013).

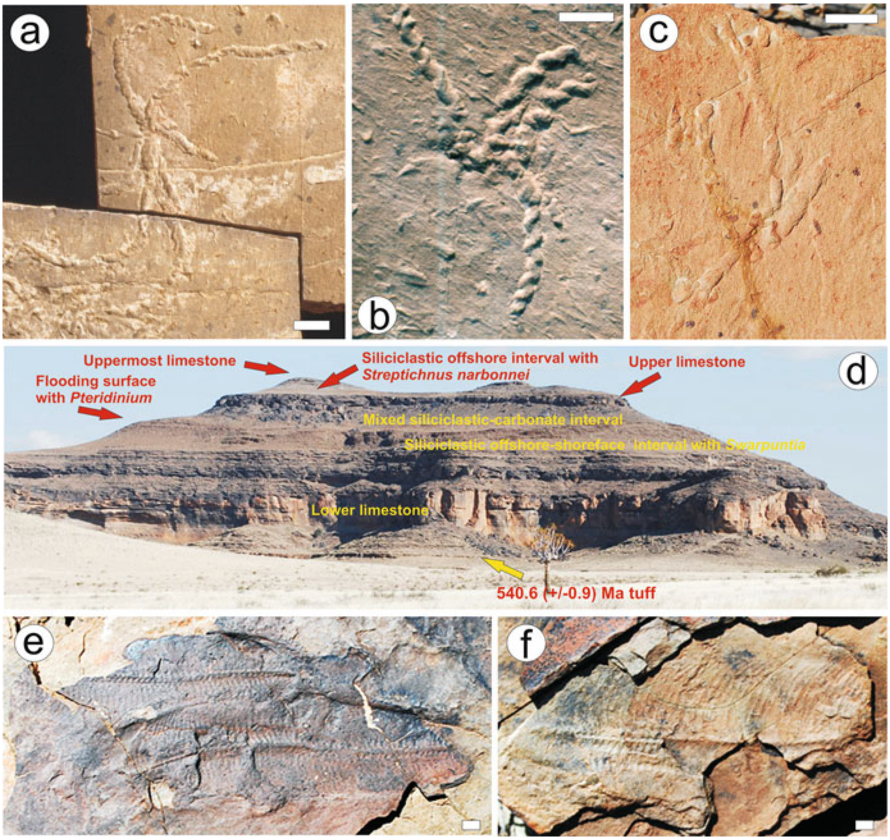

**Fig. 2.15** Horizontal burrows with horizontal to vertical branches (*Streptichnus narbonnei*) in the terminal Ediacaran. Spitskop Member, Urusis Formation, Nama Group, Swarpunt Farm, Namibia. (**a**) General view of a slab containing several specimens of *Streptichnus narbonnei*; (**b**) Close-up of specimen of *Streptichnus narbonnei* displaying diagnostic branching pattern; (**c**) Field photograph of specimen of *Streptichnus narbonnei* displaying poorly developed branching; (**d**) General view of the outcrop showing distribution of the main sedimentary facies and associated sequence-stratigraphic surfaces, including information on the precise stratigraphic occurrence of *Streptichnus narbonnei*, *Pteridinium carolinae*, and *Swarpuntia germsi*; (**e**) Field photograph of *Pteridinium carolinae*; (**f**) Field photograph of *Swarpuntia germsi*. All scale bars are 1 cm; (**a**, **b**) provided by Sören Jensen; specimens are housed with the Namibian Geological Survey, Windhoek. For details on the *Streptichnus* occurrence, see Jensen and Runnegar (2005); for information on the associated body-fossil fauna, see Narbonne et al. (1997)

On the other hand, older representatives of branching burrow systems are contentious. Chen et al. (2013) reported biogenic structures from the Ediacaran Dengying Formation in the Yangtze Gorge, South China, which were interpreted as interconnected horizontal tunnels, surface tracks/trails, and vertical trace fossils, thereby forming a complex branching system. These structures were regarded as undermat mining, epibenthic locomotion, and temporary dwelling, respectively. Biogenic structures are preserved on top and sole of beds within the bituminous limestone with silty partings of the Shibantan Member. In a subsequent study, Meyer et al. (2014a) defined the ichnotaxon *Lamonte trevallis* to include all the previously described intergradations. Retallack (2013b) rejected the metazoan interpretation of these structures, favoring comparison with slime molds, which are terrestrial eukaryotic protists. Although inconsistent with the inferred marine setting of the Dengying Formation, there is little understanding of the origin of these protists. In our view, however, the assemblage can be dismembered into horizontal undermat tunnels (collapsed) and very shallow (about 5 mm deep) vertical structures. The interpretation of discontinuous, irregular structures as "surface tracks/trails" is not supported by morphologic evidence and, in addition, "tracks," by definition imply epigenic structures consisting of appendage imprints, a feature absent in the analyzed material. Shibantan "knobs" and "series of knobs" display irregular morphologies and wide range of sizes along a specimen, and do not record distinct appendage marks. The vertical structures are also of controversial affinity. They are described as connected to and showing positive size correlation with horizontal tunnels. However, several are clearly disconnected in the figured material (e.g., their Figs. 3A; 5C, D; and 6A, D). Shallow vertical structures, however, can be equally interpreted as pits related to holdfasts recording the activity of mat encrusters (sensu Seilacher 1999) or, alternatively, as shallow-tier, plug-shaped structures. In fact, vertical structures seem to cross-cut the tunnels rather than being connected to them (cf. their Fig. 6E). In addition, vertical structures do not cross-cut the microbial mat (their Fig. 6F), being confined within the laminations of the mat (their Fig. 6F), in agreement with an encruster-style mode of life. In short, our analysis suggests that the Shibatan biogenic structures are possibly best interpreted as undermat tunnels displaying different taphonomic variants (including the so-called "tracks/trails"). These structures are relatively simple, they do not branch (i.e., true branching sensu Bromley 1996) and although producers may move up and down along their path, they are essentially confined to the microbial mat and do not strictly penetrate the underlying sediment. Based on the uncertainties regarding the overall connection of their supposed components, *Lamonte trevallis* should be regarded as an invalid ichnotaxon.

## 2.5 Ediacaran Ecosystems: The Role of Microbial Matgrounds

Ichnologic data provide a wealth of information to reconstruct Ediacaran ecosystems, particularly through their integration with high-resolution body-fossil and sedimentologic evidence. Ediacaran deposits contain a rather unusual suite of structures suggestive of sediment stabilization by microbial binding, such as wrinkled surfaces, ripple patches, palimpsest ripples, and elephant skin structures (Seilacher and Pflüger 1994; Seilacher 1999; Gehling et al. 2005; Dornbos 2006; Droser et al. 2006; Bottjer and Clapham 2006; Mángano and Buatois 2007; Gehling and Droser 2009; Buatois and Mángano 2012a), collectively known as microbially induced sedimentary structures or MISS (Noffke et al. 1996). The related term "textured organic surfaces" (TOS) have been introduced subsequently to reflect to assemblages of structures that commonly do not have a defined shape or size to be treated taxonomically (Gehling and Droser 2009). Because TOS are essentially made of MISS, there is considerable overlap between both terms, so it seems to be advisable to restrict the former to the microbial surfaces and the latter to the discrete microbial structures. Regardless of technicalities, it is clear that microbial mats were critical components in Ediacaran ecosystems and that benthic communities developed in direct association with resistant matgrounds (Seilacher 1999).

Within this framework, various categories of organism–microbial mat interactions can be recognized. In addition, animal–matground interactions can be reconstructed using the ichnoguild concept (Bromley 1990; see also Buatois and Mángano 2012a). The different categories for interactions include mat encrusters (attached to the microbial mats), mat stickers (organisms growing upward with the surrounding mats), mat scratchers (organisms rasping on the microbial mats), mat digesters (organisms able to feed from direct external digestion of the mat), mat grazers (organisms browsing through the microbial mat), and undermat miners (organisms that constructed tunnels below the mat) (Fig. 2.16). Mat encrusters (e.g., *Charniodiscus*) and mat stickers (e.g., *Cloudina*) are essentially represented by body fossils (Seilacher 1999), but trace-fossil data are key to decipher the other types of interactions (Mángano and Buatois 2007).

Mat digesters and mat scratchers have been inferred based on the integration of the trace- and body-fossil record. The former are illustrated by dickinsonids and their associated resting and locomotion traces, referred to as *Epibaion* (Ivantsov and Malakhovskaya 2002; Gehling et al. 2005; Ivantsov 2011, 2013; Sperling and Vinther 2010). The absence of preserved trails connecting discrete resting traces may indicate that the substrate did not record the epigenic locomotion on the biomat and that impressions formed where *Dickinsonia* externally digested the mat using its entire lower sole (Gehling et al. 2005). These findings are consistent with the view by Laflamme et al. (2009) that some Ediacaran organisms may have fed from osmotrophy (i.e., absorption of dissolved nutrients directly from seawater and/or from the underlying substrate across their lower surfaces). These trace fossils illustrate the *Epibaion* ichnoguild, which consists of transitory, surface mat-digester structures produced by vagile animals.

Mat scratchers are illustrated by the association of *Kimberella* with rasping traces (*Kimberichnus*) preserved on microbial mats most likely produced by a proboscis with paired teeth (Seilacher 1997; Fedonkin 2003; Seilacher et al. 2005; Gehling et al. 2005, 2014; Fedonkin et al. 2007; Ivantsov 2013). These rasping trace fossils have been included in the *Radulichnus* ichnoguild, which consists of transitory, surface mat-scratcher structures produced by vagile animals (Buatois and Mángano 2012a). Interestingly, Caron et al. (2006) suggested a similar behavior in the Burgess Shale *Odontoglyphus*, tracing a continuity in styles of microbial mat exploitation across the Ediacaran–Cambrian boundary (see also Buatois et al. 2014).

Mat grazers are by far the most abundant trace fossils in Ediacaran strata (Gehling 1999; Seilacher et al. 2005; Jensen et al. 2006; Buatois and Mángano 2012a). This interaction is illustrated by simple horizontal trails (*Helminthoidichnites*, *Helminthopsis*, *Archaeonassa*, *Gordia*) typically preserved on surfaces containing wrinkle marks and other microbially induced sedimentary structures. These trails are included in the *Helminthopsis* ichnoguild, which consists of transitory, near-surface

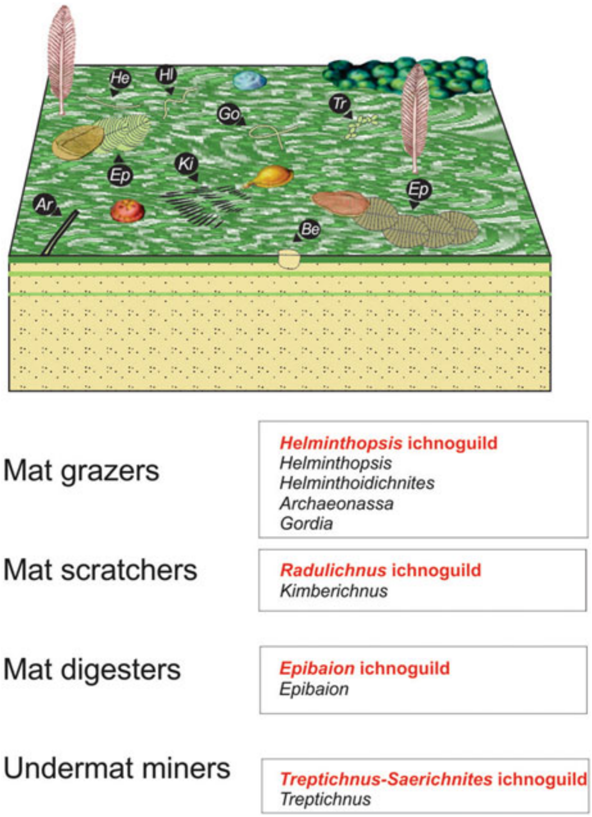

**Fig. 2.16** Categories of organisms–microbial mat interactions

to very shallow-tier, mat-grazer structures produced by vagile animals which feed from organic matter concentrated within microbial mats at the surface or right below a very thin veneer of sediment (Buatois and Mángano 2003, 2004). Simple meandering trails and, more rarely, tendency to form crude spirals have been documented (Carbone and Narbonne 2014), but more patterned, systematic meanders (e.g., *Helminthorhaphe*) and spirals (e.g., *Spirodesmos*) are strikingly absent. Carbone and Narbonne (2014) suggested that these supposed slightly more sophisticated grazing behaviors rarely represented in Ediacaran rocks reflect individual responses of organisms to specific stimuli, rather than the patterned behavior that characterizes more sophisticated Phanerozoic trace fossils (i.e., they should not be assigned to these highly patterned Phanerozoic ichnotaxa).

Although included in the original model (Seilacher 1999), undermat miners seem to have been more common in the earliest Cambrian than in the Ediacaran (Buatois and Mángano 2012a, b; Buatois et al. 2014). In fact, the persistence of matgrounds in the Fortunian coupled with the appearance of a wide variety of behavioral patterns led to extensive development of undermat mining strategies, as illustrated by the ichnogenera *Oldhamia* and *Pilichnus* (Buatois and Mángano 2012a, b). The earliest candidates for undermat mining are the branching structures illustrated by Bouougri and Porada (2007), but further description of these structures is needed. Simpler representatives may be illustrated by the Dengying structures previously analyzed (Chen et al. 2013; Meyer et al. 2014a). Ediacaran examples of this strategy seems to be restricted for the most part to the terminal Ediacaran, as indicated by the appearance of horizontal to oblique branching burrows referred to as treptichnids (Jensen et al. 2000). These structures were apparently emplaced slightly below the mat surface, representing tunnels most likely produced by undermat miners, recording a terminal Ediacaran precursor of the *Treptichnus–Saerichnites* ichnoguild, which comprises semipermanent, shallow-tier, structures of vagile to semi-vagile organisms and is widely present in the Cambrian (Buatois and Mángano 2004). In any case, the feeding strategies associated with this ichnoguild may have been quite variable. Undermat mining seems to have been involved in Ediacaran and some of the Fortunian representatives (Buatois and Mángano 2012a, b; Buatois et al. 2014). However, no association with matgrounds has been noted with most of the younger examples, suggesting deposit-feeding strategies (Buatois and Mángano 2004). In addition, the possible connection of *Treptichnus pedum* with priapulids suggests that predation may have been involved (Vannier et al. 2010).

Finally, actively filled (massive) horizontal burrows (*Torrowangea* and *Nenoxites*) do not seem to show any preferential association with matgrounds (Carbone and Narbonne 2014). The most likely interpretation is that these structures represent more typical, Phanerozoic-style interactions with soft substrates rather than Ediacaran-style exploitation of microbial mats. These structures are included in the *Torrowangea* ichnoguild, which comprises transitory, very shallow-tier structures of vagile deposit feeders. In the same vein, *Bergaueria sucta* apparently does not reflect any interaction with matgrounds. The *Bergaueria* ichnoguild consists of semipermanent, very shallow-tier structures most likely produced by predatory sessile animals. In any case, this ichnoguild became more common by the Cambrian (e.g., Seilacher 1990; Jensen 1997; Hofmann et al. 2012; Mángano et al. 2013).

Neoichnologic research with microbial mats in a modern lagoon may provide an analogy to Ediacaran marine ecosystems (Gingras et al. 2011). This hypersaline lagoon was characterized by low concentrations of dissolved $O_2$, extensive matgrounds dominated by oxygen-producing cyanobacteria, and horizontal burrows in direct connection with the mats. $O_2$ levels in these matgrounds are much higher than in the water column, suggesting that the tracemakers harvest both food and $O_2$ from the biomats (Gingras et al. 2011). This study has raised the possibility that these environments may have acted as $O_2$ oases in overall oxygen-depleted settings during the Ediacaran, favouring the evolution of early animals.

## 2.6 Comparing Shallow- and Deep-Marine Ediacaran Communities

The depositional setting and paleoenvironmental breadth of Ediacaran biotas have been a topic of some controversy (e.g., Dalrymple and Narbonne 1996; McMenamin 1998; MacNaughton et al. 2000; Gehling 2000; Wood et al. 2003; Grazhdankin 2004, 2014; Ichaso et al. 2007; Retallack 2012, 2013a, c, d; Callow et al. 2013; Gehling and Droser 2013; Xiao et al. 2013; Carbone and Narbonne 2014; Carbone et al. 2015). However, there is a general growing consensus that Ediacaran biotas inhabited two broad depositional settings: shallow- and deep-marine areas. These shallow-marine biotas are included in the White Sea and Nama Assemblages (Narbonne 2005). These shallow-marine settings may have been sporadically affected by wave action, as evident in south Australia and Namibia and more locally deltaic discharge, as indicated for South Australia and the White Sea (Gehling 2000; Grazhdankin 2004, 2014; Gehling and Droser 2013). Although the Nama deposits are typically considered as formed in shallower-water than those in South Australia, comparison of sedimentary facies in both areas indicates substantial overlap in terms of depositional environments; bathymetrically most of their siliciclastic facies ranges from the lower shoreface to the lower offshore. Deep-marine biotas are included in the Avalon Assemblage (Narbonne 2005; Narbonne et al. 2014; Liu et al. 2015). These deep-marine settings were characterized by the establishment of slope turbidite systems in some cases affected by contemporaneous volcanism and reworking by bottom currents, as is evidenced in western and eastern Canada (Dalrymple and Narbonne 1996; MacNaughton et al. 2000; Wood et al. 2003; Ichaso et al. 2007; Narbonne et al. 2014). Of particular interest is the presence in the Mackenzie Mountains of an Ediacaran succession showing the passage from deep-marine deposits having the Avalon assemblage to shallow-marine deposits containing the White Sea and Nama assemblages (Carbone et al. 2015).

Integration of ichnologic and sedimentologic information allows discriminating between shallow- and deep-marine benthic communities (Fig. 2.17). Shallow-marine ichnofaunas have been recorded from a wide variety of areas, including western (Young 1972; Fritz and Crimes 1985; MacNaughton and Narbonne 1999;

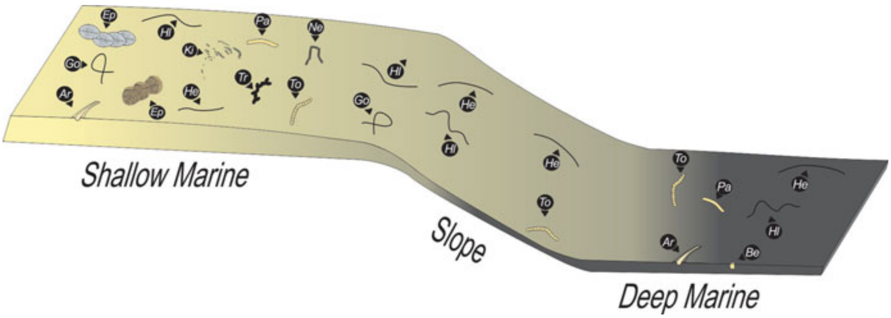

**Fig. 2.17** Ediacaran shallow- and deep-marine trace-fossil associations. The shallow-marine trace-fossil association includes *Archaeonassa* (*Ar*), *Epibaion* (*Ep*), *Gordia* (*Go*), *Helminthoidichnites* (*He*), *Helminthopsis* (*Hl*), *Nenoxites* (*Ne*), *Palaeophycus* (*Pa*), *Kimberichnus* (*Ki*), *Torrowangea* (*To*), and *Treptichnus* (*Tr*). The deep-marine trace-fossil association includes *Archaeonassa* (*Ar*), *Bergaueria* (*Be*), *Helminthoidichnites* (*He*), *Helminthopsis* (*Hl*), *Palaeophycus* (*Pa*), and *Torrowangea* (*To*)

Carbone and Narbonne 2014) and eastern Canada (Crimes and Anderson 1985; Narbonne et al. 1987; Gehling et al. 2001), eastern (Webby 1970, 1984), central (Walter et al. 1989) and southern Australia (Glaessner 1969; Jenkins 1995; Gehling 1999; Jensen 2003; Jensen et al. 2006), Mexico (Sour-Tovar et al. 2007), Norway (Banks 1970, 1973; Högström et al. 2013), Poland (Pacześna 1985, 1986, 1996), Russia (Fedonkin 1985; Ivantsov and Malakhovskaya 2002; Fedonkin et al. 2007; Ivantsov 2009, 2011, 2013; Grazhdankin 2014), Bhutan (Tangri et al. 2003), China (Weber et al. 2007; Chen et al. 2013, 2014; Meyer et al. 2014a), Namibia (Geyer and Uchman 1995; Jensen et al. 2000; Jensen and Runnegar 2005), and South Africa (Buatois et al. 2007). Deep-marine ichnofaunas are comparatively less documented, having been recorded in western Canada (Narbonne and Hofmann 1987; Narbonne and Aitken 1990; MacNaughton et al. 2000; Hofmann and Mountjoy 2010; Carbone and Narbonne 2014) and Spain (Vidal et al. 1994; Jensen et al. 2007).

Shallow-marine ichnofaunas reflect the activity of a community that inhabited offshore-transition and offshore areas between fair-weather and storm-wave base (see Buatois and Mángano 2011b for explanation of environmental terms). Overall these ichnofaunas tend to display a wider variety of architectural designs than their deep-marine counterparts. In fact, all the categories of architectural designs identified in the Ediacaran are represented in shallow-marine deposits. In contrast, deep-marine deposits host only four categories (simple horizontal trails, passively filled horizontal burrows, actively filled horizontal burrows, plug-shaped burrows). Oval-shaped impressions, rasping traces and horizontal burrows with horizontal to vertical branches are only known from shallow-marine environments. Shallow-marine ichnofaunas also display higher-diversity levels than their deep-water counterparts. Eleven ichnogenera (*Archaeonassa*, *Bergaueria*, *Epibaion*, *Gordia*, *Helminthoidichnites*, *Helminthopsis*, *Nenoxites*, *Palaeophycus*, *Kimberichnus*, *Torrowangea*, and *Treptichnus*) are known from shallow-marine deposits, whereas six ichnogenera (*Archaeonassa*, *Bergaueria*, *Helminthoidichnites*, *Helminthopsis*, *Palaeophycus*, and *Torrowangea*) have been recorded from deep-sea strata.

Alpha ichnodiversity is low in both settings (1–6), with maximum values reached for the shallow-marine Ediacara Member of the Rawnsley Quartzite in South Australia and the deep-marine Blueflower Formation of western Canada (Carbone and Narbonne 2014; Mángano and Buatois 2014). Whereas alpha ichnodiversity characterizes the trace-fossil richness of discrete paleoenvironmental zones (therefore reflecting the ecologic complexity of a benthic community), beta ichnodiversity may provide information about the degree of similarity between ichnofaunas formed along the depositional profile (Buatois and Mángano 2013; see Chap. 1). Trace-fossil associations from the offshore transition to the lower offshore are essentially identical. Also, the degree of differentiation of Ediacaran shallow- and deep-marine ichnofaunas is very low, with deep-marine trace-fossil assemblages essentially consisting of facies-crossing forms that are also present in shallow water. This is consistent with the recent observation by Carbone et al. (2015) that trace fossil assemblages in both deep- and shallow-marine deposits of the Mackenzie Mountains are quite similar. This situation may have persisted well into the early Paleozoic, starting to change with the gradual establishment of the complex patterns represented by graphoglyptids in the deep sea by the Ordovician (see Chap. 3). This supports a competition-based diversification model recently proposed by Hautmann (2014), in which three phases are distinguished: (1) niche overlap phase, (2) habitat contraction phase, and (3) niche differentiation phase. The former is characterized by very low competition, with the addition of new species having essentially negligible effect on the habitat width. Although ichnodiversity should not be equated with biologic diversity, available ichnologic information indicates that niche overlap was extensive during the Ediacaran.

Ichnoguild analysis shows that shallow-marine benthic communities were slightly more complex than those in deep-marine settings. In both cases, however, infaunal tiering structure is quite simple to nonexistent due to limited colonization of the infaunal ecospace. Infaunal activity was limited to the uppermost millimeters of the substrate, showing a very slight increase in penetration depth in shallow-water sediments by the end of the Ediacaran with the appearance of treptichnids (Jensen et al. 2000). Of the ichnoguilds previously analyzed, the *Helminthopsis*, *Palaeophycus*, *Torrowangea*, *Kimberichnus*, *Bergaueria*, and *Epibaion* ichnoguilds occur in shallow-marine deposits. An incipient *Treptichnus-Saerichnites* ichnoguild was added by the terminal Ediacaran. Of these, the former three occur in deep-marine settings as well, whereas the latter three seem to be exclusive of shallow-water deposits, pointing towards a slightly more complex niche partitioning of the infaunal ecospace in offshore areas, particularly by the terminal Ediacaran. The *Helminthopsis* ichnoguild was by far the dominant one in deep-marine deposits, revealing very simple feeding strategies based on matground exploitation. The *Palaeophycus* and *Torrowangea* ichnoguild, on the contrary, are uncommon. The *Bergaueria* ichnoguild is present in both shallow- and deep-marine environments, with *Bergaueria* isp. being present in the former (Grazhdankin 2014) and *Bergaueria sucta*, which records the lateral displacement of an anemone-like organism, in the latter (Seilacher et al. 2005). Because *Bergaueria sucta* is present in shallow-marine environments during the Cambrian (Hofmann et al. 2012; Mángano et al. 2013), this pattern may suggest origination in the deep sea and subsequent displacement to shallow water, which is somewhat unusual. In any case, the *Bergaueria* ichnoguild is poorly represented in the fossil record and further work is needed in order to test its presence and distribution.

Whereas ichnologic data provide information into infaunal tiering, body-fossil analysis yields insights into epifaunal tiering. The Ediacaran biota of Mistaken Point and adjacent localities (eastern Canada) displays three epifaunal tiers, a lower 0–8 cm tier (typically spindles, but in some cases dusters as well as short frondose forms), an intermediate 8–22 cm tier (including, among other forms, pectinates and various fronds) and an upper tier up to nearly 200 cm (comprising a number of tall frondose taxa, such as *Charnia wardi*), showing the establishment of an epifaunal community structure characterized by suspension feeding or osmotrophy (Clapham and Narbonne 2002; Narbonne and Gehling 2003; Clapham et al. 2003; Narbonne 2005; Laflamme et al. 2009; Ghisalberti et al. 2014).

The epifaunal tiering structure of shallow-water communities is less understood. However, tiered communities have been recognized in both southern Australia and the White Sea (Droser et al. 2006; Zakrevskaya 2014). Although the vast majority of these communities are dominated by organisms living immediately above the sediment surface (e.g., *Dickinsonia*, *Kimberella*, *Tribrachidium*), upper tiers are represented by large fronds and stalks, pointing to relatively complex epifaunal tiering structures (Droser et al. 2006;

Zakrevskaya 2014). Finally, the possibility that infaunal life habits may have been recorded by body fossils may be taken into account. It has been suggested that *Pteridinium* may represent growth within the sediment by successive addition of segments (Grazhdankin and Seilacher 2002; but see Elliott et al. 2011) and that *Rangea* may have lived infaunally as well (Grazhdankin and Seilacher 2005; but see Vickers-Rich et al. 2013 and Meyer et al. 2014b). A similar debate concerns *Ernietta*, which has been interpreted as fully infaunal (e.g., Crimes and Fedonkin 1996), semi-infaunal (e.g., Seilacher et al. 2003; Seilacher and Gishlick 2014), or epifaunal (Dzik 1999). A new reconstruction based on the recent discovery of complete specimens of *Ernietta* in a gutter cast supports a semi-infaunal mode of like (Ivantsov et al. in press). In any case, integration of trace- and body-fossil information indicates that the tiering structure of Ediacaran epifaunal communities in both deep- and shallow-water settings was much more complex than their infaunal counterparts.

## 2.7 Discussion

As it is the case of Ediacaran paleobiology, the field of Ediacaran ichnology is plagued with controversies and reinterpretations. Perhaps, the search for the earliest evidence of locomotion, bilaterian activity, bioturbation, or complex behavior may have been sometimes misguided by the infamous Mofaotyof Principle ("My Oldest Fossils Are Older Than Your Oldest Fossils"; Brasier 2009). Likely candidates for earliest evidence of locomotion are the structures described from the Mistaken Point and Fermeuse formations (Avalon assemblage) (Liu et al. 2010; Menon et al. 2013). These structures may reflect mobility by a Cnidarian-grade organism. However, as stated above, a conclusive trace-fossil origin cannot be demonstrated at this point. Further work in the eastern Newfoundland successions seems to be highly promising.

Because of the late Paleozoic age of the Uruguay trace fossil-bearing deposits (Gaucher et al. 2013; Verce and Netto 2015), the earliest convincing evidence of bilaterian activity apparently comes from the White Sea Assemblage (less than 560 Ma). The bilaterian origin of these trace fossils is particularly significant because there is still no consensus on the affinities of many Ediacaran body fossils (see review by Narbonne 2005). In fact, the very presence of animals in the Ediacaran is still a contentious issue (Budd 2013, 2015). Therefore, it is important to evaluate if the Seilacherian view of the dawn of animals in the shadow of large creatures of unknown affinities is still supported by the ichnologic record. The fact that alternative interpretations have been suggested for almost every type of Ediacaran trace fossil may provide ground for skepticism regarding the existence of Ediacaran animal trace fossils, at least before the appearance of treptichnids.

However, our review of the Ediacaran record suggests that, even adopting an extremely conservative view that favors alternative interpretations for each type of trace fossil, there is still robust evidence to make the case of Ediacaran animal trace fossils (Mángano and Buatois 2014). First, the direct association of *Kimberella* and *Kimberichnus* represents a rare case of a trace fossil in connection with its producer, providing clear evidence of a mat-scratching strategy by a bilaterian, irrespective of the precise phylogenetic affinity of *Kimberella*. A similar case can be made for the association of dickinsonids and the ichnogenus *Epibaion*, although in this case there is still no agreement on the animal nature of *Dickinsonia* and related forms (Harrington and Moore 1956; Glaessner and Wade 1966; Fedonkin 1983; Seilacher 1984, 1989, 1992; Retallack 2007; Sperling and Vinther 2010; Ivantsov 2011, 2013; Gold et al. 2015). Second, the presence of continuous sinuous trails with well-developed levees is hard to reconcile with a body-fossil origin (i.e., a carbonaceous filament), a protozoan trail or a microbially induced sedimentary structure. Third, the preservational styles of the structures associated to microbial mats as both positive or negative reliefs on the same surface is more consistent with a trace-fossil origin (Gehling 1999). Fourth, the view that *all* the simple horizontal structures identified as trails and burrows in Ediacaran rocks are not trace fossils is hard to support. Identical structures are present throughout the whole Phanerozoic and have been observed in modern sediments as well. Fifth, Fortunian deposits contain a similar suite of trace fossils preserved on matgrounds, with the addition of arthropod trackways (e.g., *Allocotichnus*, *Diplichnites*) and resting traces (e.g., *Rusophycus*) and sinusoidal trails, suggesting the persistence of Ediacaran taphonomic windows into the Phanerozoic (Buatois et al. 2014). This observation leaves proponents of the absence of animal trace fossils in the Ediacaran with two alternatives: (1) assuming that all the simple structures observed in these Fortunian matgrounds (and present in Ediacaran deposits already) are not trace fossils, whereas the scratch marks and trackways on the same surfaces are trace fossils despite the fact that both groups of structures display identical preservational style or (2) assuming that all the structures preserved on Fortunian matgrounds are trace fossils, but that identical ones (i.e., the simple structures) in Ediacaran matgrounds are not. In our view none of these alternatives seem to be parsimonious and, quite on the contrary, are ad hoc explanations.

The fact that our review indicates that the earliest convincing ichnologic evidence for animals is from rocks less than 560 Ma still leaves a 150–200 Myr gap with respect to estimates by molecular clocks (Erwin 2015). The absence of trace fossils in this critical time of the biosphere is hard to explain assuming the existence of ghostly ancestors. The most common reason invoked is that this absence is due to the small size of these presumed Ediacaran bilaterians, assuming that only the activity of large organisms capable to plow across the sea floor is reflected in the trace-fossil record (Wray 2015). This view is unsupported by ichnologic research. Microbial mats enhance preservation of fine morphologic details allowing visibility of tiny structures (Budd and Jensen 2000; Buatois and Mángano 2012a). The widespread presence of microbial mats without any evidence of trace fossils in rocks predating the terminal Ediacaran argues against a taphonomic explanation.

The earliest evidence of bioturbation is another controversial issue. Intense bioturbation has been indicated recently for the Siberian deposits (Rogov et al. 2012). However, the figured structures consist of serially repeated elements, quite reminiscent of those in problematic body fossils, commonly referred to as *Helanoichnus*, *Palaeopascichnus*, and *Shaanxilithes* (Shen et al. 2007; Meyer et al. 2012). Because of this, Brasier et al. (2013) argued against a trace-fossil origin for these structures. Moderate levels of bioturbation have been mentioned for a marine limestone of the 551–541 Ma Dengying Formation of South China, suggesting that the presence of

Ediacaran body fossils in these deposits may indicate tolerance to moderate levels of sediment disturbance (Chen et al. 2014). However, the illustrated associated structures (their Fig. 6e–g) resemble superficial to very shallow-tier grazing trails that typically produce negligible disturbance of the primary fabric and no significant exchange of nutrients between the sediment water interface and the underlying sediment. In a way, the problem here deals with the very same definition of bioturbation. Bioturbation refers to the process by which the consistency and structure of the sediment are modified by organism activity, implying various degrees of sediment mixing (Bromley 1996). In particular, Taylor and Goldring (1993) established bioturbation indexes (BI) based on the categories previously defined by Reineck (1963, 1967), adding a more precise characterization in terms of in terms of burrow density, amount of burrow overlap, and the sharpness of the original fabric (see Chap. 1). Accordingly, bioturbation indexes are specifically measured in cross-sectional views, allowing for an appreciation of the disturbance of the primary fabric. Similar schemes established for bedding planes by Miller and Smail (1997) and referred to as bedding-plane bioturbation index (BPBI) actually deal with density of biogenic structures on bedding surfaces, rather than bioturbation in strict sense. When the bioturbation indexes of Taylor and Goldring (1993) are used, it is clear that Ediacaran sediments displayed almost invariably no bioturbation (BI 0) to very locally sparse bioturbation (BI 1) (Mángano and Buatois 2014).

Another relevant point to address is the early evidence of complex behavior as recorded by trace fossils. As with the term “bioturbation,” the use of the term “complex trace fossil” has been used by some Precambrian paleobiologists in a very loose way, which precludes establishing a serious assessment of trace-fossil evolution through time. To complicate things further, the very same definition of a complex trace fossil remains somewhat unclear despite previous efforts in that direction (Miller 1998, 2002, 2003). However, some clarifications are essential to evaluate the claim of Ediacaran complex behavior from an ichnologic standpoint. One approach particularly useful regarding grazing traces is to frame ichnologic observations within the optimal foraging theory, which states that organisms are driven by a tendency to maximize net energy gained per unit of time feeding (e.g., Schoener 1987). This may help to illuminate on how organisms can potentially respond to what has been termed their “information landscape” (Plotnick et al. 2010), providing an indirect measurement of complexity. A critical evaluation of the trace-fossil record suggests that animals displaying sophisticated feeding strategies involving strophotaxis (i.e., proclivity to make U-turns so that the animal turns around 180° at intervals), phobotaxis (i.e., tendency to avoid crossing its own and other trails), or thigmotaxis (i.e., propensity to keep close contact with a former segment of the trail) were absent in the Ediacaran (Mángano and Buatois 2014). This view is quite strong given the growing consensus on the lack of evidence to ascribe a trace-fossil origin to *Yelovichnus* and *Palaeopascichnus* (Haines 2000; Seilacher et al. 2003, 2005; Jensen et al. 2006; Shen et al. 2007; Antcliffe et al. 2011).

Regarding feeding structures, systematic branching and specialized spreiten may be regarded as evidence of complex behavior. In this regard, two contenders for complex trace fossils have emerged recently. One of these candidates is the structures recorded from the Dengying Formation of China (Chen et al. 2013; Meyer et al. 2014a). The Dengying material displays unusual high density for Ediacaran assemblages showing overcrossing and intergradations among structures that provide a first impression of complexity. However, as discussed above, these structures do not actually display true branching and are in fact relatively simple on morphological and ethological grounds. A second candidate is the structures described from the Zaris Formation of the Nama Group in Namibia (MacDonald et al. 2014). However, as previously discussed, these structures are most likely not trace fossils. To conclude, critical evaluation of the available information and a more careful use of pertinent ichnologic concepts place the earliest evidence of complex behavior in the treptichnids recorded by the end of the Ediacaran (Jensen et al. 2000), certainly representing the prelude of the dramatic increase in complexity evidenced by the Cambrian explosion (see Chap. 3).

Finally, the temporal and spatial overlap between Ediacaran organisms represented by body fossils and bilaterians mostly recorded by their trace fossils may prompt the question of the type of relationship between the two, a topic that may bear implications on the disappearance of the Ediacaran biota (Laflamme et al. 2013; Buatois et al. 2014; Darroch et al. 2015; Budd and Jensen in press). Three alternative hypotheses have been proposed to explain the disappearance of the Ediacaran biota and its replacement by a Phanerozoic-style metazoan fauna, namely closing of the unique Ediacaran taphonomic window, a mass extinction of Ediacaran organisms, and biotic replacement (Laflamme et al. 2013). The persistence in the Cambrian of matgrounds (particularly in the Fortunian) showing direct evidence of bilaterian activity in the absence of members of the Ediacara biota suggests that the typical Ediacaran taphonomic window persisted well into the Phanerozoic, arguing against the taphonomic hypothesis (Buatois et al. 2014). A systematic analysis of the terminal Ediacaran assemblage present in the Farm Swartpunt succession of Namibia demonstrated that this site has significantly lower diversity than older assemblages, which provides support to the hypothesis of a more gradual disappearance instead of a catastrophic event (Darroch et al. 2015). In this scenario, the Ediacara biota was gradually affected by competition with the newly evolving bilaterians which were eventually conducive to their demise (Laflamme et al. 2013; Darroch et al. 2015).

This view has been recently challenged by Budd and Jensen (in press), who made an analogy between the Ediacaran biota playing an enabling role in bilaterian evolution with the role of the Savannah for human evolution and bipedality (their "Savannah hypothesis"). In this scenario, the mostly immobile Ediacaran organism served as sites for concentration of organic matter creating heterogeneities in an otherwise homogeneous landscape (Budd and Jensen in press). These authors adapted the whale fall analogy put forward by Mángano et al. (2012) to explain the role of carapaces as attractors in Cambrian Burgess Shale-type settings, in this case with the living and dead Ediacaran soft-bodied organisms creating sites rich in organics that may have attracted the newly evolved bilaterians. According to the Savannah hypothesis, a positive relationship was established between the Ediacaran biota and the bilaterians rather than the displacement of the former by the latter.

These two views remain to be further tested, but we note that they may not be mutually exclusive. In contrast to the extensive presence of trace fossils associated with carapaces in Cambrian Burgess Shale-type deposits (e.g., Mángano 2011; Mángano et al. 2012; Mikuláš et al. 2012; see Chap. 3), no analogous occurrences have been reported so far from the Ediacaran. The search for empirical support for the Savannah hypothesis is promising and the proposed scenario is plausible on theoretical grounds. In any case, a third view emphasizing passive coexistence of Ediacaran biotas and bilaterians without any positive or negative interactions is also a possibility, particularly given the absence of trace fossils in direct association with Ediacaran body fossils. In fact, both bilaterians and Ediacarans may have coexisted peacefully for almost 20 My. In this scenario, it is not the appearance of bilaterians per se that are responsible for the decline of the Ediacaran biota, but the onset of bilaterians capable of bioturbation. As discussed above, incipient penetration of the substrate took place by the end of the Namibian time span (e.g., Jensen et al. 2000; Jensen and Runnegar 2005) to exponentially accelerate in the early Cambrian (see Chap. 3). The rise of bioturbation is coincident with the decline of the Ediacarans (Darroch et al. 2015), suggesting that sediment disturbance may have played a major role in the disappearance of the Ediacaran biota.

## 2.8 Conclusions

Although a growing number of molecular-clock studies show a clear trend towards increased consistency with the body-fossil record, divergence times are still placed deeper back in time (i.e., Cryogenian) than strictly indicated by the fossil record. Because it is assumed that these evolutionary ghosts did not leave a record as body fossils, scrutinizing the Proterozoic record in the search for trace fossils may yield insights into the early evolution of animals. Until now, the earliest convincing evidence of bilaterian activity comes from the White Sea Assemblage (less than 560 Ma). Trace-fossil evidence is particularly significant in these Ediacaran rocks, given the absence of consensus on the affinities of many Ediacaran body fossils. A critical reevaluation of the trace-fossil record indicates reduced global ichnodiversity and ichnodisparity during the Ediacaran, with only seven categories of architectural designs present [simple horizontal trails, passively filled horizontal burrows, actively filled (massive) horizontal burrows, plug-shaped burrows, oval-shaped impressions, rasping traces, and horizontal burrows with horizontal to vertical branches], the latter restricted to the terminal Ediacaran. Benthic communities developed in direct association with microbial mats. Mat encrusters and mat stickers are represented by body fossils, whereas trace-fossil data provide information on mat scratchers (organisms rasping on the microbial mats), mat digesters (organisms able to feed from direct external digestion of the mat), mat grazers (organisms browsing through the microbial mat), and undermat miners (organisms that constructed tunnels below the mat). Shallow- and deep-marine benthic communities are distinguished based on their ichnologic record. However, limited beta ichnodiversity indicates substantial niche overlap during the Ediacaran. Bioturbation was limited, with primary fabrics pristinely preserved and showing delicate microbially induced sedimentary structures. Only by the end of the Ediacaran, the appearance of treptichnids may have contributed to a very subtle and limited disruption of the sedimentary fabric and only very locally. These branching burrow systems record the appearance of the first complex behaviors, representing the prelude of the dramatic increase in complexity that took place subsequently as a result of the Cambrian explosion.

**Acknowledgments** We are happy to have been able to interact with Dolf Seilacher, who was a huge influence for us. Discussions with Guy Narbonne have always been both fruitful and enjoyable. Sören Jensen has always been there for valuable exchanges on Ediacaran ichnofaunas. Sören Jensen is also thanked for providing the photographs for Figs. **2.14**b, c and **2.15**a, b. Jakob Vinther generously provided all photographs included in Fig. **2.12**. A large number of colleagues guided us in Ediacaran outcrops all over the world, including John Almond (South Africa, Namibia), Jim Gehling (Australia), Gerard Germs (Namibia), Sören Jensen (Spain), Alex Liu (Newfoundland), and Guy Narbonne (Australia, Newfoundland). Peter Crimes gave access to his trace fossil collection and inspired us to tackle some of the issues discussed in this chapter. Richard Jenkins and Jim Gehling showed us material from Australia. Ludvig Loewemark and Jorge Genise provided valuable comments on the controversial Nama structures. This chapter has been benefitted from careful reviews by Sören Jensen and Guy Narbonne. Financial support for this study was provided by Natural Sciences and Engineering Research Council (NSERC) Discovery Grants Discovery Grant 311726-05/08/13 awarded to Buatois.

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# Chapter 3
# The Cambrian Explosion

M. Gabriela Mángano and Luis A. Buatois

## 3.1 Introduction

The Cambrian explosion represents one of the most dramatic episodes in the history of the biosphere. Following a period during the Ediacaran when biotas were dominated by soft-bodied organisms, some of which seemingly unrelated with modern metazoans (Seilacher 1989; Narbonne 2005), the fossil record changed rapidly as revealed by the first appearance of fossilized representatives of almost all the major animal body plans in lower Cambrian rocks (Marshall 2006; Erwin et al. 2011; Erwin and Valentine 2013). During the last decades, there has been a strong interest in deciphering the evolutionary events that mark the Ediacaran–Cambrian transition. There are two opposing views on the early evolution of animals. One view considers the fossil record essentially at face value, favoring a scenario of rapid origination of modern phyla (the Cambrian explosion). On the contrary, the other view stresses the imperfect nature of the fossil record, putting forward the notion of deep Precambrian roots in metazoan evolutionary history (the "slow phylogenetic fuse") (Fortey et al. 1996; Conway Morris 2000). According to this second perspective, there is no such a thing as the Cambrian explosion and the sudden appearance of fossils near the beginning of the Phanerozoic is essentially an artifact resulting from an increase in preservability of body fossils related to the acquisition of mineralized skeletons (Fortey et al. 1996, 2004). In turn, mineralization may reflect major changes in the chemistry of the oceans (Brasier 1992; Maloof et al. 2010). More recently, an emerging third view points to the robustness of the fossil record and the Cambrian explosion, but indicates an early divergence of animal clades during the Cryogenian

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M.G. Mángano, L.A. Buatois (eds.), *The Trace-Fossil Record of Major Evolutionary Events*, Topics in Geobiology 39,
DOI 10.1007/978-94-017-9600-2_3

(850–635 Ma), suggesting a macroevolutionary lag between the initial construction of the bilaterian developmental toolkit and the first appearance in the fossil record (Erwin et al. 2011). In the latter perspective, the Cambrian explosion emerges as the product of a long history of evolution of developmental networks, and increasing ecologic interactions within the context of favorable environmental conditions near the beginning of the Phanerozoic. This view may be regarded as a refinement of the phylogenetic fuse hypothesis because it assumes a relatively long time of hidden evolution not reflected in the fossil record (Erwin 2015).

Historically two different datasets have illuminated this debate, the body-fossil record and molecular clocks. Undoubtedly the body-fossil record supports the notion that the Cambrian event of diversification is real and unparalleled in the history of life (Conway Morris 2000; Budd and Jensen 2000; Valentine 2004; Budd 2013, 2015), whereas the interpretation of molecular-clock evidence has been quite controversial (dos Reis et al. 2015; Pisani and Liu 2015). Some early studies opposed the explosion scenario, suggesting deeper divergence among animals (Wray et al. 1996; Blair and Blair Hedges 2005), but a growing number of more recent studies that have tried to take account of problems in the implementation of molecular clocks show a tendency to decrease the gap with the body-fossil record (Peterson et al. 2004, 2008). However, even this latter set of studies shows divergence times that are still hard to reconcile with the explosion scenario (Mángano and Buatois 2014; Erwin 2015; dos Reis et al. 2015; see Chap. 2).

Because trace fossils are commonly produced by soft-bodied animals, they offer a line of evidence independent of the body-fossil record to calibrate the Cambrian explosion. The underlying hypothesis here is that the appearance of new body plans must have been signaled by new ways of animal–sediment interactions. Most important, this ichnologic signal was not dependent on the taphonomic rules that may have governed the appearance of mineralized body parts. In addition, there is an approximately 20 Ma gap between the youngest exceptional preservation of Ediacaran body-fossil assemblages (549–541 Ma) and that of the Cambrian Stage 3 Burgess Shale-type assemblages (521–514 Ma) (Mángano and Buatois 2014). In contrast, the trace-fossil record across the Ediacaran–Cambrian boundary is far more continuous than the body-fossil record, providing information on a critical time of diversification and ecosystem construction across the Ediacaran–Cambrian transition. In addition, because trace fossils reflect animal–substrate interactions, they allow a better integration with sedimentologic data, resulting in finely calibrated interpretations on the associated depositional environments.

Since the seminal paper by Seilacher (1956), the ichnologic record associated with the Cambrian radiation has been explored in numerous studies, demonstrating the potential of trace fossils to illuminate hidden facets of this evolutionary event (e.g., Crimes 1987, 1992, 1994; Jensen 1997, 2003; McIlroy and Logan 1999; MacNaughton and Narbonne 1999; Buatois and Mángano 2004; Mángano and Buatois 2004, 2014; Seilacher et al. 2005; Gámez Vintaned et al. 2006; Mángano et al. 2012; Jensen et al. 2013). The aim of this chapter is to provide an updated review of the ichnologic record of the Cambrian explosion, emphasizing how trace-fossil data can provide information on the chronology of the diversification event and the associated changes at ecosystem scale.

## 3.2 The Cambrian Revolutions

Before analyzing the potential of the trace-fossil record to shed light on the Cambrian explosion, it is necessary to clarify some terminological issues because a number of related concepts have been introduced. The notion of the "Cambrian explosion" itself refers to the event by which essentially all of the readily fossilizable animal phyla occur in the fossil record for the first time (Valentine 2002; Marshall 2006; Erwin and Valentine 2013). This dramatic appearance of body fossils near the base of the Phanerozoic has been noted since Darwin's times (see Chap. 2).

More recently, some other concepts pertaining to the dramatic changes that occurred during the Cambrian have been proposed. One of these is the "Agronomic revolution," originally introduced by Seilacher and Pflüger (1994) and further developed by Seilacher (1999). This concept refers to the replacement of matground-related communities by mixground-related communities that took place during the early Cambrian. Seilacher and Pflüger (1994) made an analogy of this breakthrough with the development of agriculture and efficient plowing and its resulting effects upon soils. Given the fact that Dolf Seilacher tended to convey a significant amount of information in his highly elaborated drawings instead of using long written explanations, it is essential to look at his original illustration (Seilacher and Pflüger 1994, Fig. 2, repeated in Seilacher 1999, Fig. 1). This artistic illustration depicts an Ediacaran habitable benthic zone that was essentially restricted to the proximities of the sediment–water interface. Widespread matgrounds effectively sealed the infaunal ecospace, precluding any fluid or efficient nutrient exchange with the water column. In addition, microbial mats allowed for a number of feeding strategies and lifestyles for the benthic fauna (see Chap. 2). The Ediacaran picture sharply contrasts with that from the Cambrian, which underscores the role of penetrative bioturbation, particularly recorded by vertical burrows, such as *Arenicolites*, *Diplocraterion*, *Lingulichnus*, and *Syringomorpha*. Also in the picture are some mid-tier horizontal structures as well as shallow-tier trilobite structures; the importance of predation is highlighted by the icon of *Anomalocaris*. Animal activity within the sediment broke the seal, allowing for exchange between the water column and the infaunal space. In Cambrian sediments, microbes were abundant but mostly coated sediment grains rather than forming extensive surfaces. The vertical expansion of the habitable benthic zone was dramatic, with the opening of the infaunal ecospace.

A closely related concept is that of the "Cambrian substrate revolution", proposed by Bottjer et al. (2000) and further explored in a number of other papers (e.g., Dornbos and Bottjer 2000; Dornbos et al. 2004, 2005; Álvaro et al. 2013). It highlights the evolutionary and ecological effects of Cambrian substrate changes on benthic metazoans. Therefore, the concept of the Cambrian substrate revolution shows some overlap with that of the Agronomic revolution. Emphasis was placed on adaptations by hard body organisms, such as echinoderms and mollusks to cope with the new Phanerozoic-style substrates.

Finally, the concept of the "Cambrian information revolution" proposed by Plotnick et al. (2010) is also relevant as it adds to reveal the complexity of the Cambrian evolutionary event at the dawn of the Phanerozoic. Central to this concept is the notion of information landscape, which refers to the distribution of environmental signals that an organism can potentially respond to. The Ediacaran–Cambrian transition was characterized by an increased complexity and heterogeneity of marine environments and this must have played a major role as a driving force of further evolutionary change (Plotnick 2007; Plotnick et al. 2010). The Cambrian information revolution implies a coevolutionary increase in the information content of marine ecosystems and in the ability of animals to obtain and process this information (see also Parker 2003). Diverse and abundant mobile bilaterians with macroscopic sense organs are a signature of this evolutionary breakthrough. From an ichnologic perspective, the Cambrian information revolution is reflected by the appearance of trace fossils with complex morphologic patterns, indicating sophisticated strategies to exploit resources in a heterogeneous landscape.

In subsequent sections we will further explore how the trace-fossil record reveals these events. In addition, we will use ichnologic information to evaluate if these evolutionary events were synchronous or if, on the contrary, diachronism was involved.

## 3.3 Assessment of Ichnodiversity and Ichnodisparity

The early Cambrian (Terreneuvian and Series 2) displayed a dramatic increase in both global and alpha ichnodiversity and ichnodisparity of bioturbation structures (see Chap. 1 for discussion of these terms). Whereas a maximum of 11 ichnogenera may be present in Ediacaran strata (see Chap. 2), 42 ichnogenera have been recorded in the Fortunian (Fig. 3.1 and Table 3.1) (Mángano and Buatois 2014). The rapid increase in behavioral patterns is also displayed at the scale of ichnodisparity, with a maximum of seven categories of architectural designs in the Ediacaran (see Chap. 1) in contrast to 21 in the Fortunian (Fig. 3.2 and Table 3.2) (Mángano and Buatois 2014). Maximum alpha ichnodiversity is 28 by the end of the early Cambrian (Fig. 3.1 and Table 3.1) (Stages 3 and 4). The uniqueness of the Cambrian radiation is also evident when this evolutionary event is compared with the Great Ordovician Biodiversification Event (GOBE), which shows an increase in ichnodiversity, but roughly Cambrian levels of ichnodisparity for bioturbation structures (Buatois et al. 2016) (see Chap. 4).

Based on body-fossil faunas, three possible relationships between taxonomic diversity and morphological disparity have been identified (Foote 1993, 1997). These are (1) limited disparity with diversification unrelated to disparity; (2) a rapid disparity increase exceeding initial diversification (implying early large steps in disparity and smaller ones subsequently); and (3) concordance between disparity and diversity. In the former two cases, diversity and disparity are decoupled. Erwin (2007) summarized a number of case studies, concluding that there seems to be a

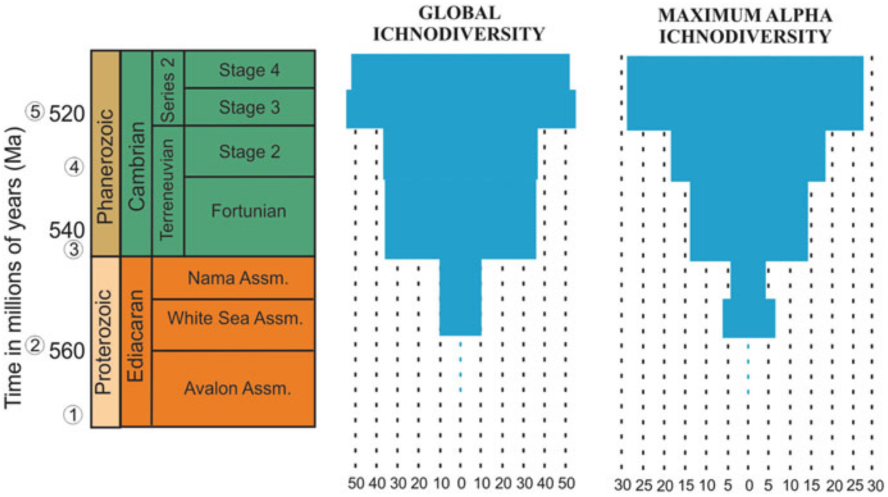

**Fig. 3.1** Summary diagram of changes in global and alpha ichnodiversity during the Ediacaran–Cambrian transition (after Mángano and Buatois 2014). 1 = appearance of the Ediacaran biota; 2 = first uncontroversial evidence of bilaterian trace fossils; 3 = major diversification of trace-fossil bauplans; 4 = onset of vertical bioturbation and coupling of benthos and plankton; 5 = earliest fossil Lagerstätte (Chengjiang) and Cambrian explosion according to body fossils. In contrast to fossil Lagerstätte, the trace-fossil record is continuous through the critical Ediacaran–Cambrian interval. Assm. = assemblage

relatively consistent pattern of more rapid increase in morphological disparity rather than taxonomic diversity early in the history of clades. More recently, Hughes et al. (2013), based on the analysis of 98 metazoan clades radiating throughout the Phanerozoic, supported the view that clades reach highest morphological disparity early in their evolution. Interestingly, the same pattern of initial rapid increase in morphological disparity is observed in the ichnologic record by comparing ichnodisparity and ichnodiversity trajectories during the Cambrian radiation and the GOBE (Buatois et al. 2016; see Chap. 4).

Typical Cambrian architectural designs reveal the appearance of new producers interacting in an innovative way with the sediment (Fig. 3.3 and Table 3.2). Trackways, scratch marks and bilaterally symmetrical, short, scratched impressions represent the earliest evidence of arthropods in the fossil record, as shown by the presence of *Rusophycus avalonensis* and *Allocotichnus dyeri* in Fortunian strata of Member 2 of the Chapel Island Formation in Newfoundland, significantly predating the FAD of trilobites (Crimes and Anderson 1985; Narbonne et al. 1987; Buatois et al. 2014). The presence of pentameral-shaped impressions, represented by *Asteriacites lumbricalis*, in Fortunian rocks of the Zhongyicun Member of the Zhijiaqing Formation, Yunnan Province, China (Luo et al. 1984; Crimes and Jiang 1986; Zhu 1997), provides early evidence for asterozoans, most likely ophiuroids. Given the uncertainties surrounding the presence of plug-shaped burrows in the Ediacaran (see Chap. 2), the occurrence of this type of structures (e.g., *Conichnus conicus*) in Fortunian strata of Member 2 of the Chapel Island Formation (Narbonne et al. 1987) and Cambrian

**Table 3.1** Quantitative summary of ichnofaunal changes across the Ediacaran–Cambrian transition

| | Ediacaran (Vendian) | Ediacaran (Nama) | Fortunian | Cambrian Stage 2 | Cambrian Stage 3 | Cambrian Stage 4 |
|---|---|---|---|---|---|---|
| Global ichnodiversity | 10 | 7 | 42 | 43 | 53 | 49 |
| Global ichnodiversity (standardized per Ma) | 1.0 | 0.8 | 3.5 | 5.4 | 7.6 | 9.8 |
| Appearance of new ichnogenera | 10 | 1 | 33 | 14 | 12 | 2 |
| Maximum alpha ichnodiversity | 6 | 4 | 14 | 18 | 28 | 28 |
| Average alpha ichnodiversity | 2.6 | 2.0 | 3.3 | 4.0 | 5.4 | 4.8 |
| Global ichnodisparity | 6 | 5 | 21 | 24 | 30 | 28 |
| Maximum local ichnodisparity | 4 | 4 | 11 | 13 | 15 | 15 |
| Maximum bioturbation index | 0 | 1 | 3 | 6 | 6 | 6 |
| Average bioturbation index | 0 | 0.1 | 0.5 | 2.3 | 2.4 | 2.3 |
| Maximum depth of bioturbation (cm) | 0.2 | 1.0 | 8 | 100 | 100 | 100 |

Only bioturbation structures are included. Degree of bioturbation based on Taylor and Goldring (1993). The Ediacaran bin has been further divided using the informal subdivision of Vendian (560–550 Ma) and Nama (550–541 Ma), proposed by Jensen et al. (2006). The oldest subdivision (Avalon; 575–560 Ma) does not contain undisputed bilaterian trace fossils and, therefore, has not been considered (see Chap. 2). This table represents actual occurrences and, therefore, there are slight differences with the curves plotted as "range-through" data presented in Chap. 16. Modified from Mángano and Buatois (2014)

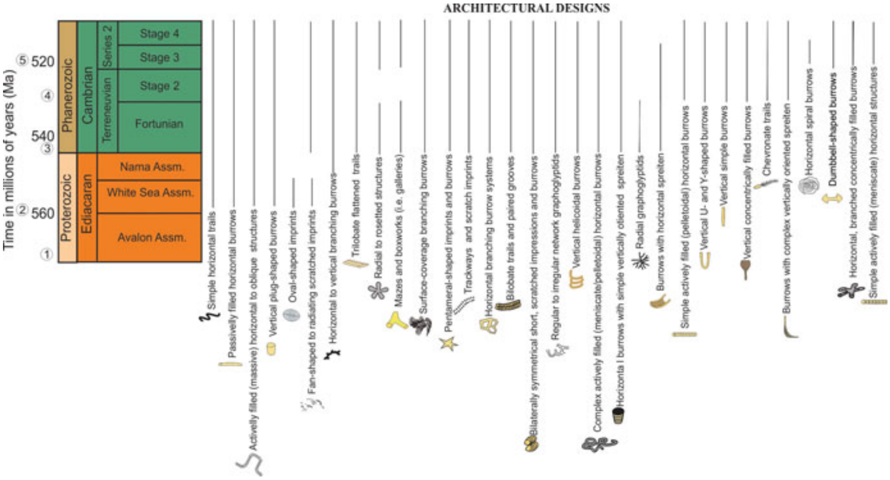

**Fig. 3.2** Summary diagram of changes in architectural designs (after Mángano and Buatois 2014). 1 = appearance of the Ediacaran biota; 2 = first uncontroversial evidence of bilaterian trace fossils; 3 = major diversification of trace-fossil bauplans; 4 = onset of vertical bioturbation and coupling of benthos and plankton; 5 = earliest fossil Lagerstätte (Chengjiang) and Cambrian explosion according to body fossils. The appearance of a wide repertoire of behavioral strategies occurred by the terminal Ediacaran and particularly the Fortunian. Assm. = assemblage

**Table 3.2** Summary of categories of architectural designs used to assess ichnodisparity of bioturbation structures, ichnogenera present in each category, ethologic and trophic information, and first appearance datum (FAD) for each ichnogenus

| Architectural designs | Behavioral and trophic interpretation | Ichnogenera | FAD |
|---|---|---|---|
| Simple horizontal trails | Grazing trails of deposit and detritus feeders (including mat grazers) | *Archaeonassa* | Ediacaran (Vendian) |
| | | *Circulichnis* | Fortunian |
| | | *Cochlichnus* | Fortunian |
| | | *Gordia* | Ediacaran (Vendian) |
| | | *Helminthoidichnites* | Ediacaran (Vendian) |
| | | *Helminthopsis* | Ediacaran (Vendian) |
| Trilobate flattened trails | Locomotion traces of active predators | *Curvolithus* | Fortunian |
| Chevronate trails | Locomotion traces of deposit feeders | *Protovirgularia* | Stage 2 |
| Bilobate trails and paired grooves | Locomotion traces of deposit and detritus feeders | *Cruziana* | Fortunian |
| | | *Didymaulichnus* | Fortunian |
| | | *Diplopodichnus* | Fortunian |
| Trackways and scratch traces | Locomotion traces of deposit and detritus feeders and feeding traces of mat grazers and detritus feeders | *Allocotichnus* | Fortunian |
| | | *Asaphoidichnus* | Fortunian |
| | | *Dimorphichnus* | Fortunian |
| | | *Diplichnites* | Fortunian |
| | | *Monomorphichnus* | Fortunian |
| | | *Petalichnus* | Stage 2 |
| | | *Protichnites* | Stage 4 |
| | | *Tasmanadia* | Fortunian |
| Bilaterally symmetrical short, scratched burrows | Resting traces of deposit and detritus feeders | *Cheiichnus* | Stage 2 |
| | | *Rusophycus* | Fortunian |
| Browsing traces | Feeding trace of mat grazers and detritus feeders | *Kimberichnus* | Ediacaran (Vendian) |
| Passively filled horizontal to oblique burrows | Dwelling burrows of suspension feeders and active predators | *Palaeophycus* | Ediacaran (Vendian) |
| Simple actively filled (massive) horizontal to oblique burrows | Feeding structures of deposit feeders | *Nenoxites* | Ediacaran (Vendian) |
| | | *Planolites* | Fortunian |
| | | *Sericichnus* | Stage 4 |
| | | *Torrowangea* | Ediacaran (Vendian) |
| Simple actively filled (meniscate) horizontal to oblique burrows | Feeding structures of deposit feeders | *Taenidium* | Stage 3 |

(continued)

**Table 3.2** (continued)

| Architectural designs | Behavioral and trophic interpretation | Ichnogenera | FAD |
|---|---|---|---|
| Simple actively filled (pelletoidal) horizontal burrows | Feeding structures of deposit feeders | *Alcyonidiopsis* | Stage 2 |
| Complex actively filled (meniscate/pelletoidal) horizontal burrows | Feeding structures of deposit feeders | *Nereites* | Fortunian |
| | | *Psammichnites* | Fortunian |
| Horizontal branching burrow systems | Feeding structures of deposit feeders (including undermat miners) | *Multina* | Fortunian |
| | | *Pilichnus* | Fortunian |
| Horizontal burrows with horizontal to vertical branches | Feeding structures of deposit and detritus feeders (including undermat miners) | *Phycodes* | Fortunian |
| | | *Saerichnites* | Fortunian |
| | | *Streptichnus* | Fortunian |
| | | *Treptichnus* | Ediacaran (Nama) |
| Surface-coverage branching burrows | Feeding structures of undermat miners | *Oldhamia* | Fortunian |
| Radial to rosetted burrows | Feeding structures of deposit feeders | *Dactyloidites* | Fortunian |
| | | *Helichone* | Fortunian |
| | | *Scotolithus* | Stage 3 |
| | | *Volkichnium* | Fortunian |
| Horizontal burrows with simple vertically oriented spreiten | Feeding structures of deposit feeders | *Halopoa* | Stage 3 |
| | | *Teichichnus* | Fortunian |
| | | *Trichophycus* | Stage 3 |
| Horizontal spiral burrows | Feeding burrows of deposit feeders | *Multilaqueichnus* | Stage 3 |
| Burrows with complex vertically oriented spreiten | Feeding burrows of deposit feeders (including feeding from epigranular bacteria) | *Syringomorpha* | Stage 2 |
| Burrows with horizontal spreiten | Feeding structures of deposit feeders | *Multilamella* | Stage 3 |
| | | *Rhizocorallium* | Fortunian |
| Burrows with helicoidal spreiten | Feeding structures of deposit feeders (other feeding strategies involved) | *Zoophycos* | Stage 3 |
| Pentameral-shaped impressions and burrows | Resting trace of passive predators or detritus feeders | *Asteriacites* | Fortunian |
| Oval-shaped impressions | Resting trace of mat digesters (among other potential feeding strategies) | *Epibaion* | Ediacaran (Vendian) |
| Dumbbell-or arrow-shaped burrows | Dwelling burrows of suspension feeders | *Bifungites* | Stage 3 |
| Plug-shaped burrows | Dwelling burrows of suspension feeders and passive predators | *Astropolichnus* | Stage 3 |
| | | *Bergaueria* | Ediacaran (Vendian) |
| | | *Conichnus* | Fortunian |
| | | *Dolopichnus* | Stage 2 |

(continued)

**Table 3.2** (continued)

| Architectural designs | Behavioral and trophic interpretation | Ichnogenera | FAD |
|---|---|---|---|
| Vertical simple burrows | Dwelling burrows of suspension feeders and passive predators | *Altichnus* | Stage 2 |
| | | *Lingulichnus* | Stage 2 |
| | | *Monocraterion* | Stage 3 |
| | | *Skolithos* | Stage 2 |
| Vertical single U- and Y-shaped burrows | Dwelling burrows of suspension feeders and passive predators | *Arenicolites* | Stage 2 |
| | | *Diplocraterion* | Stage 2 |
| Vertical helicoidal burrows | Feeding burrows of deposit feeders | *Gyrolithes* | Fortunian |
| Vertical concentrically filled burrows | Dwelling burrows of detritus feeders | *Cylindrichnus* | Stage 2 |
| | | *Rosselia* | Stage 2 |
| Horizontal, branched concentrically filled burrows | Feeding structures of detritus and deposit feeders | *Asterosoma* | Stage 3 |
| Radial graphoglyptids | Farming traces | *Dendrorhaphe* | Fortunian |
| Regular to irregular network graphoglyptids | Farming traces | *Megagrapton* | Stage 3 |
| | | *Paleodictyon* | Stage 2 |
| | | *Protopaleodictyon* | Fortunian |
| Mazes and boxwork burrows (i.e., galleries) | Feeding structures of deposit feeders | *Thalassinoides* | Fortunian |

Ethologic and trophic interpretations are based on a review of the ichnologic literature. Bacterial farming has been postulated for some post-Palaeozoic *Zoophycos*, but there is no clear evidence of this feeding strategy in the Cambrian examples. FAD follows informal Ediacaran divisions. Modified from Mángano and Buatois (2014)

Stage 3 rocks of the Upper Member of the Wood Canyon Formation in the Death Valley, USA (Mata et al. 2012) unquestionably indicates the activities of actinarians or ceriantharians, both orders characterized by a meager fossil record (although see Han et al. 2010). In addition, many of the architectural designs that occur for the first time in the early Cambrian reveal the appearance of a wide variety of worm-like organisms, whose actual phylogenetic identities are, in most cases, extremely difficult to pinpoint, but that in all probability include nematodes, phoronids, and annelids, among others. Based on fine morphologic features and fabricational design, it is now thought that the occurrence of *Treptichnus pedum* at the Ediacaran–Cambrian boundary records the activities of priapulids (Vannier et al. 2010).

Regardless of the precise taxonomic affinity of the producers, the high ichnodiversity and ichnodisparity indicate complex behavioral patterns, strikingly unknown in the Ediacaran and recording the activities of a wide biologic pool. Although horizontal burrows with horizontal to vertical branches, referred to as "treptichnids," have been recorded in the terminal Ediacaran (Jensen et al. 2000), these are still quite simple in comparison with the wide variety of more complex forms present in the early Cambrian, including the appearance of the index ichnotaxon *Treptichnus pedum* together with other *Treptichnus* ichnospecies, as well as *Phycodes*,

**Fig. 3.3** Schematic reconstructions of the main Ediacaran and early Cambrian architectural designs

*Saerichnites*, and *Streptichnus*. Increased morphologic complexity is also expressed by the appearance of horizontal branching burrow systems (e.g., *Multina*, *Pilichnus*), surface-coverage branching burrows (e.g., *Oldhamia*), radial to rosetted burrows (e.g., *Dactyloidites*), actively filled and complex meniscate burrows showing guided meandering patterns (e.g., *Psammichnites*), mazes and boxworks (e.g., *Thalassinoides*), vertical helicoidal burrows (e.g., *Gyrolithes*), burrows with horizontal (e.g., *Rhizocorallium*), vertical (e.g., *Teichichnus*) and helicoidal (*Zoophycos*) spreiten, radial (e.g., *Dendrorhaphe*) and regular to irregular network graphoglyptids (e.g., *Protopaleodictyon*, *Paleodictyon*), horizontal, branched concentrically filled burrows (e.g., *Asterosoma*), vertical simple burrows (e.g., *Skolithos*, *Lingulichnus*), vertical single U-shaped burrows (e.g., *Arenicolites*, *Diplocraterion*), and burrows with complex vertically oriented spreiten (*Syringomorpha*), among other forms. In particular, *Syringomorpha* and *Oldhamia* seem to be restricted to the Cambrian (Figs. 3.4 and 3.5) (Mángano and Buatois 2004; Herbosch and Verniers 2011; Engelhardt and Hoffmann 2012; Jensen et al. 2013).

Hendricks et al. (2014) underscored the problems of what they called "the generification of the fossil record," that is, the unjustified reification of genera in an evo-

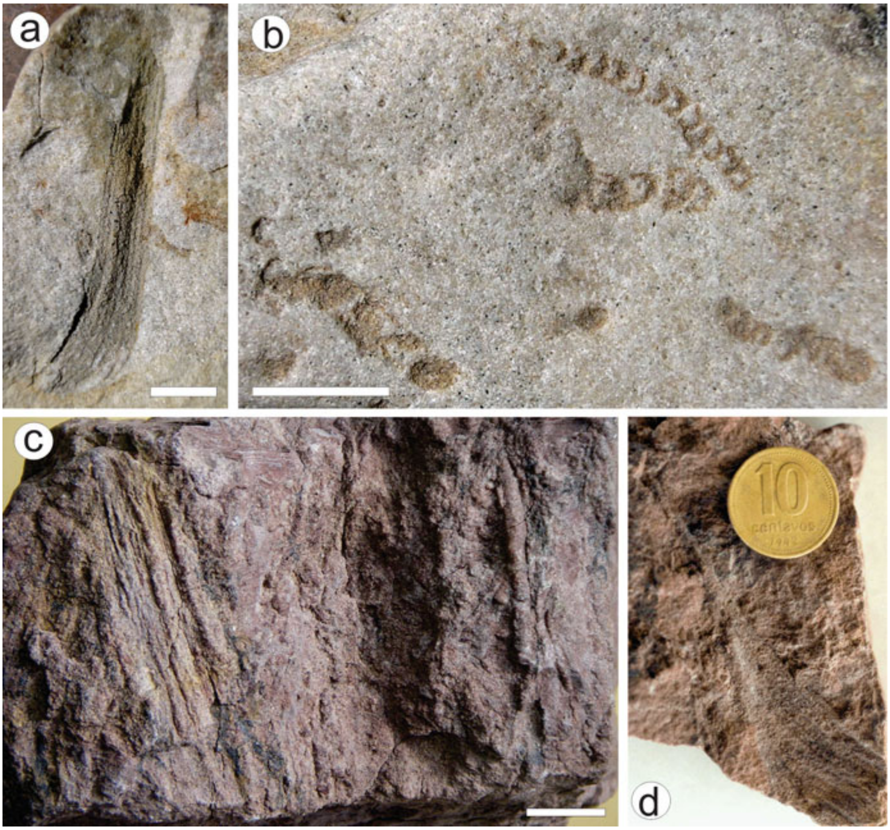

**Fig. 3.4** The Cambrian ichnogenus *Syringomorpha*. (**a**) *Syringomorpha nilssoni* in an erratic block, Kiersgoube Pastz, Berlin, Germany; identical forms are known from Cambrian Stage 2–4 strata in Scandinavia; (**b**) bedding-plane view of *Syringomorpha nilssoni* showing the horizontal expression of the spreite, erratic block, Kiersgoube Pastz, Berlin, Germany; (**c**) *Syringomorpha* isp., early to middle Cambrian Campanario Formation, Angosto del Morro de Chucalezna, northwest Argentina; (**d**) *Syringomorpha nilssoni*, early to middle Cambrian Campanario Formation, Cordón de Alfarcito, northwest Argentina. Specimens illustrated in (**a**) and (**b**) are housed in the Berlin Museum of Natural History, (**c**) is a field photograph, and the specimen in (**d**) is housed at the Miguel Lillo Institute (Tucumán). All scale bars are 1 cm, coin diameter is 1.8 cm

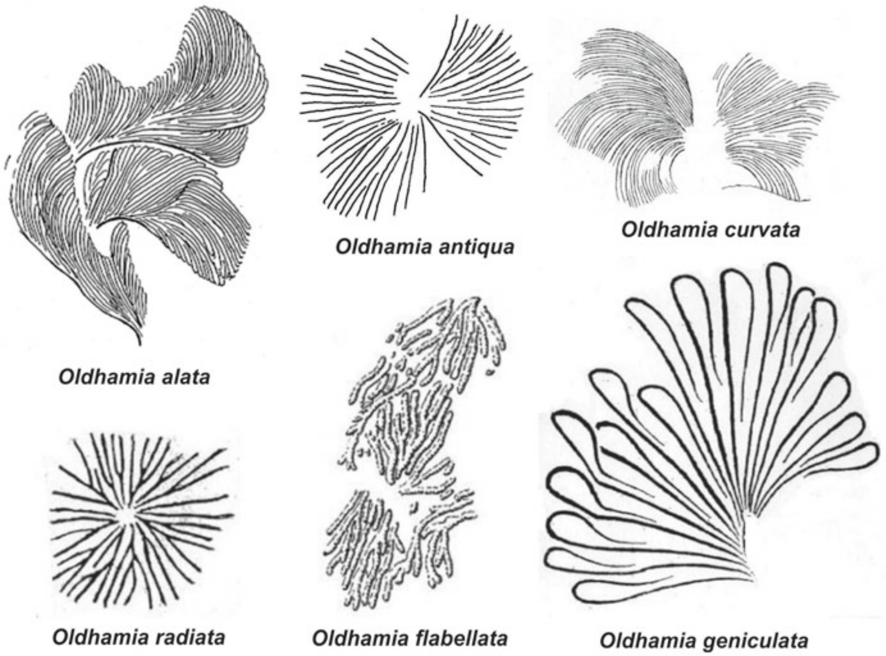

**Fig. 3.5** Behavioral variability of the ichnogenus *Oldhamia* as illustrated by its high diversity at ichnospecies level in the early Cambrian (modified from Seilacher et al. 2005)

lutionary context. Their main concern is both ontological and epistemological because of the uncritical assumption of the validity of genera as meaningful proxies for species. As a strategy to underscore ichnotaxonomic inconsistencies, ichnodiversity is usually measured at ichnogeneric level. For different reasons to those concerning the body-fossil record, ichnodiversity analysis at ichnogeneric rank may also be insufficient to reveal certain trends. Because ichnospecies reflect minor behavioral variations within broader ethologic plans recorded at ichnogeneric rank, they may be useful to detect more subtle trends in behavioral innovations, which may be overlooked if the analysis is performed at ichnogeneric rank. A large majority of lower Cambrian ichnogenera are monotaxic or comprise a few ichnospecies. Examples are *Rosselia* (only *R. socialis* is known from the lower Cambrian), *Phycodes* (*P. palmatum*), *Rhizocorallium* (*R. commune*), *Thalassinoides* (*T. horizontalis*), *Asteriacites* (*A. lumbricalis*), *Halopoa* (*H. imbricata*), *Lingulichnus* (*L. verticalis*), and *Nereites* (*N. macleayi* and *N. missouriensis*). In other cases, only the basic ichnogeneric bauplan is evident but ichnospecific assessment remains unclear (e.g., *Asterosoma*, *Conostichus*, *Paleodictyon*, *Protopaleodictyon*, *Megagrapton*, *Dendrorhaphe*, *Zoophycos*). In general, all these ichnogenera would undergo further "speciation" later in the Phanerozoic (see Chap. 9).

There are a few ichnogenera that show marked departures from this pattern. One of these is *Oldhamia*, an ichnogenus which is in fact restricted to the Cambrian (Herbosch and Verniers 2011; Jensen et al. 2013); post-Cambrian recordings should belong most likely in other ichnogenera. *Oldhamia* encompasses six ichnospecies, *O. alata*, *O. antiqua*, *O. curvata*, *O. flabellata*, *O. geniculata*, and *O. radiata*, all of them present in lower Cambrian rocks, with a few ichnospecies persisting into the middle Cambrian (Fig. 3.5) (Seilacher et al. 2005; Herbosch and Verniers 2011; Jensen et al. 2013). There is now significant evidence that *Oldhamia* is associated with microbial mats, most likely representing an undermat mining structure (Seilacher 1999; Buatois and Mángano 2003a, 2012a). Therefore, the notable diversity of morphologic plans reached by this ichnogenus by the early Cambrian may be a reflection of the combination of Ediacaran-style matgrounds with the appearance of new behavioral programs most likely genetically wired.

Another exception is *Treptichnus*, which is represented in the early Cambrian by eight ichnospecies, *T. bifurcus*, *T. coronatum*, *T. lublinensis*, *T. pedum*, *T. pollardi*, *T. rectangularis*, *T. tripleurum*, and *T. triplex* (Fig. 3.6a–f). The reasons for this unusual early high ichnodiversity at ichnospecies rank are more debatable. However, it has been noted that intergradation among some of these ichnospecies is extremely common, as evidenced by extensive collections from South Africa (Buatois et al. 2007; Almond et al. 2008) and Namibia (Wilson et al. 2012). This may reflect a high degree of behavioral plasticity coupled with a taphonomic overprint.

Trilobite resting and locomotion trace fossils also display an early diversification event at ichnospecies rank during the Cambrian (Fig. 3.7a–h). In particular, 21 ichnospecies of *Rusophycus* have been recorded in the lower Cambrian, namely *R. avalonensis*, *R. barbatus*, *R. bikanerus*, *R. bilobatus*, *R. bonnarensis*, *R. carbonarius*, *R. carinatus*, *R. cerecedensis*, *R. crebrus*, *R. didymus*, *R. dispar*, *R. eutendorfensis*, *R. jenningsi*, *R. latus*, *R. leifeirikssoni*, *R. leonensis*, *R. marginatus*, *R. parallelum*, *R. pectinatus*, *R. radwanskii*, and *R. transversensis*. In turn, 11 ichnospecies of *Cruziana* are known from the lower Cambrian, namely *C. barbata*, *C. brannae*, *C. cantabrica*, *C. fasciculata*, *C. irregularis*, *C. magna*, *C. pectinata*, *C. plicata*, *C. pormensis*, *C. problematica* (= *C. tenella*), and *C. rusoformis*. Irrespective of the fact that many *Cruziana* are gradational with related *Rusophycus* ichnospecies, this list shows the ongoing diversification of trilobites and trilobitomorphs. Even allowing for significant room for synonymies, the pattern of high ichnodiversity for *Rusophycus* and *Cruziana* at ichnospecific rank is robust. This is hardly surprising given the fact that trilobites and related clades are central components of the Cambrian Evolutionary Fauna (Sepkoski 1981).

Finally, the architectural category of plug-shaped burrows is particularly diverse in the lower Cambrian, both at ichnogeneric and ichnospecific ranks (Fig. 3.8). All the ichnogenera included in this category, *Astropolichnus*, *Bergaueria*, *Conichnus*, *Conostichus*, and *Dolopichnus*, are in fact present in the lower Cambrian, with *Astropolichnus* being actually restricted to the lower Cambrian. In addition, *Bergaueria* shows a wide variety of patterns, being represented by five ichnospecies, *B. baltica*, *B. hemisphaerica*, *B. perata*, *B. radiata*, and *B. sucta* (Pemberton et al. 1988; Seilacher 1990). Plug-shaped burrows are comparatively rare in younger rocks. The reasons for this pattern are not completely clear. It has been argued that coelenterates were very abundant in the Cambrian, but later declined most likely as a result of increased competition with more mobile animals (Crimes et al. 1977).

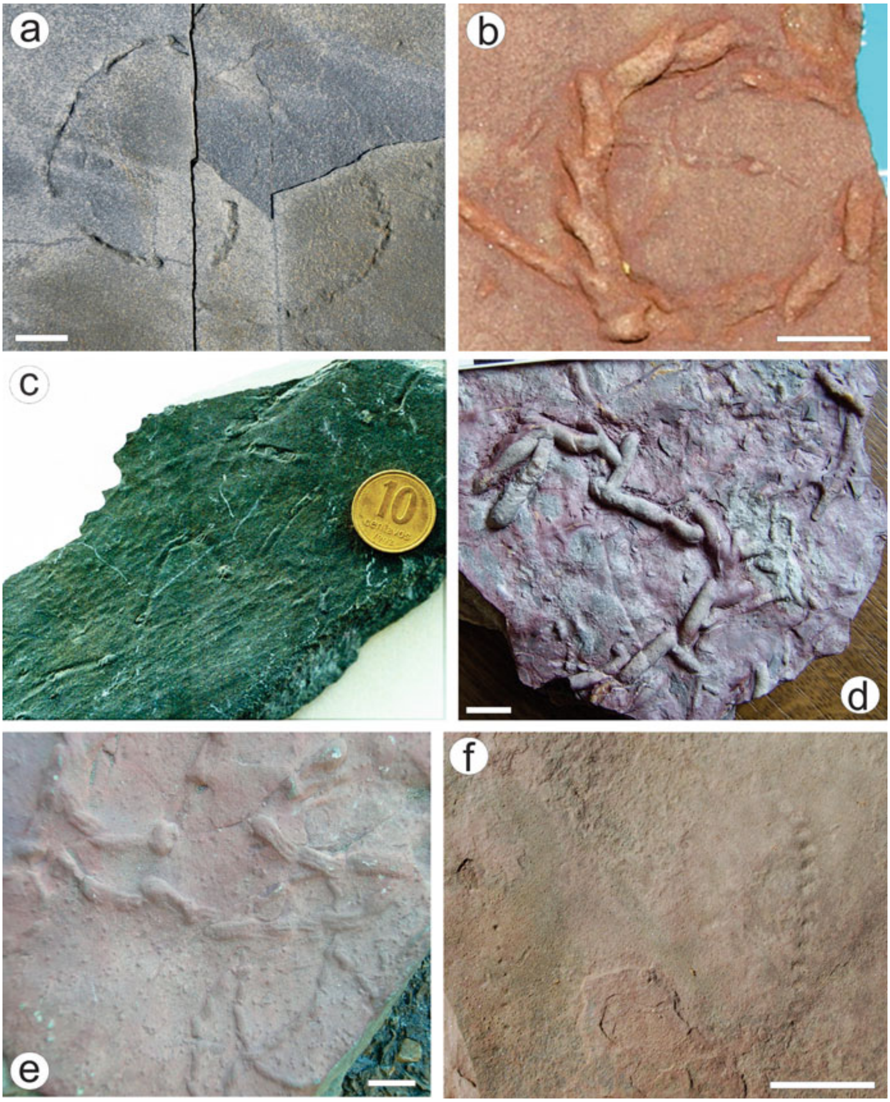

**Fig. 3.6** Behavioral variability of the ichnogenus *Treptichnus* as illustrated by its high diversity at ichnospecies level in the early Cambrian (the illustrated specimen of *T. rectangularis* is from the Furongian, but this ichnospecies is also known from the lower Cambrian). (**a**) *Treptichnus coronatum*, Member 2, Chapel Island Formation, Fortune Head, Newfoundland, field photo; (**b**) *Treptichnus pedum*, Klipbak Formation, near Brandkop, South Africa, field photo; (**c**) *Treptichnus pollardi*, Puncoviscana Formation, Quebrada del Toro, northwest Argentina, specimen housed at the Miguel Lillo Institute (Tucumán); (**d**) *Treptichnus rectangularis*, Wiśniówka Sandstone Formation, Wiśniówka Duża Quarry, Holy Cross Mountains, Poland, specimen housed at the Museum of the Faculty of Geology, University of Warsaw; (**e**) *Treptichnus tripleurum*, Dolkraals Formation, near Bloukrans Farm, South Africa, specimen housed at the South Africa Geological Survey (Cape Town); (**f**) *Treptichnus* isp. displaying a linear pattern, Nomtsas Formation, Sonntagsbrunn, Namibia, field photo. All scale bars are 1 cm, coin diameter is 1.8 cm

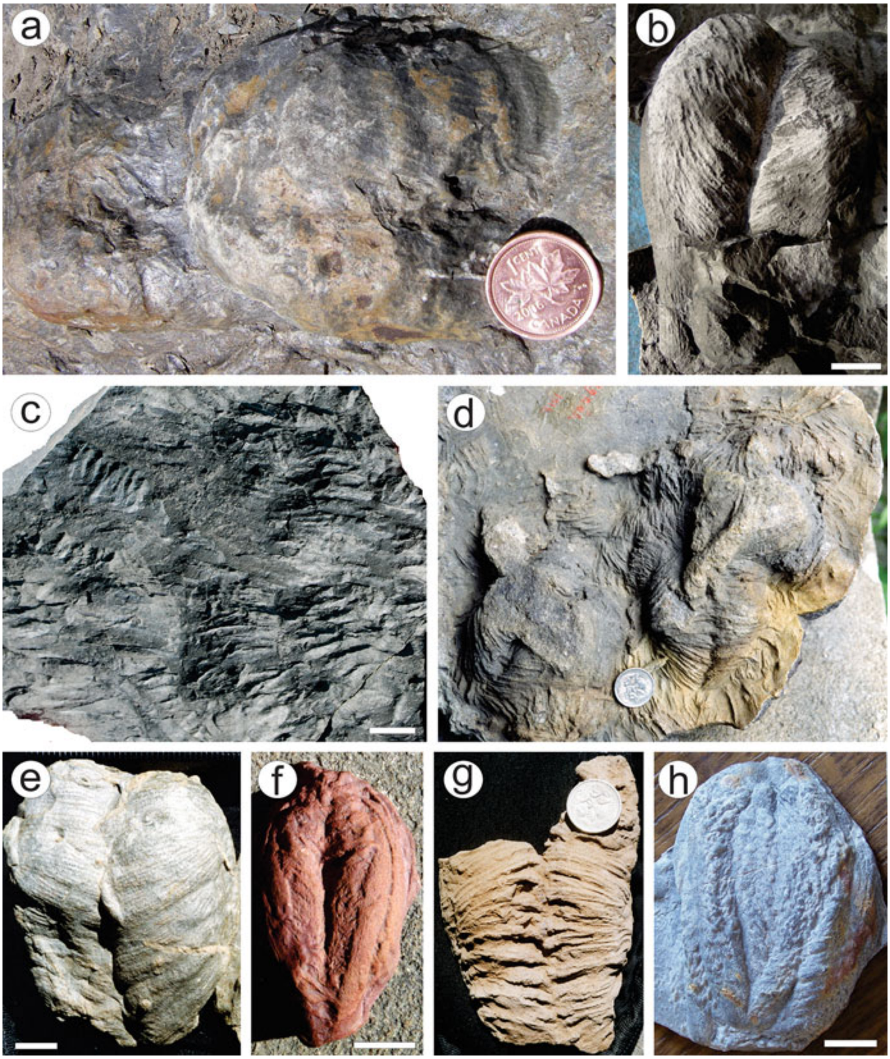

**Fig. 3.7** Examples of Cambrian trilobite-produced trace fossils. (**a**) *Rusophycus pectinatus*, Lake Louise Member, Gog Group, Lake Louise, Canadian Rockies, Cambrian Stage 3, field photo, coin diameter is 1.6 cm; (**b**) *Rusophycus jenningsi*, Gog Group, Mount Assiniboine, Canadian Rockies, Cambrian Stage 3, field photo; (**c**) *Rusophycus avalonenesis*; Chapel Island Formation, Fortune Head, Burin Peninsula, Newfoundland, Canada, Fortunian, field photo; (**d**) *Rusophycus dispar* forming clusters, Mickwitzia Sandstone, Västergötland, Sweden, Cambrian Stage 3–4, specimen housed at Geologisches Institut of Tübingen University, coin diameter is 1.9 cm; (**e**) *Cruziana fasciculata*, Member 3, Herrería Sandstone, Boñar, Spain, Cambrian Stage 2–3, specimen housed at Geologisches Institut of Tübingen University; (**f**) *Rusophycus arizonensis*, Tapeats Sandstone, Kaibab Trail, Grand Canyon, Arizona, United States, Cambrian Series 3, specimen housed at Geologisches Institut of Tübingen University; (**g**) *Cruziana salomonis*, Hanneh Member, Burj Formation, Zerka Main, Jordan, Cambrian Series 3, field photo, coin diameter is 1.9 cm; (**h**) *Rusophycus polonicus*, Wiśniówka Sandstone Formation, Wiśniówka Duża Quarry, Holy Cross Mountains, Poland, Furongian. All scale bars are 1 cm

**Fig. 3.8** High-density clusters of the plug-shaped burrow *Bergaueria* (*B. hemisphaerica*) in the lower Cambrian Moraine Lake Member of the Gog Group, Canadian Rockies, field photo (see Pemberton and Magwood 1990 for detailed descriptions of specimens in the same region)

However, as noted by Thayer (1983) burrowing anemones seem to be common elements in modern shallow-marine environments. This author suggested that this trend can be explained taphonomically by the fact that sea anemone are slow burrowers and their resting structures were most likely obliterated by more active faster burrowers, which increased in significance in younger benthos.

As noted elsewhere (e.g., Mángano and Buatois 2014), this dramatic increase in ichnodiversity and ichnodisparity at the dawn of the Phanerozoic supports the hypothesis of a real diversification event. Based on ichnologic evidence, the sudden appearance of body plans and new ways of interaction with the sediment cannot be explained simply as a taphonomic artifact related to the acquisition of mineralized skeletons. However, body-fossil information places the appearance of the main animal body plans by Cambrian Epoch 2 (Marshall 2006). In contrast, the trace-fossil record shows that the main diversification event took place by the Fortunian, allowing for a relatively short time (approximately 20 Ma) of phylogenetic fuse (Mángano and Buatois 2014; Buatois et al. 2016).

## 3.4 Sediment Mixing, Ecosystem Engineering, and the Timing of the Cambrian Revolutions

The macroevolutionary significance of ecosystem engineering, which involves modifications to the abiotic environment by species that affect resource availability for other species (Jones et al. 1997; Wright and Jones 2006), has been underscored recently for the Cambrian (Erwin 2008; Erwin and Tweedt 2012; Mángano and

Buatois 2014). There is now widespread recognition that ichnologic data are essential to understand ecosystem engineering and that bioturbation may have been the ecologic driver of further diversifications and increased nutrient recycling (e.g., Erwin and Tweedt 2012; Mángano and Buatois 2014; Boyle et al. 2014). Yet, there are still fundamental disagreements about the timing and nature of some of these changes and the different lines of evidence are apparently difficult to reconcile.

Based on a global dataset of Ediacaran–Cambrian body fossils and a more detailed compilation restricted to exceptionally preserved early Cambrian faunas of southeast China, Erwin and Tweedt (2012) classified the modes of modifying the environment by different groups of animals resulting from the Cambrian radiation. They concluded that the Cambrian explosion was associated with the onset of metazoan ecosystem engineers that for the first time in the history of the biosphere significantly affected the physical and chemical environment. Physical ecosystem engineering included structural or architectural activities (e.g., reef construction), sediment bioturbation and bulldozing, and sediment stabilization. Chemical ecosystem engineering encompassed oxygenation and ventilation of the water column or sediment, and nutrient transfer (Erwin and Tweedt 2012).

Based on information from a database comprising 369 stratigraphic units, Mángano and Buatois (2014) compiled trace-fossil data across the Ediacaran–Cambrian in order to detect if ichnodiversity and ichnodisparity trajectories were coincident with changes in ecosystem engineering and structuring. The absence of preserved soft-bodied faunas and, in fact, the overall paucity of body fossils, during the Terreneuvian is a major problem to provide an assessment of the role of ecosystem engineering macroevolutionary novelties and innovations at the dawn of the Phanerozoic. Fortunately, the ichnologic record helps to bridge this gap, providing finely tuned information on animal–substrate interactions. These authors noted that the Fortunian diversification event expressed by the appearance of a wide variety of trace-fossil morphologies (Fig. 3.9) was decoupled from the major shift in benthic ecologic structure that took place later during Cambrian Age 2, and is referred to as the Agronomic revolution (Seilacher 1999).

The Fortunian diversification event marks the establishment of novel ways of interacting with the sediment resulting from the appearance of distinctive body plans and a wide repertoire of behavioral strategies, as evidenced by the high ichnodiversity and ichnodisparity levels. Sediment bulldozing in diffusion-dominated benthic systems (Mermillod-Blondin and Rosenberg 2006), such as reworking of fine-grained offshore deposits, was characteristic of this phase of ecosystem engineering (Mángano and Buatois 2014). Diffusion-dominated benthic systems are characterized by fine-grained sediments and low hydrological connections between bottom and interstitial waters (Mermillod-Blondin and Rosenberg 2006). Bedding planes totally covered by trace fossils occur for the first time in the Fortunian (Fig. 3.10a–c) (Crimes and Anderson 1985; Narbonne et al. 1987). Biogenic reworking must have contributed to significant changes in both the sediment and the water column. These may have included increase in seawater sulfate concentration, promotion of water fluxes at the sediment–water interface, release of nitrogen from the sediment, average deepening of the redox discontinuity surface, increase in the

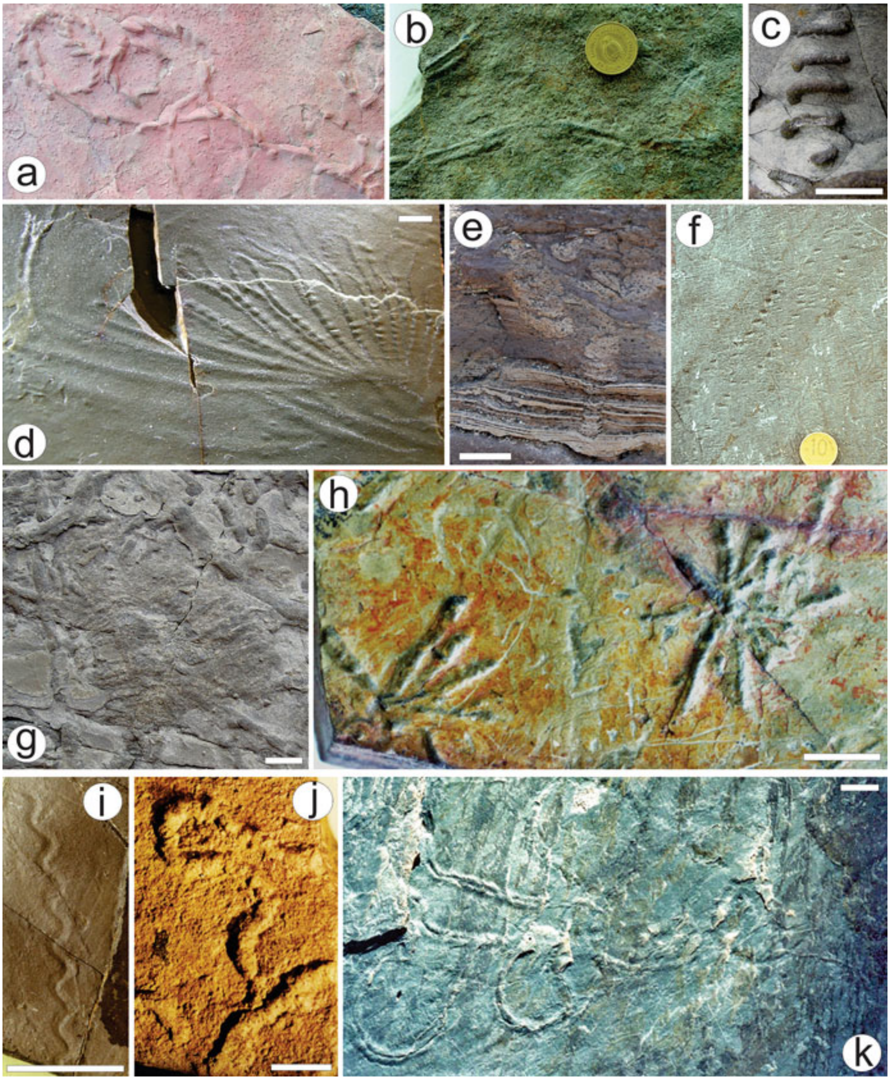

**Fig. 3.9** Representative Fortunian trace fossils. Note the wide variety of architectural designs and the overwhelming dominance of horizontal shallow-tier trace fossils. All are bedding-plane views with the exception of (**c**) and (**e**). (**a**) Horizontal to oblique branching burrows (*Treptichnus pedum* intergradational with *T. tripleurum*), Dolkraals Formation, near Bloukrans Farm, South Africa, specimen housed at the South Africa Geological Survey (Cape Town); (**b**) Bilobate trails and paired grooves (*Didymaulichnus lyelli*), Puncoviscana Formation, near the city of Salta, northwest Argentina, specimen housed at the Miguel Lillo Institute (Tucumán), coin diameter is 1.8 cm; (**c**) Vertical helicoidal burrows (*Gyrolithes* isp.), Chapel Island Formation, Fortune Head, Burin Peninsula, Newfoundland, Canada, field photo; (**d**) Surface-coverage branching burrows (*Oldhamia geniculata*), Puncoviscana Formation, Los Chorrillos, Quebrada del Toro, northwest Argentina, specimen housed at the Museo Egidio Feruglio (Trelew); (**e**) Burrows with vertical spreiten (*Teichichnus rectus*), Chapel Island Formation, Fortune Head, Burin Peninsula, Newfoundland,

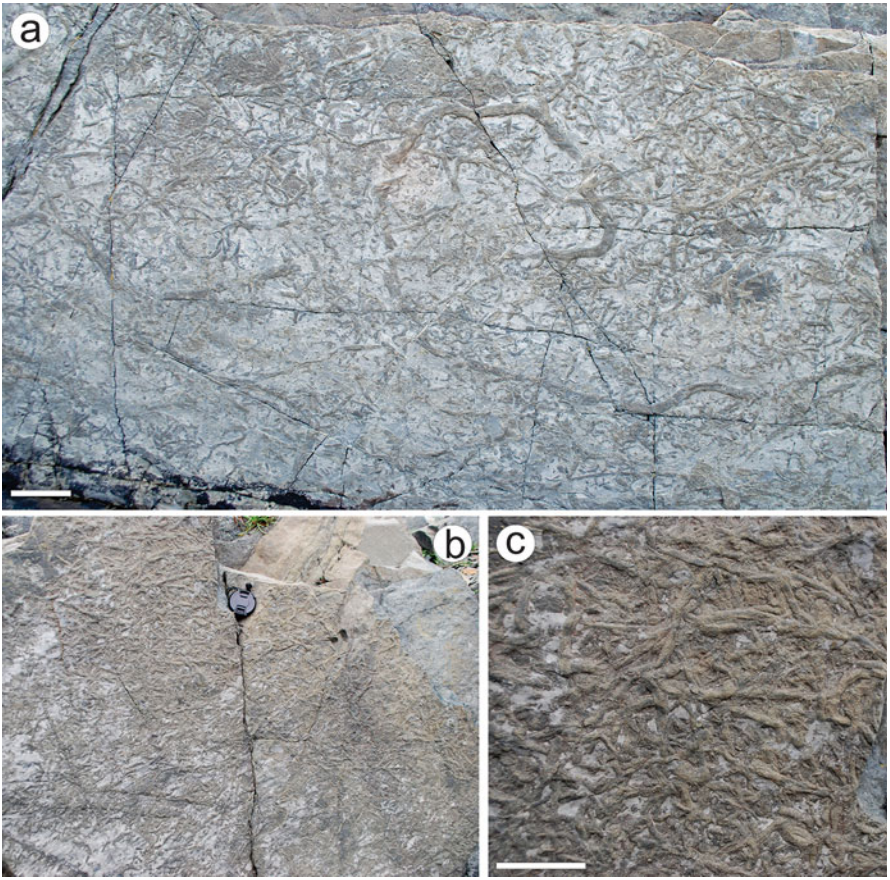

**Fig. 3.10** Bed soles covered by trace fossils in the Grand Banks section of the Chapel Island Formation, Burin Peninsula, Newfoundland, field photos. (**a**) General view showing a high density of small to medium-sized burrows overprinted by a large trail (most likely a preservational variant of *Psammichnites*); (**b**) General view of another surface showing high density of shallow-tier burrows; (**c**) Close-up of (**b**) showing intense burrow overlap; the extent of burrow overlap complicates distinction of discrete trace fossils, but branching seems to be apparent in some specimens, suggesting affinities with *Phycodes*. All scale bars are 1 cm; lens cap diameter is 5.5 cm

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**Fig. 3.9** (continued) Canada, field photo; (**f**) Trackways (*Tasmanadia cachii*), Puncoviscana Formation, Cachi, northwest Argentina, specimen housed at the Miguel Lillo Institute (Tucumán); (**g**) Bilaterally symmetrical short, shallow to deep scratched impressions (*Rusophycus avalonenesis*), Chapel Island Formation, Fortune Head, Burin Peninsula, Newfoundland, Canada, field photo; (**h**) Radial branching structures (*Volkichnium volki*), Puncoviscana Formation, Cachi, northwest Argentina, specimen housed at the Miguel Lillo Institute (Tucumán); (**i**) Simple horizontal trails (*Cochlichnus anguineus*), Puncoviscana Formation, Cuesta Muñano, northwest Argentina, specimen housed at the Miguel Lillo Institute (Tucumán); (**j**) Actively filled (massive) horizontal burrows (*Torrowangea rosei*), Lintiss Vale Formation, Barrier Ranges, southern Australia, Australian Museum (Sydney); (**k**) Actively filled (complex meniscate) horizontal burrows (*Psammichnites saltensis*), Puncoviscana Formation, Cachi, northwest Argentina, field photo. All scale bars are 1 cm sediment–water flux of iron and manganese, increase of the overall biomass of organisms, expansion of aerobic bacteria, increase in the rate of organic matter decomposition, and promoting regeneration of nutrients (McIlroy and Logan 1999; Butterfield 2001; Mermillod-Blondin and Rosenberg 2006; Canfield and Farquhar 2009; Brasier et al. 2011). This is consistent with recent work involving the connections between bioturbation and oxygen and phosphorous cycles (Boyle et al. 2014).

Interestingly, this evolutionary breakthrough in the way animals interacted with the sediment may have coexisted with the exploitation of matgrounds, probably as a result of the low levels of bioturbation and the restriction of most trace fossils to lithological interfaces (Buatois et al. 2014). Recent studies in the type section of the basal Cambrian in Fortune Head, Newfoundland, Canada, have documented widespread microbially induced sedimentary structures associated with trace fossils, showing that Ediacaran-style matground-based ecology persisted well into the Fortunian (Figs. 3.11 and 3.12) (Buatois et al. 2014). Similar interactions between animals and matgrounds have been recorded in roughly coeval deposits in China (Dornbos et al. 2004) and Argentina (Buatois and Mángano 2012a) (Fig. 3.13a–d). This is consistent with the presence in this succession and elsewhere in the Cambrian of biogenic structures indicative of a widespread development of relatively firm substrates near or at the sediment–water interface, the virtual absence of a mixed layer, and the presence of benthic faunas adapted to firmgrounds (Droser et al. 2002a, b, 2004; Dornbos et al. 2004; Jensen et al. 2005; Dornbos 2006; Mángano et al. 2013; Kloss et al. 2015). Ichnologic features indicative of firm substrates are the presence of open burrows in mudstone without any wall reinforcement, presence of bioglyphs and scratch trace fossils, unusually high quality of preservation (particularly of minute structures), preservational bias towards very shallow-tier structures, and absence of well-developed mottled textures (Droser et al. 2002a, b, 2004; Dornbos et al. 2004; Jensen et al. 2005; Mángano et al. 2013). Body-fossil evidence includes presence of helicoplacoid echinoderms living as sediment stickers and edrioasteroids living unattached on the seafloor (Bottjer et al. 2000; Dornbos 2006; Kloss et al. 2015).

The second event in ecosystem engineering took place by Cambrian Age 2, and involves an evolutionary breakthrough in ecologic structuring (Mángano and Buatois 2014). The ichnologic signature of this event was the appearance of deep-tier suspension feeders, revealing bioturbation in advection-dominated benthic systems (Mermillod-Blondin and Rosenberg 2006), as clearly illustrated by the *Skolithos* piperock in sandstone (Fig. 3.14a–h). These vertical burrows are typically attributed to lophophorate phoronids and tentacular-crowned polychaetes (Desjardins et al. 2010). Advection-dominated benthic systems are characterized by coarse-grained sediment and strong hydrological connections between bottom and interstitial water (Mermillod-Blondin and Rosenberg 2006). The establishment of suspension-feeding infaunal communities, in addition to the presence of more complex tiering structure consisting of multiple ichnoguilds, suggests plankton closely coupled to benthos (Butterfield 1997, 2001). The diversification of filter-feeding mesozooplankton was responsible for repacking unicellular phytoplankton as nutrient-rich particles more than one order of magnitude larger, therefore triggering a remarkable increase in the

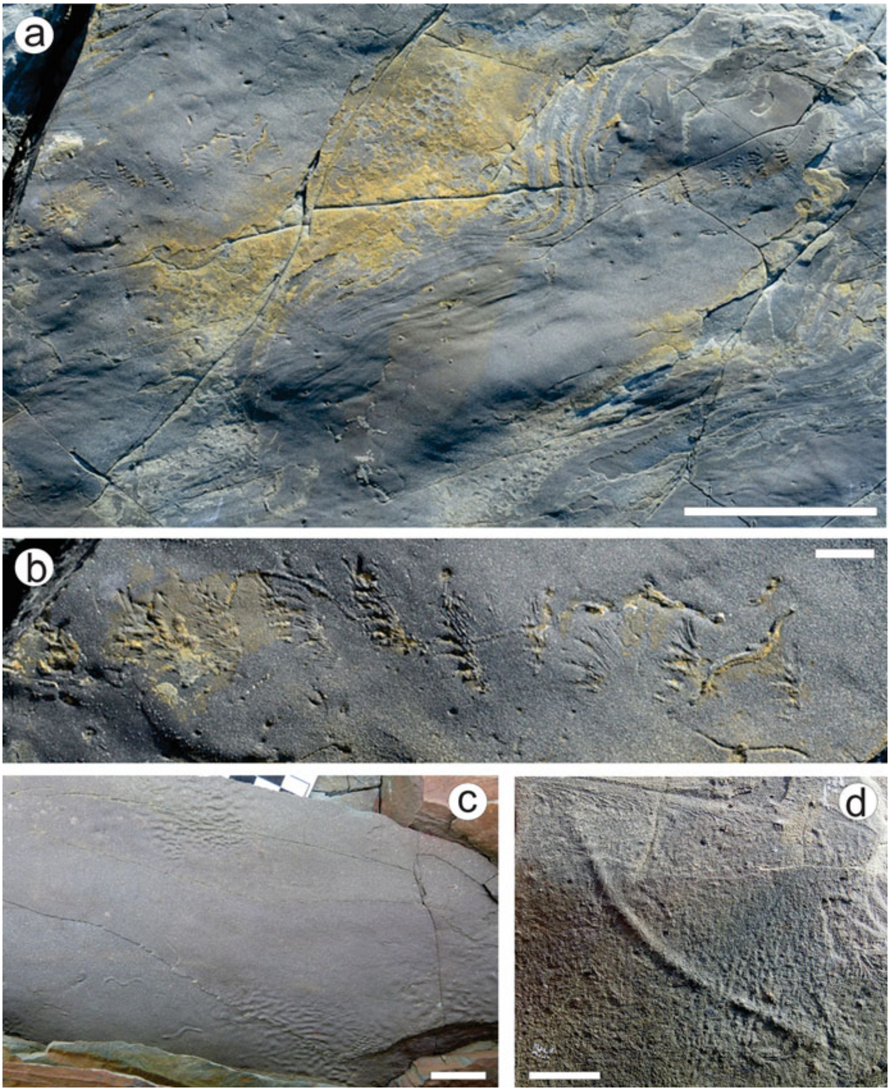

**Fig. 3.11** Trace fossils and microbial mats in the Fortune Head section of the Chapel Island Formation, Burin Peninsula, Newfoundland, field photos. (**a**) Microbially stabilized surface covered with *Allocotichnus dyeri*, scale bar is 10 cm; (**b**) Close-up of *Allocotichnus dyeri*, scale bar is 1 cm; (**c**) Patches of wrinkle marks and *Cochlichnus anguineus*, scale bar is 2 cm; (**d**) Close-up of *Helminthoidichnites tenuis* associated with wrinkle marks, scale bar is 1 cm. For details see Buatois et al. (2014)

delivery of organics into the sediment and providing a concentrated food resource for the benthos (Butterfield 2001, 2009a). In addition, as indicated by evidence from marine benthic ecology, suspension-feeding communities may have been able to play a major role in nutrient cycling, including regeneration of nitrogen and phosphorous

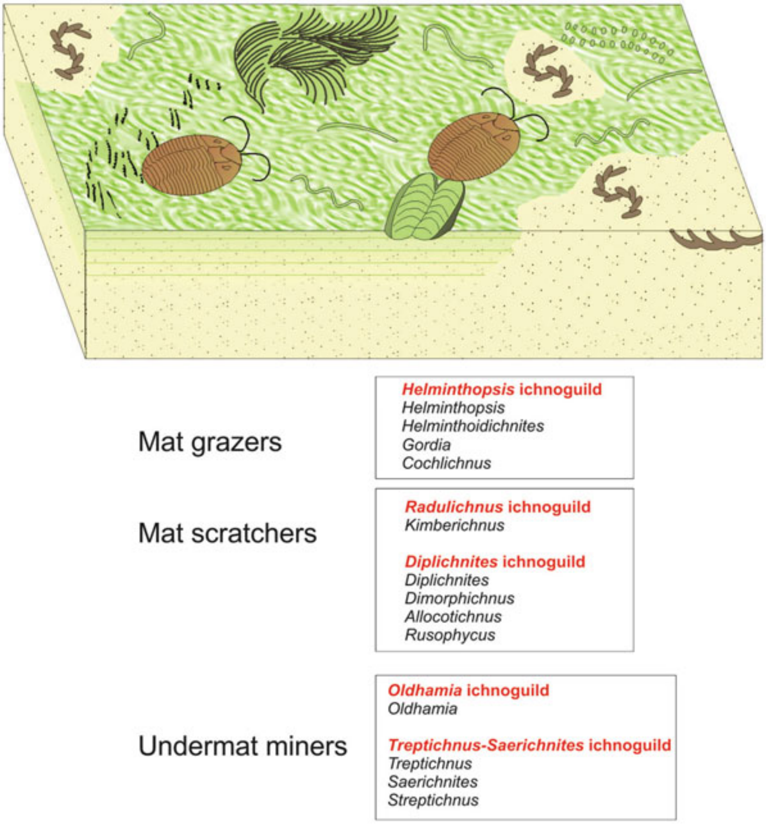

**Fig. 3.12** Categories of Fortunian animal–matground interactions (modified from Buatois et al. 2014)

to the water column (Dame et al. 2001; Newell et al. 2005; Boyle et al. 2014). Because Cambrian Age 2 witnessed an exponential increase in the intensity and depth of bioturbation, irrigation levels may have increased, resulting in a further deepening of the redox discontinuity surface (Fig. 3.15) (Mángano and Buatois 2014). In addition, the establishment of suspension-feeder communities in shallow-marine settings may have triggered a dramatic increase in ocean ventilation, filtering large volumes of water, preventing eutrophication and reducing water turbidity, therefore making light available for microphytobenthos (Hily 1991; Dame et al. 2001; Newell et al. 2005; Butterfield 2009b). This evolutionary event is coincident with the rise to modern levels of ocean oxygenation (Chen et al. 2015). In turn, capture of organic particles by infaunal suspension feeders may have promoted diversification of deposit feeders by increasing the content of organic matter through biodeposition (Hily 1991). Accordingly, suspension feeders may have been ecological drivers of a subsequent diversification phase that took place during Cambrian Age 3, providing an example of ecological spillover (Fig. 3.15) (Mángano and Buatois 2014).

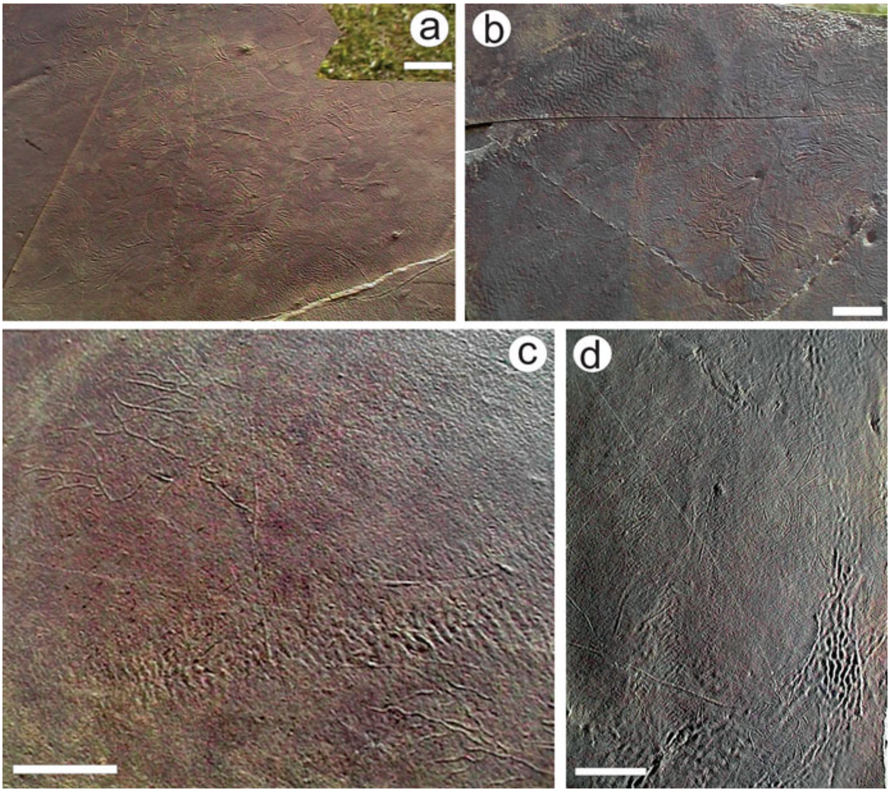

**Fig. 3.13** Trace fossils and microbial mats in the Puncoviscana Formation of northwest Argentina. All photos from El Mollar trace-fossil locality, Quebrada del Toro. (**a**, **b**) Several specimens of *Oldhamia alata* on corrugated surfaces showing evidence of microbial mats. (**c**, **d**) *Pilichnus* cf. *dichotomus* on a matground, note corrugations on the surface. All scale bars are 1 cm. Specimens housed in the Museo Egidio Feruglio (Trelew). For detailed information on this ichnofauna, see Buatois and Mángano (2012b)

By Cambrian Ages 3 and 4, there is significant body-fossil evidence of a dramatic increase in the complexity of food webs (e.g., Vannier and Chen 2002, 2005; Vannier et al. 2007; Vannier 2007, 2012; Dunne et al. 2008; Williams et al. 2015), further supporting the view emerging from the trace-fossil record (see also Mángano and Buatois 2004). Models of Cambrian food webs suggest that the key principles regulating present-day ecosystem functioning were in place by Cambrian Epoch 2. Ecological categories include primary production by phytoplankton (e.g., acritarchs), primary zooplanktonic consumers (e.g., crustaceans), secondary planktonic and nektonic consumers (e.g., chaetognaths, protoconodont animals), suspension feeders (e.g., sponges), detritivores and scavengers (e.g., worms, arthropods), and benthic-nektobenthic primary consumers (e.g., priapulids, anomalocarids, arthropods) (Vannier 2007; Vannier et al. 2007).

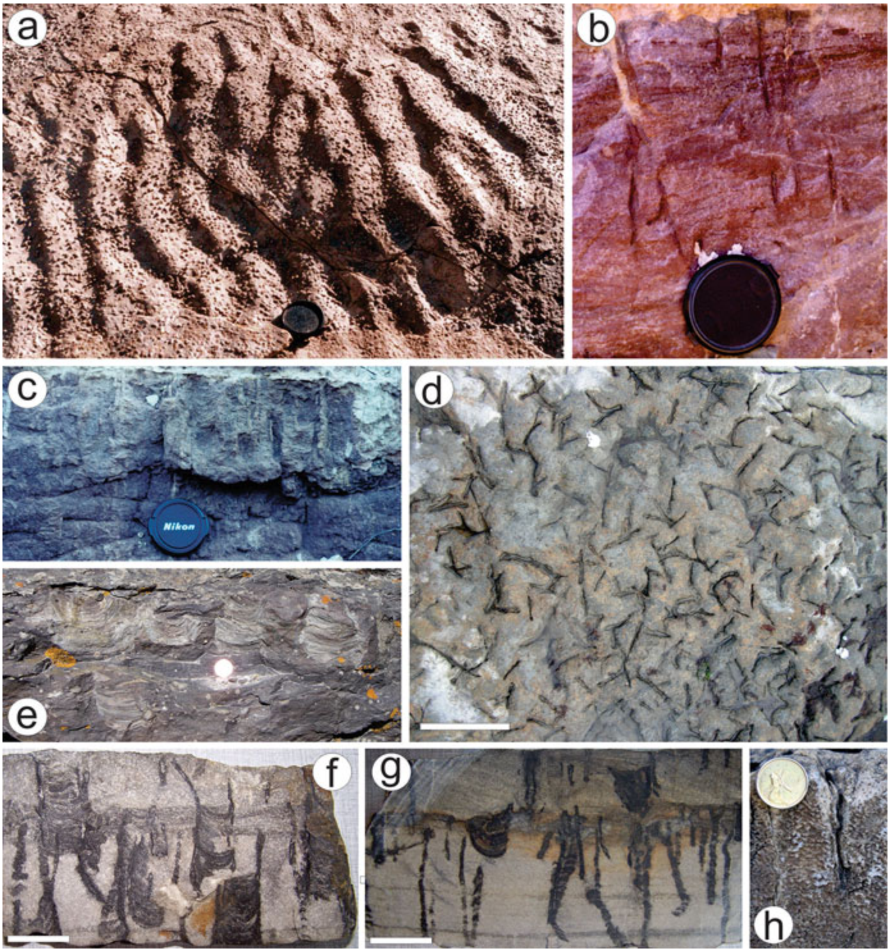

**Fig. 3.14** Representative vertical burrows typifying the second phase of ecologic changes. (**a**) Bedding-plane view of *Skolithos linearis* on a rippled surface, Campanario Formation, Angosto de Perchel, northwestern Argentina, Cambrian Series 2–3, field photo, lens cap diameter is 5.5 cm; (**b**) *Arenicolites* isp., Campanario Formation, Angosto de Perchel, northwestern Argentina, Cambrian Series 2–3, field photo, lens cap diameter is 5.5 cm; (**c**) *Diplocraterion parallelum* in cross-sectional view, Parachilna Formation, Flinders Ranges, southern Australia, Cambrian Stage 2, field photo, lens cap diameter is 5.5 cm; (**d**) High density of *Diplocraterion parallelum* in bedding-plane view, Balka Sandstone, Bornholm, Denmark, Cambrian Stages 2–3, field photo, scale bar is 10 cm; (**e**) *Diplocraterion parallelum* in cross-sectional view, Lake Louise Member, Gog Group, Lake Louise, Canadian Rockies, Cambrian Stage 3, field photo, coin diameter is 2.5 cm; (**f**, **g**) *Diplocraterion parallelum* in cross-sectional view, Dividalen Group, Imobekken, northern Norway, Cambrian Stages 2–3, scales bars are 5 cm; (**h**) *Rosselia* isp. St. Piran Formation, Gog Group, Lake Magot, Canadian Rockies, Cambrian Stages 3–4, field photo, coin diameter is 2.3 cm

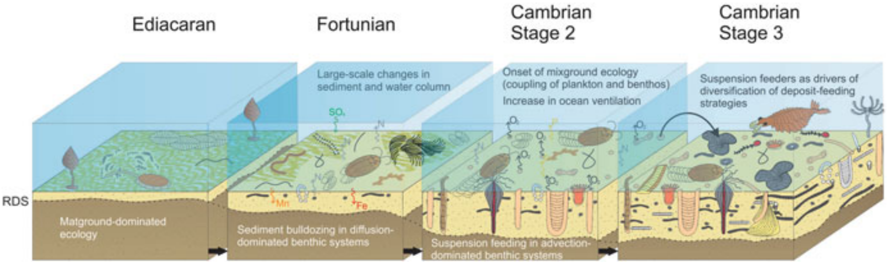

**Fig. 3.15** Evolutionary changes in benthic faunas and ecosystem engineering through the Ediacaran–Cambrian transition. Note deepening of the redox discontinuity surface (RDS) and complex feedback loops

A different view has been put forward recently by Tarhan and Droser (2014) and Tarhan et al. (2015), who suggested that sediment mixing was suppressed at a global scale across early and middle Cambrian marine environments and limited until the late Silurian. Their conclusion was based on the analysis of heterolithic facies in selected stratigraphic intervals measured in 22 units spanning the lower Cambrian to the upper Silurian (nine for the whole lower to middle Cambrian). In particular, Tarhan and Droser (2014) noted that lower to middle Cambrian deposits were characterized by preservation of mm- to cm-scale well-defined layers, overall low intensities of bioturbation, shallow-tier bioturbation (all observed lower and middle Cambrian burrows were less than 3 cm deep), dominance of trace fossils preserved along lithologic interfaces, well-preserved trace fossils having well-developed bioglyphs, and delicate preservation of superficial physical structures. According to this scenario, the increased infaunalization that characterized the early Cambrian did not result in sediment mixing, despite the appearance of a wide variety of types in animal–substrate interactions and the appearance and diversification during this time span of organisms that are thought to be capable of efficient sediment reworking (e.g., trilobites).

Although shallow-tier trace fossils were undoubtedly dominant in heterolithic facies during the early to middle Cambrian, maximum burrow depths were higher than 3 cm if ichnologic information is compiled at a global scale (e.g., Mángano and Buatois 2014). Bioturbation depths of 8 cm have been recorded in Fortunian tempestites (Buatois and Mángano 2004, 2012a). Burrows almost 10 cm deep are known in deltaic heterolithics from Stages 2 and 3 (Loughlin and Hillier 2010). Middle Cambrian tidal heterolithics contain burrows up to 27 cm deep (Hofmann et al. 2012; Mángano et al. 2013). If nearshore sandstone is considered, increase in burrowing depth is exponential with *Skolithos* reaching 1 m (Fig. 3.16) (Hallam and Swett 1966; Davies et al. 2009; Mángano and Buatois 2014). It has long been noted that dwelling burrows, such as *Skolithos*, do not significantly mix sediment because they are permanent structures (Thayer 1983; Tarhan and Droser 2014). However, as discussed above, this view overlooks the significance of the suspension-feeding infauna in nutrient cycling to the water column. In addition, the vertical burrow *Rosselia*, which is present in relatively high-energy lower Cambrian sands (e.g., Desjardins et al. 2010), records the activity of detritus feeders that further contributed to add organics into the sediment and to promote nutrient recycling.

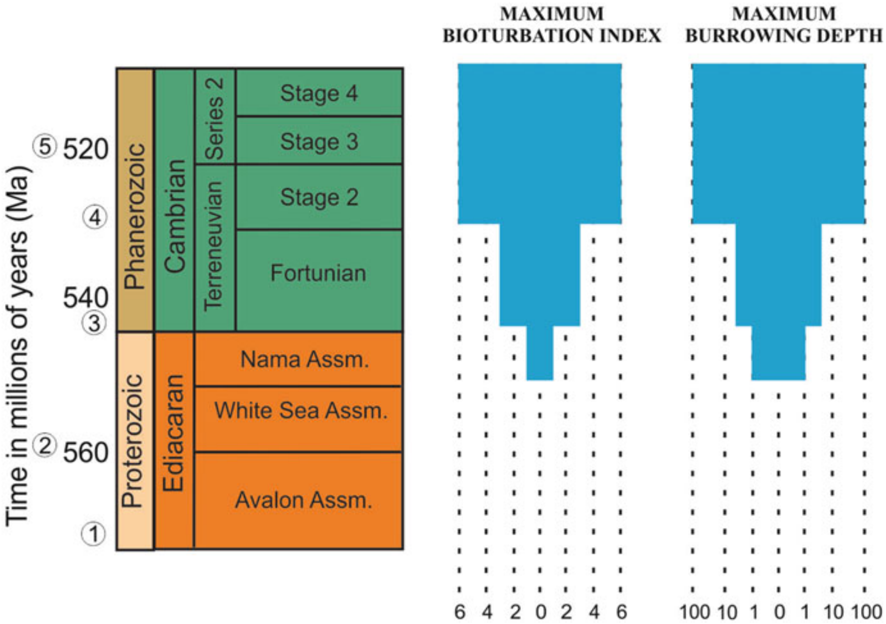

**Fig. 3.16** Summary diagram of changes in average degree of bioturbation, maximum degree of bioturbation, and maximum burrowing depth during the Ediacaran–Cambrian transition (after Mángano and Buatois 2014). Maximum burrowing depth is expressed in a logarithmic scale. Biotubation index is based on the scheme by Taylor and Goldring (1993). 1 = appearance of the Ediacaran biota; 2 = first uncontroversial evidence of bilaterian trace fossils; 3 = major diversification of trace-fossil bauplans; 4 = onset of vertical bioturbation and coupling of benthos and plankton; 5 = earliest fossil Lagerstätte (Chengjiang) and Cambrian explosion according to body fossils. The establishment of a modern ecologic structure took place during Cambrian Age 2. This ecologic structure was characterized by the appearance of a suspension-feeder infauna, an increased complexity of the food route, and trophic web and a reorganization of the infaunal ecospace, resulting in a dramatic increase in depth and degree of bioturbation. Assm. = assemblage

Extreme caution should be exercised in global extrapolation from a limited number of cases, particularly if depositional setting is not critically evaluated. Heterolithic facies encompass a wide variety of environmental settings, such as offshore, prodelta, estuary basin, and tidal flats, which display remarkable different depth and intensity of bioturbation even in modern environments. For example, global values of bioturbation for the Upper Ordovician are calculated based on one example, the Juaniata Formation (Tarhan et al. 2015), whose depositional environment is most likely marginal marine and not open marine (Davies et al. 2010). Colonization of marginal-marine, brackish-water settings has lagged well behind that of fully marine environments and limited sediment mixing by bioturbators in these setting has long been noted (Buatois et al. 2005; see Chap. 5).

Another problem with the hypothesis of suppressed global sediment mixing is the underlying assumption that the absence of a well-developed mixed layer implies no sediment mixing and limited sediment ventilation at a global scale. Relatively deeply penetrating bioturbation is evidenced by the establishment of infaunal communities displaying tiering patterns that, albeit simple and limited (e.g., Mángano et al. 2013), reflect incipient colonization of the infaunal ecospace that resulted in sediment mixing by the early Cambrian. In addition, there is growing evidence that infaunalization may have been diachronous (Mángano and Buatois 2011; see Chap. 4), which suggests that firmground conditions may have persisted in some areas with the mixed layer already established in others. For example, burrow mottling of Phanerozoic aspect has been recorded as early as Cambrian Stage 2 (Fig. 3.17) (Goldring and Jensen 1996). In addition, a scenario of sediment mixing is more consistent with available information on the complexity of trophic webs (e.g., Vannier 2007, 2012; Dunne et al. 2008), which is difficult to reconcile with globally delayed sediment mixing.

The major ecosystem changes previously discussed can be framed within the perspective that differentiates between novelties and innovations in evolutionary biology, as recently emphasized in a number of studies (Erwin and Krakauer 2004; Erwin 2012). These studies draw an analogy between novelty and innovation in evolutionary biology, and invention and innovation in technology. Whereas invention is the creation of something new, innovation refers to a successful development of an invention. Evolutionary novelties do not necessarily become ecologically significant (Erwin 2012). However, some novelties may result in innovations that may drive ecologic transformation. The appearance of coelomate animals during the Ediacaran–Cambrian transition represented an evolutionary novelty that was conducive later during the early Cambrian to an evolutionary innovation recorded by the ecosystem-scale changes resulting from bioturbation (Erwin 2012).

When the different proposed Cambrian revolutions are seen within this framework, it is possible to delineate a chronology of major evolutionary breakthroughs. Systematic evaluation of the ichnologic record indicates that the Agronomic revolution is not coincident with the Ediacaran-Cambrian boundary, but rather occurred during Cambrian Age 2 (Mángano and Buatois 2004, 2014). The Cambrian sub-

**Fig. 3.17** Cambrian Stage 2 intensely bioturbated sandstone showing well-developed mixed layer, Unit 18 of the Bayan Gol Formation of Govi-Altay, Mongolia (see Goldring and Jensen 1996, for detailed ichnologic descriptions of this formation), specimen housed at Oxford Museum, scale bar is 1 cm

strate revolution partially overlaps with the Agronomic revolution, but its most definite expression in epibenthic communities is actually during the middle and late Cambrian (Bottjer et al. 2000). In contrast, the Cambrian information revolution involved the appearance of sophisticated, innovative feeding strategies that allowed benthic organisms to exploit resources in an increasingly more heterogeneous sea bottom (Plotnick 2007; Plotnick et al. 2010). The occurrence in the Fortunian of highly patterned grazing trails, such as *Psammichnites*, reflects strophotactic (i.e., proclivity to make U-turns so that the animal turns around 180° at intervals), phobotactic (i.e., tendency to avoid crossing its own and other trails) and thigmotactic (i.e., propensity to keep close contact with a former segment of the trail) behaviors indicative of highly developed navigational devices (Fig. 3.18) (Plotnick 2007;

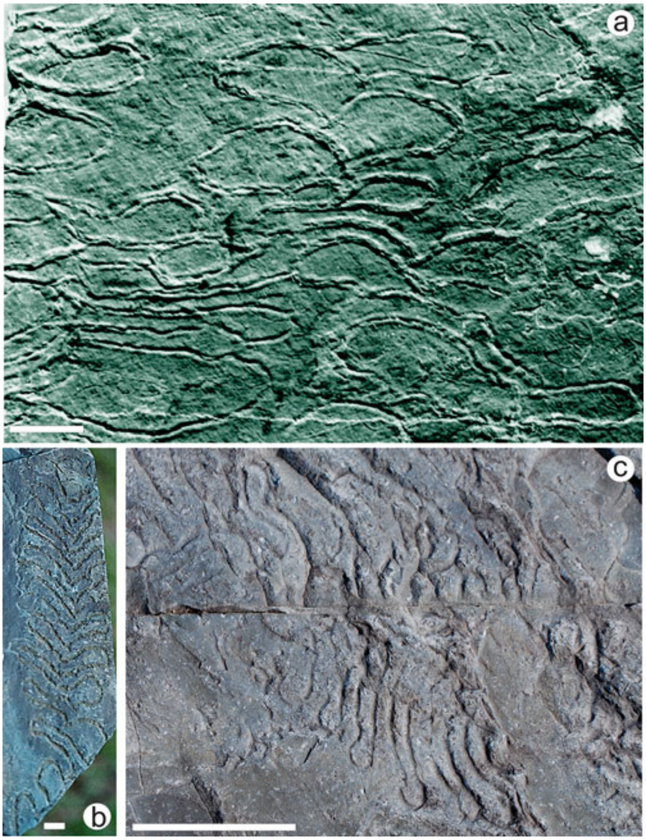

**Fig. 3.18** *Psammichnites* displaying guided meandering patterns, which reflect the establishment of strophotactic, phobotactic and thigmotactic behaviors, signaling the appearance of the Cambrian information revolution. (**a**) Puncoviscana Formation at Campo Quijano, specimen housed at the Miguel Lillo Institute (Tucumán), scale bar is 5 cm; (**b**) Puncoviscana Formation at Cachi, specimen housed in the Museo Egidio Feruglio (Trelew), scale bar is 1 cm; (**c**) Chapel Island Formation at Fortune Head, field photo, scale bar is 5 cm

Plotnick et al. 2010; Mángano and Buatois 2014). This is consistent with the appearance of more sophisticated digestive systems that allowed organisms to exploit richer and more abundant food (Vannier et al. 2014). The provided chronology suggests that the Cambrian information revolution started before the Cambrian substrate revolution and the Agronomic revolution and was probably a protracted process operating during most of the Cambrian.

## 3.5 Environmental Breadth of the Cambrian Explosion

The body-fossil record of the Cambrian explosion is for the most part restricted to shallow-marine shelfal environments as revealed by the preferred habitat of the dominant components of the Cambrian evolutionary fauna, such as trilobites, as well as some of its other elements, most notably inarticulate brachiopods, hyolithids, monoplacophorans, eocrinoids, and hexactinellid sponges (Sepkoski 1981). Even Burgess Shale-type deposits, although formed in deeper water than the typical shelly fauna, do not record deep-marine conditions in the sense of hundreds of meters of water depth at the base of the continental slope (e.g., Ineson and Peel 2011). In contrast to the diverse body-fossil record of deep-marine Ediacaran settings, as revealed by the Avalon assemblage (e.g., Clapham et al. 2003; Narbonne 2005; Narbonne et al. 2009; Wilby et al. 2011; Liu et al. 2012), Cambrian deep-sea strata are essentially barren in terms of body fossils. However, the picture emerging from the trace-fossil record reflects a much more complex situation in terms of environmental breadth of the Cambrian explosion.

It has been noted that limited beta ichnodiversity indicates substantial niche overlap between shallow- and deep-marine benthic communities during the Ediacaran (see Chap. 2). The picture that emerges from the Cambrian is somewhat different (Fig. 3.19). The vast majority of lower Cambrian ichnologic information comes from open shallow-marine environments (e.g., Seilacher 1955; Crimes and Anderson 1985; Crimes and Jiang 1986; Hofmann and Patel 1989; Pacześna 1996; Goldring and Jensen 1996; Jensen 1997; MacNaughton and Narbonne 1999; Orłowski and Żylińska 2002; Buatois and Mángano 2004, 2012a; Gámez Vintaned et al. 2006). Maximum alpha ichnodiversity (measured at ichnogeneric rank) in lower Cambrian shallow-marine settings is 28. Typical early Cambrian shallow-marine ichnotaxa are *Asteriacites*, *Asterosoma*, *Astropolichnus*, *Arenicolites*, *Bergaueria*, *Cheiichnus*, *Conichnus*, *Cruziana*, *Curvolithus*, *Dactyloidites*, *Didymaulichnus*, *Diplocraterion*, *Gyrolithes*, *Lingulichnus*, *Pilichnus*, *Psammichnites*, *Rhizocorallium*, *Rosselia*, *Rusophycus*, *Skolithos*, *Syringomorpha*, *Taenidium*, *Teichichnus*, *Treptichnus*, *Trichophycus*, *Saerichnites*, and *Zoophycos* (Fig. 3.20). These ichnotaxa are essentially restricted to shallow water during the early Cambrian. Lower Cambrian shallow-marine deposits show the establishment of two archetypal assemblages illustrating the *Skolithos* Ichnofacies of moderate- to relatively high-energy nearshore areas and the *Cruziana* Ichnofacies of lower-energy offshore to lower-shoreface settings. Colonization of low-energy muddy to

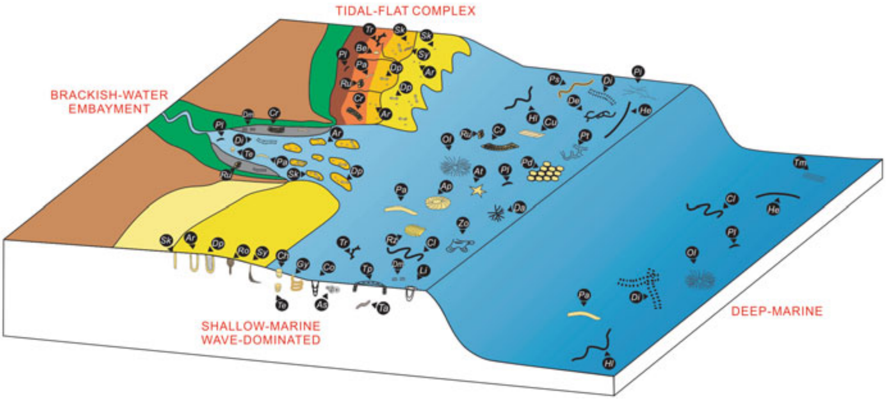

**Fig. 3.19** Environmental breadth of the Cambrian explosion. Lower Cambrian marginal-, shallow- and deep-marine trace-fossil associations. The shallow-marine trace-fossil association corresponding to nearshore settings of wave-dominated shorelines is dominated by vertical burrows, such as *Arenicolites* (*Ar*), *Diplocraterion* (*Dp*), *Rosselia* (*Ro*), *Skolithos* (*Sk*), and *Syringomorpha* (*Sy*), whereas the offshore association tends to display a wider variety of ichnotaxa, such as *Asteriacites* (*At*), *Asterosoma* (*As*), *Astropolichnus* (*Ap*), *Cheiichnus* (*Ch*), *Cochlichnus* (*Cl*), *Conichnus* (*Co*), *Cruziana* (*Cr*), *Curvolithus* (*Cu*), *Dactyloidites* (*Da*), *Dendrorhaphe* (*De*), *Dimorphichnus* (*Dm*), *Diplichnites* (*Di*), *Gyrolithes* (*Gy*), *Helminthoidichnites* (*He*), *Helminthopsis* (*Hl*), *Lingulichnus* (*Li*), *Oldhamia* (*Ol*), *Palaeophycus* (*Pa*), *Paleodictyon* (*Pd*), *Pilichnus* (*Pi*), *Planolites* (*Pl*), *Protopaleodictyon* (*Pt*), *Psammichnites* (*Ps*), *Rusophycus* (*Ru*), *Taenidium* (*Ta*), *Teichichnus* (*Te*), *Treptichnus* (*Tr*), *Trichophycus* (*Tp*), and *Zoophycos* (*Zo*). The deep-marine association is of moderate ichnodiversity, including *Cochlichnus* (*Cl*), *Diplichnites* (*Di*), *Helminthoidichnites* (*He*), *Helminthopsis* (*Hl*), *Oldhamia* (*Ol*), *Palaeophycus* (*Pa*), *Planolites* (*Pl*), and *Tasmanadia* (*Tm*). Tidal-flat areas also display evidence of animal activity, as recorded by the presence of the ichnogenera *Arenicolites* (*Ar*), *Diplocraterion* (*Dp*), *Skolithos* (*Sk*), and *Syringomorpha* (*Sy*) in the higher-energy sandy deposits and *Bergaueria* (*Be*), *Cruziana* (*Cr*), *Rusophycus* (*Ru*), *Palaeophycus* (*Pa*), *Planolites* (*Pl*), and *Treptichnus* (*Tr*) in the lower-energy, mixed sandy-muddy deposits. Colonization of brackish-water, marginal-marine environments is recorded by the presence of *Arenicolites* (*Ar*), *Dimorphichnus* (*Dm*), *Diplocraterion* (*Dp*), *Cruziana* (*Cr*), *Rusophycus* (*Ru*), *Palaeophycus* (*Pa*), *Planolites* (*Pl*), *Skolithos* (*Sk*), and *Teichichnus* (*Te*)

**Fig. 3.20** (continued) Tübingen University, coin diameter is 1.9 cm; (**f**) *Bergaueria sucta*, Hanneh Member, Burj Formation, Wadi Uhaymir, middle Cambrian, field photo; (**g**) *Cheiichnus gothicus*, Mickwitzia Sandstone, Västergötland, Sweden; Cambrian Stages 3–4, specimen housed at Geologisches Institut of Tübingen University; (**h**) *Treptichnus pedum*, Klipbak Formation, near Brandkop, South Africa, Fortunian, field photo; (**i**) *Saerichnites* isp., Dolkraals Formation, near Bloukrans Farm, South Africa, Fortunian, field photo; (**j**) *Didymaulichnus miettensis*, Box Hole Formation, Amadeus Basin, Australia, Cambrian Stage 3, specimen housed at the South Australia Museum; (**k**) *Cruziana salomonis*, Hanneh Member, Burj Formation, Wadi Uhaymir, middle Cambrian, field photo; (**l**) *Dactyloidites asteroides*, Metawee Slate Formation, vicinity of Middle Granville, New York State, United States, Cambrian Stage 4, Burke Museum (Seattle); (**m**) *Psammichnites* isp., Bayan Gol Formation, Govi-Altay, Mongolia, Cambrian Stage 2, specimen housed at Oxford Museum. All scales bars are 1 cm

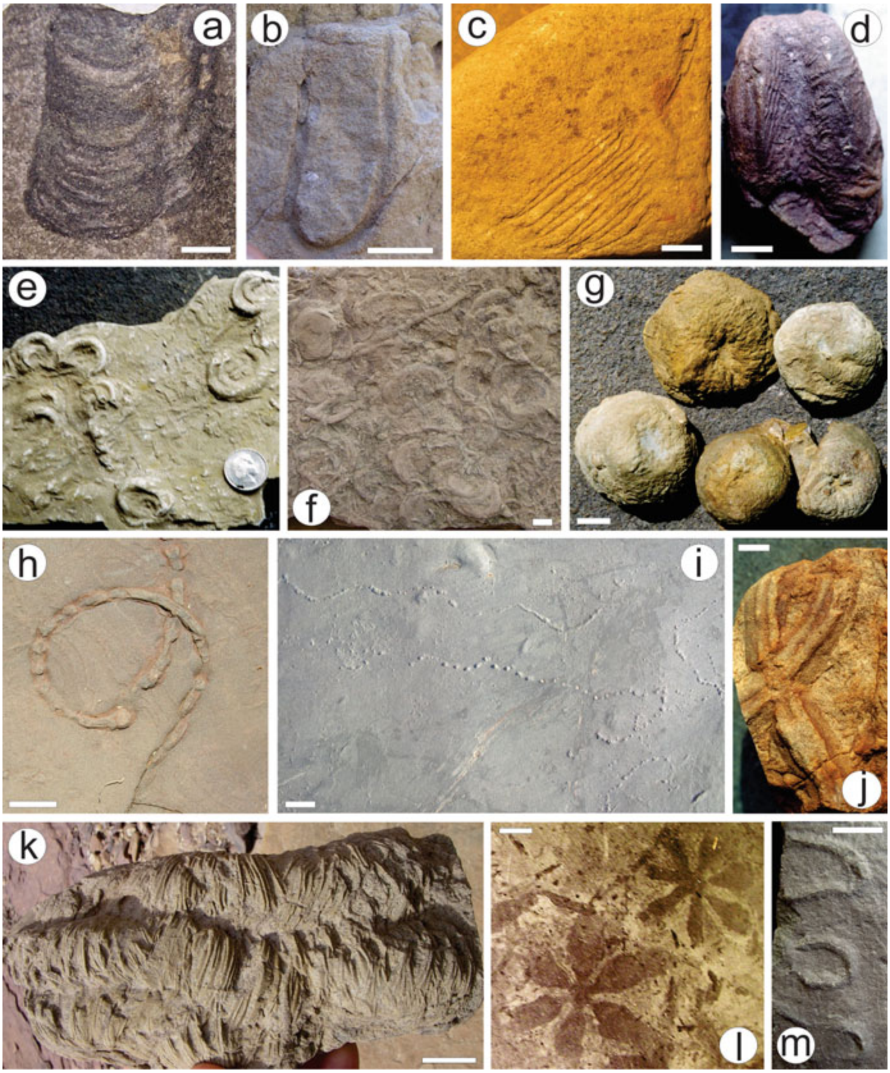

**Fig. 3.20** Typical trace fossils in Cambrian shallow-marine settings. (**a**) *Diplocraterion parallelum*, Dividalen Group, Imobekken, northern Norway, Cambrian Stages 2 to 3 (**b**) *Arenicolites* isp., Hanneh Member, Burj Formation, Wadi Issal, Jordan, middle Cambrian, field photo; (**c**) *Syringomorpha nilssoni*, erratic block, Kiersgoube Pastz, Berlin, Germany; identical forms are known from Cambrian Stages 2–4 strata in Scandinavia, specimen housed at the Berlin Museum of Natural History; (**d**) *Rusophycus leifeirikssoni*, Campanario Formation, Angosto del Morro de Chucalezna, Quebrada de Humahuaca, northwest Argentina, Cambrian Series 2–3, specimen housed at the Miguel Lillo Institute (Tucumán); (**e**) *Gyrolithes polonicus*, Mickwitzia Sandstone, Västergötland, Sweden; Cambrian Stage 3–4, specimen housed at Geologisches Institut of

silty sandy substrates by this benthic community took place in the Fortunian, whereas the establishment of an infauna in relatively high-energy nearshore sands occurred by Cambrian Age 2, as indicated by the appearance of dense ichnofabrics dominated by vertical burrows of suspension feeders (Mángano and Buatois 2014). As is the case of their younger counterparts, offshore and lower-shoreface assemblages show a wide range of ethologies, including feeding, grazing, locomotion and dwelling trace fossils, mostly produced by deposit and detritus feeders and, to a lesser extent, suspension feeders. Interestingly, information from shell bioerosion suggests limited durophagous predation in the Cambrian (Bromley 2004; Wilson 2007; Buatois et al. 2016). In contrast to younger examples, shallow-marine low-energy communities tend to show a dominance of shallow- to mid-tier ichnoguilds. Another major difference with respect to younger ichnofaunas in these shallow-marine settings is the presence of graphoglyptids (farming structures), which otherwise tend to be typical of deep-marine environments. This departure with respect to the standard bathymetric range of graphoglyptids is illustrated by the presence of *Protopaleodictyon*, *Paleodictyon* and *Dendrorhaphe* in Cambrian shallow-marine deposits (e.g., Crimes and Anderson 1985; Pacześna 1996; Jensen and Mens 1999; Jensen et al. 2013).

Although the tiering structure and overall complexity of the Cambrian shallow-marine benthos point to relatively simple community structures and limited utilization of the infaunal ecospace in comparison with younger counterparts (Mángano et al. 2013), Cambrian shallow-marine communities certainly display much more sophisticated niche partitioning than contemporaneous deep-water communities. Cambrian nearshore communities, typically upper- to middle shoreface deposits, tend to be dominated by dwelling, escape and equilibrium structures of suspension feeders. In contrast to low-energy offshore to lower-shoreface infaunal communities, the deep tiers of nearshore sands were exploited by a suspension-feeding infauna, as evidenced by the presence of *Skolithos* piperock, showing bioturbation depths of up to 1 m (e.g., Davies et al. 2009).

Cambrian deep-marine ichnofaunas have been documented from a number of areas (e.g., Crimes and Crossley 1968; Aceñolaza and Durand 1973; Dhonau and Holland 1974; Crimes 1976; Churkin and Brabb 1965; Hofmann and Cecile 1981; Lindholm and Casey 1990; Sweet and Narbonne 1993; Hofmann et al. 1994; Buatois and Mángano 2003a, 2004). Maximum alpha ichnodiversity in deep-marine deposits is 8, revealing that evolutionary innovations lagged behind in the deep sea. Higher diversity levels have been noted in the Meguma Terrane of Nova Scotia (Gingras et al. 2011; White et al. 2012) and ongoing analysis may provide further clarification on the taxonomy and environmental setting of this ichnofauna (Jensen et al. 2015). By far, the dominant element of deep-marine assemblages is the ichnogenus *Oldhamia* (Fig. 3.21a), typically displaying a wide variety of ichnospecies. However, although dominant in Cambrian deep-sea assemblages, *Oldhamia* is not restricted to these settings, having been recognized in shallow-marine deposits as well (Fig. 3.22a-c) (Buatois and Mángano 2004; Seilacher et al. 2005; Jensen et al. 2013). In fact, early Cambrian deep-marine trace fossil assemblages tend to comprise facies-crossing ichnotaxa (Fig. 3.21), such as grazing trails (e.g., *Cochlichnus*,

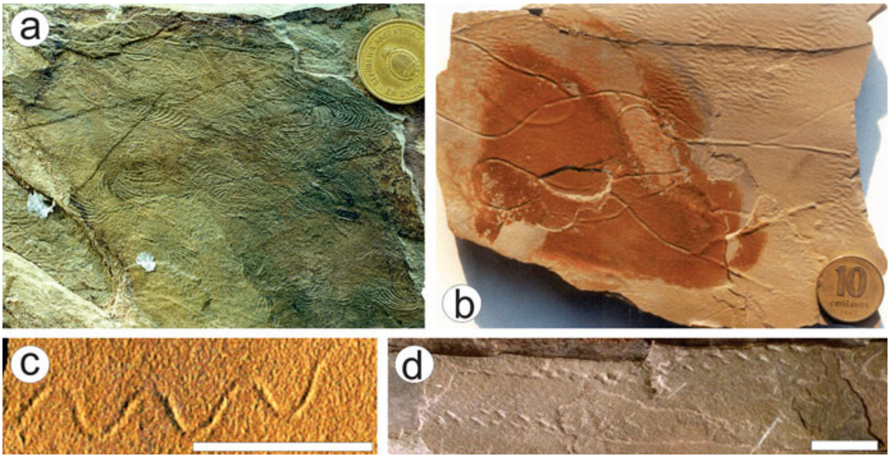

**Fig. 3.21** Typical trace fossils in Cambrian deep-marine settings. All trace fossils from the Puncoviscana Formation of northwest Argentina, Fortunian. (**a**) *Oldhamia curvata*, Sierra de la Ovejería; (**b**) *Helminthopsis tenuis* associated with wrinkle marks, San Antonio de Los Cobres; (**c**) *Cochlichnus anguineus*, San Antonio de Los Cobres; (**d**) *Diplichnites* isp., San Antonio de Los Cobres. All specimens housed at the Miguel Lillo Institute (Tucumán). All scale bars are 1 cm, coin diameter is 1.8 cm

*Helminthopsis*, *Helminthoidichnites*) (Fig. 3.21b and c) and simple burrows (*Planolites*, *Palaeophycus*). Arthropod trackways (e.g., *Diplichnites*, *Tasmanadia*) (Fig. 3.21d), which in younger rocks are mostly present in shallow-marine deposits, are relatively common in deep-marine lower Cambrian deposits (Orr 2001).

Strictly speaking, there are almost no ichnotaxa exclusive of the deep sea during the Cambrian. Limited beta ichnodiversity indicates substantial niche overlap between shallow- and deep-marine communities in the Cambrian. This represents a sharp departure with respect to the Ordovician radiation, which signals the establishment of a deep-marine community dominated by graphoglyptids, the archetypal structures of this setting (see Chap. 4). The uniqueness of Cambrian deep-marine ichnofaunas and its marked differences with respect to their younger counterparts have been noted elsewhere (Orr 2001). From an ecological standpoint, Cambrian deep-marine ichnofaunas suggest feeding strategies linked to the exploitation of microbial matgrounds. Therefore, deep-marine assemblages indicate that microbial matground ecology persisted in the deep sea during the early Cambrian, and may be regarded as Ediacaran relicts in this regard (Buatois and Mángano 2003a). The fact that these strategies persisted in the deep sea long after the onset of infaunal bioturbation in shallow water indicates the diachronic nature of the Agronomic revolution (Buatois and Mángano 2003a; Mángano 2011).

The paucity of deep deposit-feeding burrowers in low-energy offshore to deeper-water deposits during the Cambrian has been taken as an evidence of limited amounts of food buried in the sediment (Bambach 1993). Following this line of reasoning, the presence of graphoglyptids in shallow-marine deposits may suggest

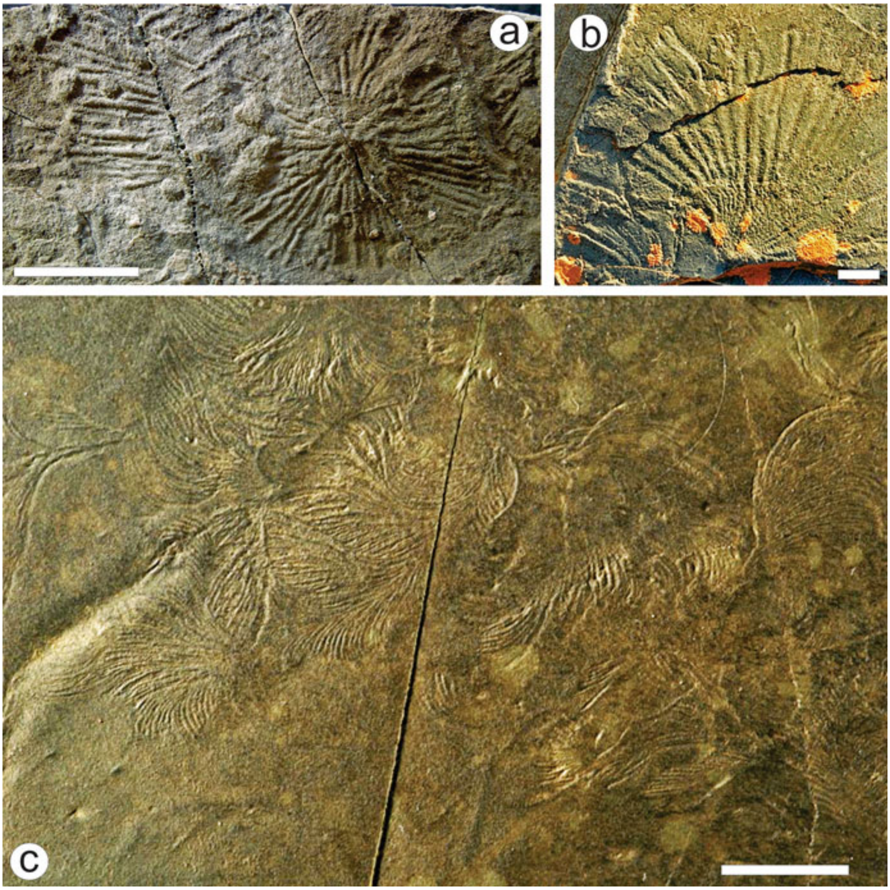

**Fig. 3.22** Shallow-marine occurrences of the ichnogenus *Oldhamia*. (**a**) *Oldhamia radiata*, Bayan Gol Formation, Govi-Altay, Mongolia, Cambrian Stage 2; (**b**) *Oldhamia geniculata*, Besonderheid Formation, Bokkeveld escarpment, South Africa, Fortunian; (**c**) *Oldhamia alata*, Puncoviscana Formation, El Mollar trace-fossil locality, Quebrada del Toro, Argentina, Fortunian. All scale bars are 1 cm

that farming and trapping strategies were already developed during the Cambrian, and later migrated into the deep sea. Because these sophisticated strategies involved in the formation of graphoglyptids are most likely a response to scarce food resources, this pattern seems to be consistent with comparatively more limited food in shallow seas during the Cambrian (Buatois and Mángano 2003b).

Although the bulk of paleobiologic and ichnologic information comes from fully marine environments, Cambrian ichnofaunas have been documented from marginal-marine settings as well (Fig. 3.19) (see Chap. 5). Two different environmental contexts may be recognized here: very shallow intertidal settings connected to the open sea (Fig. 3.23a–g) and brackish-water embayed settings (Fig. 3.24a-f). The former set of settings includes tidal flats, ranging from the lower-intertidal sand flat to the

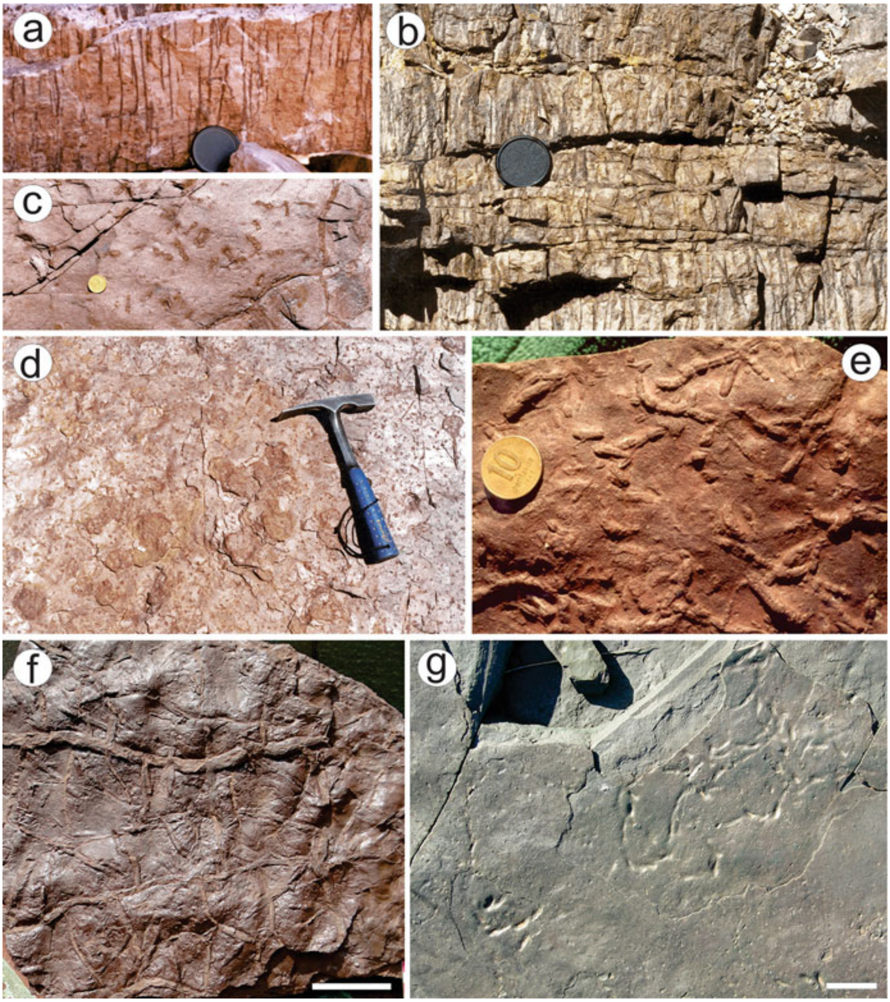

**Fig. 3.23** Typical trace fossils in Cambrian tidal-flat settings. (**a**) *Arenicolites* isp., Campanario Formation, Angosto de Perchel, northwest Argentina, Cambrian Series 2–3, field photo, lens cap diameter is 5.5 cm; (**b**) *Syringomorpha* isp., Campanario Formation, Angosto del Morro de Chucalezna, northwest Argentina, Cambrian Series 2–3, field photo, lens cap diameter is 5.5 cm; (**c**) Bedding plane view of a high-density association of *Diplocraterion parallelum*, note associated desiccation cracks, Campanario Formation, Quebrada de Moya, northwest Argentina, Cambrian Series 2–3, field photo, coin diameter is 1.8 cm; (**d**) Clusters of *Rusophycus leifeirikssoni*, Campanario Formation, Angosto del Morro de Chucalezna, northwest Argentina, Cambrian Series 2–3, field photo, hammer is 33.5 cm long; (**e**) *Cruziana problematica*, Campanario Formation, Angosto de Perchel, northwest Argentina, Cambrian Series 2–3, specimen housed at the Miguel Lillo Institute (Tucumán), coin diameter is 1.8 cm; (**f**) General view of pavement of *Cruziana irregularis* crosscut by different sizes of desiccation cracks, Rome Formation, Pine Ridge, Tennessee, Cambrian Stages 2–3, field photo, scale bar is 5 cm; (**g**) *Treptichnus pedum*, Kalk Gat Formation, Vanrhynsdorp Group, creek near Kalk Gat Noord Farm, South Africa, Fortunian, field photo, scale bar is 5 cm

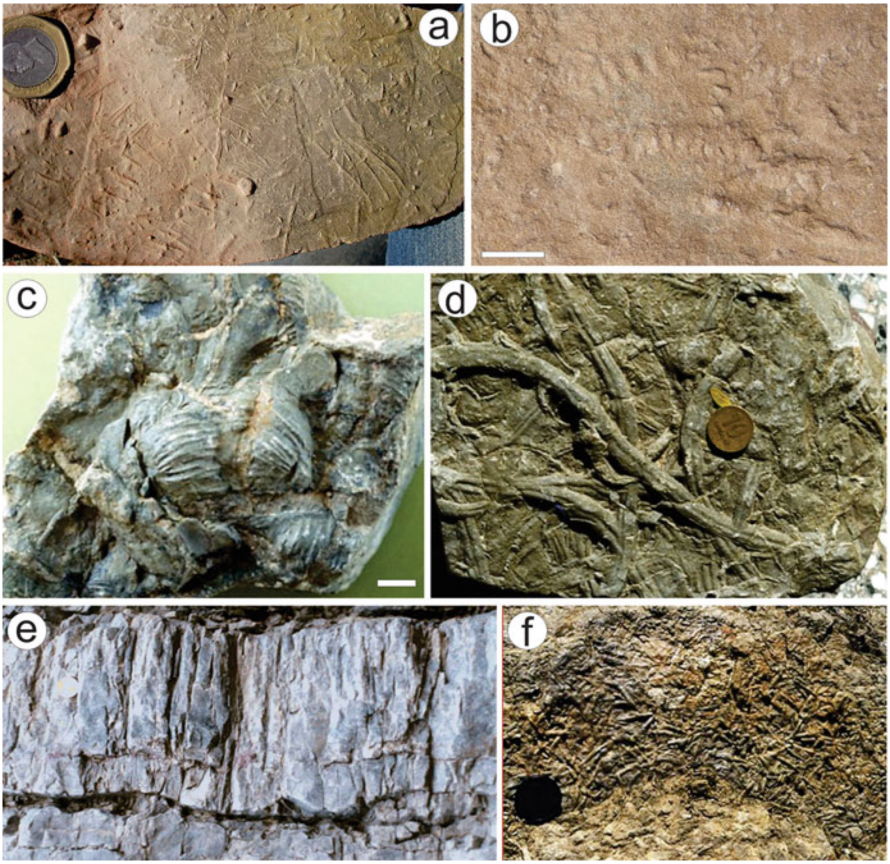

**Fig. 3.24** Typical trace fossils in Cambrian brackish-water settings. (**a**) *Dimorphichnus* cf. *D. obliquus*, Hanneh Member, Burj Formation, Wadi Uhaymir, Jordan, middle Cambrian, field photo, coin diameter is 2.9 cm; (**b**) *Diplichnites* isp., Umm Ishrin Formation, Wadi Issal, Jordan, middle Cambrian, field photo, scale bar is 1 cm; (**c**) *Rusophycus latus*, Pico de Halcón Member, Santa Rosita Formation, Quebrada del Salto Alto, northwest Argentina, Furongian, scale bar is 2 cm; (**d**) *Cruziana semiplicata*, Pico de Halcón Member, Santa Rosita Formation, Quebrada del Salto Alto, northwest Argentina, Furongian, specimen housed at the Miguel Lillo Institute (Tucumán), coin diameter is 1.8 cm; (**e**) *Skolithos linearis*, Pico de Halcón Member, Santa Rosita Formation, Quebrada del Salto Alto, northwest Argentina, Furongian, field photo, coin diameter is 1.8 cm; (**f**) *Palaeophycus tubularis*, Pico de Halcón Member, Santa Rosita Formation, Quebrada del Salto Alto, northwest Argentina, Furongian, field photo, lens cap diameter is 5.5 cm

upper-intertidal mud flat of tide-dominated shorelines (e.g., Mángano and Buatois 2004, 2015; Desjardins et al. 2012; Mángano et al. 2014). Lower-intertidal sand flats typically display relatively high-energy conditions, and are dominated by elements of the *Skolithos* Ichnofacies, whereas arthropod trackways and burrows, the giant locomotion trail *Climactichnites* and its related resting trace *Musculopodus*, paired scratch marks arranged in meandering patterns, referred to as *Radulichnus* and simple vermiform structures, are the most common components in shallower-water, upper- to middle-intertidal flats formed under lower-energy conditions (Mángano and Buatois 2004, 2015; Pandey et al. 2014). *Syringomorpha* has also been recorded in sand-flat areas (Mángano and Buatois 2004). *Treptichnus pedum* occurs in Fortunian tidal-flat deposits, underscoring its environmental tolerance (Buatois et al. 2013).

In particular, the presence of *Rusophycus* most likely produced by olenellid trilobites in lower Cambrian very shallow intertidal deposits suggests that trilobites were able to foray into the upper intertidal zone very early in their evolutionary history (Mángano et al. 2014). Four hypotheses have been suggested in an attempt to explain trilobite incursions to tidal flats: the trilobite nursery, trilobite pirouette, hunting burrow, and microbial garden hypotheses (Mángano and Buatois 2004; Mángano et al. 2014). Whereas the first hypothesis implies reproductive behavior, the others involve feeding activities. The trilobite nursery hypothesis is based on the observation that modern tidal flats are nursery sites where eggs and juveniles are protected from marine predators (Reise 1985). In particular, limulids (Eldredge 1970) using the head to shovel burrows to lay their eggs that are grouped in clusters resemble some *Rusophycus* occurrences in Cambrian tidal flats (Mángano and Buatois 2004). As an analogy, it has been suggested that *Rusophycus* clusters in tidal-flat deposits may represent nesting sites. In the case of the trilobite pirouette hypothesis, trilobite trails may display circular and scribbling patterns that record deposit feeding activities (Seilacher 1970), reflecting incursions in the search of organic detritus during the high tide. The hunting burrow hypothesis is based on the interpretation of some deep *Rusophycus* as predation traces, reflecting trilobites preying on worms (Jensen 1990). In the light of this hypothesis, trilobite incursions to intertidal areas reflect increased predation pressures. The microbial garden hypothesis suggests that trilobites may have forayed into tidal flat areas to graze on microbially enriched sediments. Information from marine benthic ecology indicates that bioturbation by infaunal organisms results in microbial growth significantly changing the organic content of the sediment (Reise 1985).

The second set of settings includes marginal-marine brackish-water environments, such as embayments, estuaries, and distal reaches of braidplains, where the stress associated with salinity fluctuations is extreme, becoming a limiting factor. Ichnofaunas documented from these settings are almost invariably of low diversity and dominated by arthropod trackways and burrows or by simple facies-crossing vermiform trace fossils (Mikuláš 1995; Mángano and Buatois 2003; Baldwin et al. 2004; Buatois et al. 2005; Mángano et al. 2013) (Fig. 3.19), suggesting tolerance to salinity fluctuations and dilution of normal marine salinities.

In short, ichnologic information shows that the Cambrian explosion was not limited to fully marine environments, and that representatives of the Cambrian evolutionary fauna were able to regularly visit extremely shallow-water settings and in some cases colonized brackish-water environments (Buatois et al. 2005;

Mángano et al. 2014) in what may be regarded as a prelude to the invasion of the land (see Chap. 5).

## 3.6 Cambrian Provincialism in Trace Fossils

A recent study by Jensen et al. (2013) attempted to explore if potential paleogeographic trends can be discerned based on Cambrian trace-fossil distributions. These authors noted that a number of Cambrian ichnotaxa, namely *Astropolichnus hispanicus*, *Climactichnites*, *Syringomorpha nilssoni*, and *Paleodictyon* have a restricted paleogeographic distribution. *Astropolichnus hispanicus* is mostly present in Europe, in terranes located along the margins of Gondwana (Pillola et al. 1994; Jensen et al. 2013). The ichnogenus *Climactichnites* is restricted to eastern North America, most likely reflecting facies controls (Getty and Hagadorn 2009). *Syringomorpha nilssoni* occurs in Baltica and Gondwana occupying in both cases mid-latitudes (Jensen et al. 2013). Most of recordings of *Paleodictyon* in the Cambrian occur along the margin of Gondwana, probably in connection with the opening of the Rheic Ocean, probably reflecting the restricted paleogeographic distribution of the tracemakers (Jensen et al. 2013).

In contrast, a cosmopolitan distribution has been noted for *Didymaulichnus miettensis*, and in early examples of *Rusophycus* isp. and *Dactyloidites* isp., ranging from equatorial to polar regions. The ichnogenus *Oldhamia* displays a wide distribution in lower Cambrian deep-sea deposits, albeit with a restricted occurrence of *Oldhamia geniculata* and *O. alata.*

## 3.7 A Picture from Burgess Shale-Type Deposits

Although Burgess Shale (BS)-type faunas were originally regarded as transported from shallower water to an anoxic deeper-water setting (Conway Morris 1979), subsequent work has documented the presence of trace fossils in BS-type deposits, providing uncontroversial evidence of an in situ benthic community (e.g., Rudkin 1992; Allison and Brett 1995; Gaines and Droser 2005; Zhang et al. 2007; Wang et al. 2009; Lin et al. 2010; Mángano 2011; Mángano et al. 2012; Minter et al. 2012; Caron et al. 2014). In particular, Mángano (2011) summarized ichnologic features of BS-type deposits by grouping biogenic structures based primarily on distinct preservational styles, and secondarily by morphology and size range in: (1) diminutive structures directly associated to non-mineralized carapaces; (2) trace fossils with extensive distribution along bedding surfaces; (3) burrows containing their producers; and (4) three-dimensional, typically early mineralized, vermiform structures.

Spectacular examples of the former group are known from the lower Cambrian Sirius Passet of Greenland, where simple trails, annulated tubes, irregular polygonal networks, and thin, crenulated branching burrows occur in direct association with the large, weakly mineralized arthropod *Arthroaspis bergstroemi* (Mángano et al. 2012) (Fig. 3.25a–e). In particular, the interconnected burrow systems seem restricted to the carapaces and have been regarded as evidence for reuse, and a feeding strategy of bacterial farming and grazing. Trails and burrows also occur in carapaces from Burgess Shale-type deposits elsewhere, such as Stanley Glacier, Canadian Rockies (Mángano 2011) (Fig. 3.25f and g), Chengjiang, China (Zhang et al. 2007) (Fig. 3.25 h–j), and the Barrandian area, Czech Republic (Fatka et al. 2011; Mikuláš 2000; Mikuláš et al. 2012), among other sites. It has been postulated that in BS-type settings carcasses and molds of weakly or non-biomineralized organisms may have acted as attractors, favoring the establishment of a community of small invertebrates, in the same fashion that whale falls do in modern sea bottoms (Mángano et al. 2012). At some stratigraphic surfaces with low sedimentation rate, non-biomineralized carapaces accumulated, creating a sharp boundary on the sea floor, further decreasing oxygen diffusion into the sediment and promoting the growth of sulfur-bacteria that could have served as the primary food for small macrofauna and meiofauna. These carapaces and their associated communities signal an increased heterogeneity of the sea floor during the Cambrian, and record an expression of the Information Revolution".

The second category, stratigraphic horizons covered with trace fossils, is superbly recorded at Stanley Glacier (Fig. 3.26a–e) (Mángano 2011). Bedding planes with abundant and varied trace fossils seem to record improvement in oxygen content, recording colonization of the shallow infaunal ecospace. Preservation of delicate morphologic details was enhanced by early diagenetic processes (i.e., early carbonate cement) or biomat stabilization, generating firmground conditions at or very close to the sediment–water interface.

The unusual association of burrows containing their own producers deserves further investigation. Famous examples in Walcott Quarry include *Ottoia* within its J-shaped burrows (Rudkin 1992), whereas in Chengjiang are represented by priapulids found within their burrows (Zhang et al. 2006; Huang et al. 2014). Although organic tubes locally containing their producers (Caron et al. 2013) are not biogenic sedimentary structures, they could be considered as an extension of this category in the sense that they also provide direct paleobiologic information.

Finally, 3D burrows recording early pyritization within the sulfate reduction zone were documented at Stanley Glacier (Mángano 2011). However, these conspicuous structures are not hosted within the mudstone facies containing soft-bodied fossils, but typically within the limestone facies that capped the Stanley Glacier shallowing-upward cycles (Gaines 2011).

Overall, BS-type ichnofaunas reveal a complex interplay of taphonomic, ecologic, and evolutionary controls. General characteristics of ichnofaunas from BS-type deposits, such as minute size, shallow penetration depth, and low diversity, support a discontinuity redox surface very close to the sediment–water interface (Mángano 2011). Also, bedding surfaces containing trace fossils typically alternate with parallel-laminated deposits totally barren of biogenic structures, suggesting fluctuations of the redox discontinuity surface. In addition to oxygen as a control-

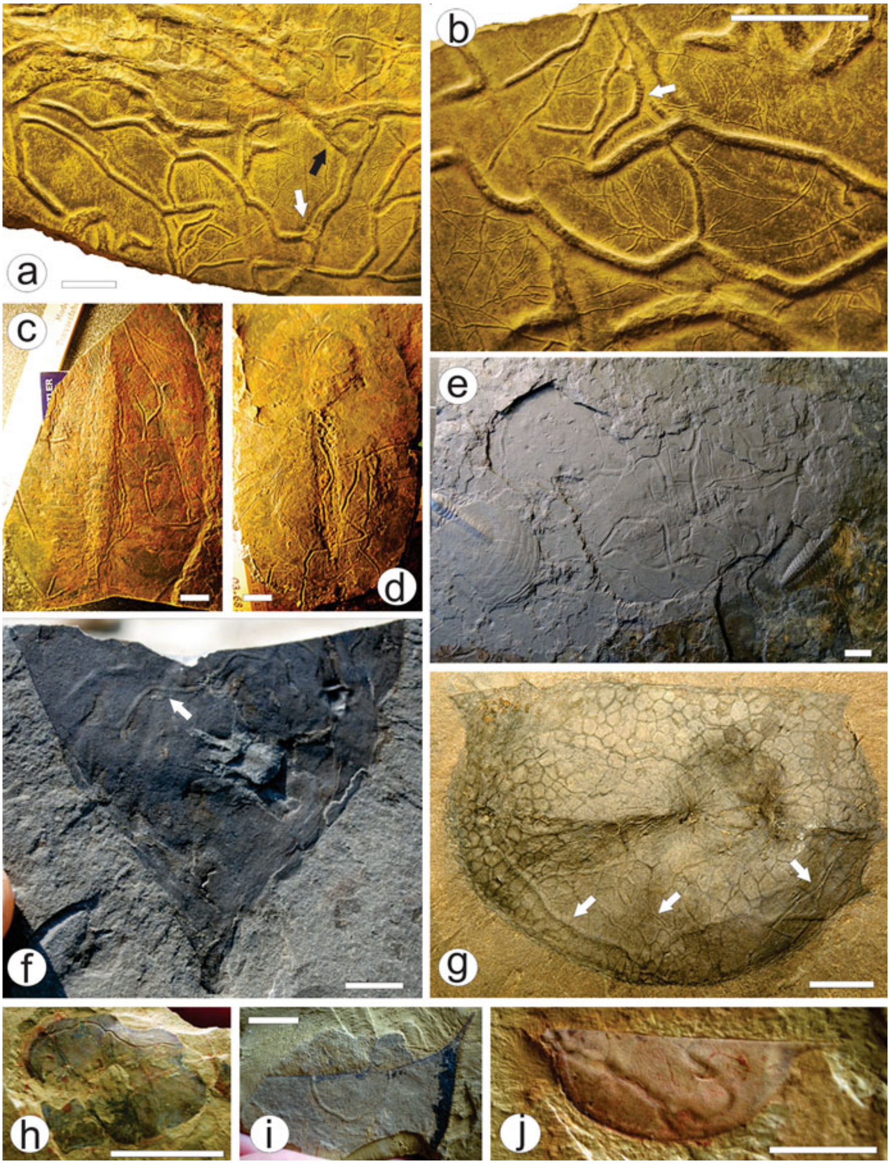

**Fig. 3.25** Trace fossils associated with non-biomineralized carapaces in Burgess Shale-type deposits. (**a**) The arthropod *Arthroaspis bergstroemi* showing regular polygonal networks displaying true branching (*black arrows*) and secondary successive branching (*white arrow*), Sirius Passet, Greenland, specimen housed at the Natural History Museum (Copenhagen); (**b**) Close-up of (**a**) showing annulated structures (*arrow*) and delicate, narrow-caliber, filament-like structures mostly confined to areas among network branches; (**c**, **d**) General view of *Arthroaspis bergstroemi* showing several irregular networks, Sirius Passet, Greenland, specimen housed at the Natural History Museum (Copenhagen); (**e**) Pavement with *Arthroaspis bergstroemi* containing several trails, note the presence of the trilobite *Buenellus higginsi*, Sirius Passet, Greenland, specimen housed at the Natural History Museum (Copenhagen); (**f**) *Hurdia* containing *Cochlichnus anguineus* (*arrow*); Stanley Glacier, Canadian Rockies, specimen housed at the Royal Ontario Museum (Toronto); (**g**) *Tuzoia* in lateral preservation displaying several specimens of *Helminthoidichnites tenuis* of different sizes (*arrow*); note reticular pattern recording the microstructure of the carapace; Stanley Glacier, Canadian Rockies, specimen housed at the Royal Ontario Museum (Toronto);

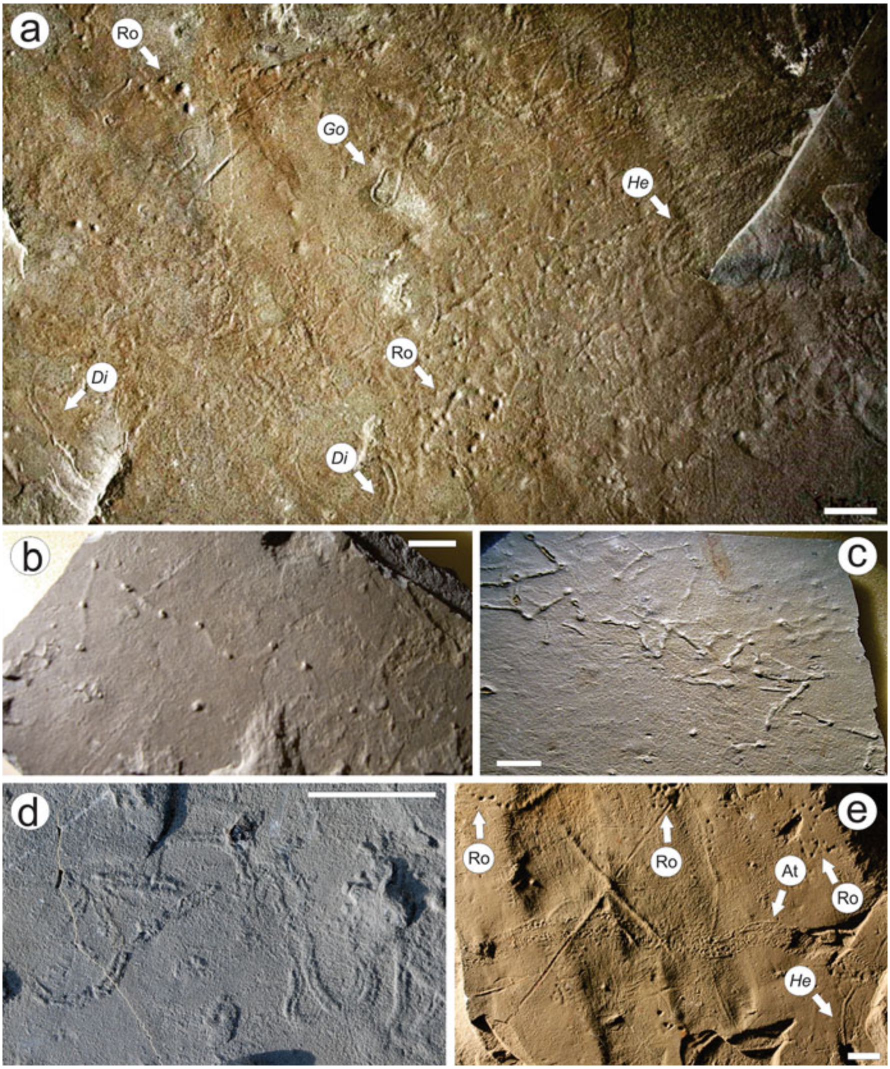

**Fig. 3.26** Trace fossils in Burgess Shale-type deposits, Stanley Glacier, Canadian Rockies. (**a**) General view of a bedding plane containing relatively high diversity of trace fossils, including rosary-like structures (Ro), *Diplopodichnus biformis* (*Di*), *Gordia marina* (*Go*), and *Helminthoidichnites tenuis* (*He*); (**b**, **c**) Close-up of rosary-like structures; (**d**) *Cruziana problematica*; (**e**) Arthropod trackway (At), *Helminthoidichnites tenuis* (*He*) and rosary-like structures (Ro). All specimens housed at the Royal Ontario Museum (Toronto). All scale bars are 1 cm

◄

**Fig. 3.25** (continued) (**h**) Trail on fragment of *Vetulicola cuneata*, Chengjiang, China, specimen housed at the Natural History Museum (Copenhagen); (**i**) undetermined arthropod cuticle with *Helminthoidichnites tenuis*, Chengjiang, China, specimen housed at the Natural History Museum (Copenhagen); (**j**) Carapace of the arthropod *Isoxys auritus* with *Helminthoidichnites tenuis*, Chengjiang, China, specimen housed at the Natural History Museum (Copenhagen). All scale bars are 1 cm ling factor, it has been noted that a variable degree of substrate consistency may have been responsible for the observed variations in morphology, burrow sharpness, and degree of deformation of some biogenic structures. Some trace-fossil assemblages record fine morphologic features indicative of firmground conditions resulting from early cementation (Gaines et al. 2012) or microbial stabilization. In terms of evolutionary controls, absence of deep-tier colonization in Cambrian dysoxic settings and of a well-developed mixed layer opened a taphonomic window for the exceptional preservation of diminutive, delicate surficial and shallow-tier trace fossils in BS-type deposits (Mángano 2011). These conditions coexisted with intensely bioturbated deposits in more oxygenated, typically shallower-water deposits, pointing to the unusual environmental and taphonomic conditions of BS-type settings. Interestingly, the recent discovery of the Marble Canyon locality in the Canadian Rockies provides evidence of medium-sized burrows, forming dense ichnofabrics that noticeably disturb the primary laminated fabric, signaling a departure from the more classical BS-type ichnofaunas (Caron et al. 2014).

## 3.8 The Fortunian as a Critical Time in Macroevolution

As stated by Knoll (2004), “there is nothing like the Cambrian until the Cambrian.” However, given the unique character of the Cambrian, it is equally fair to say that “there is nothing like the Cambrian after the Cambrian” (Buatois and Mángano 2011). In addition to witnessing the most dramatic evolutionary radiation in the history of life, the Cambrian is a pivotal point in macroevolution. This is particularly illustrated by the Fortunian, a critical time to understand the chronology of the evolutionary novelties and innovations involved in the Cambrian explosion. The fact that there are no Burgess Shale-type deposits of Fortunian age, and that this stage as a whole has a meager body-fossil record makes ichnologic evidence the most remarkable.

The Fortunian seems to express a dual nature. On the one hand, the high ichnodiversity and ichnodisparity are clear signatures of the evolutionary innovations represented by the interactions of new animal body plans and the sediment. On the other, the widespread occurrence of feeding strategies associated with the exploitation of microbial mats seems to suggest that a relict Ediacaran, matground-based ecology persisted into the Phanerozoic (Buatois and Mángano 2003a, 2012b; Dornbos et al. 2004; Buatois et al. 2014). In fact, it is precisely the uniqueness of this association of sophisticated undermat miners in Fortunian substrates and its contrast with the simple strategies of the Ediacaran that eliminates the possibility of a taphonomic artifact. The coexistence during the Fortunian of mixground and microbial-mat ecologies within the same environmental setting is dramatically illustrated in the Global Stratotype (GSSP) for the Cambrian System in Fortune Head by the presence of bioturbated siltstone, which is interbedded with extensive microbial mats (Buatois et al. 2014). These matgrounds typically occur on the top of sandy event beds, which record minor omission surfaces. Reestablishment of background fair-weather sedimentation was accompanied by more intense bioturbation, signaling a change in animal–sediment interactions. However, even this more intense fair-weather bioturbation is not strictly of Phanerozoic-style because this ichnofauna consists of well-defined structures with clear burrow boundaries (Fig. 3.27a-f) instead of poorly defined, soft-sediment mottled textures, such as

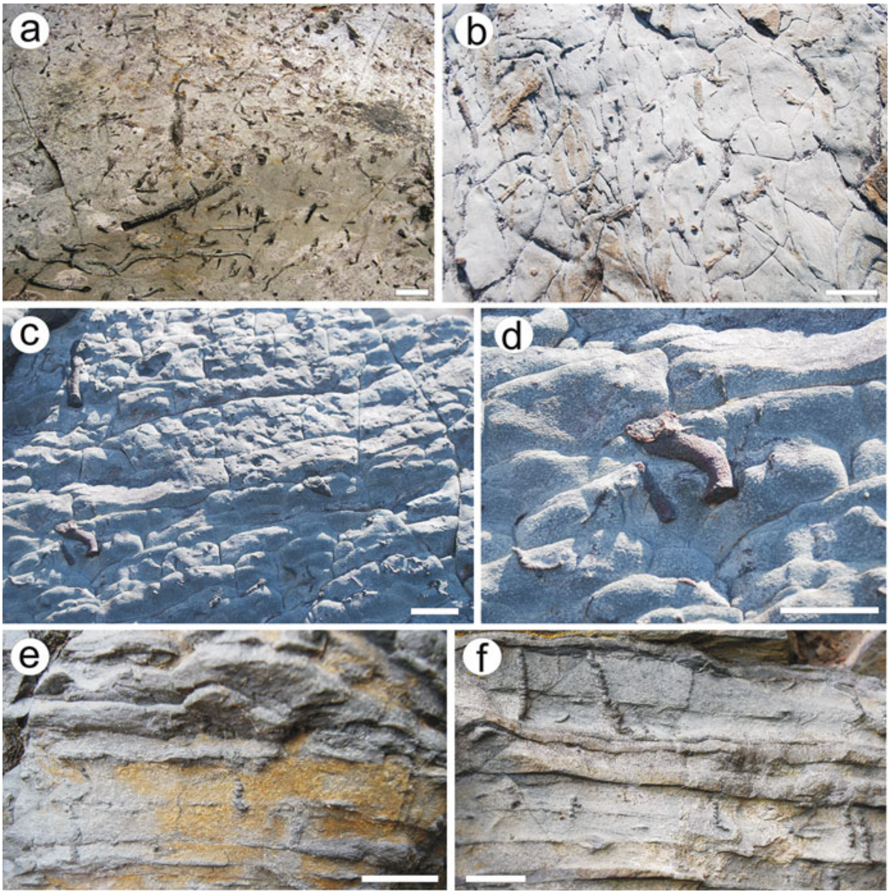

**Fig. 3.27** Trace fossils indicative of firmground conditions, Chapel Island Formation at Fortune Head (see Droser et al. 2002a and Buatois et al. 2014 for discussion). (**a**–**c**) General view of bedding planes showing fair-weather siltstone ichnofauna with well-defined trace-fossil morphologies and infill coming from overlying coarser-grained deposits, scale bars in (**a**) and (**b**) are 1 cm and in (**c**) is 2 cm; (**d**) Close-up of firmground burrows shown in (**c**), scale bar is 1 cm; (**e**, **f**) Cross-sectional view of tiny vertical burrows in siltstone with infill coming from overlying coarser-grained deposits, scale bars are 1 cm. Although these burrows have been typically assigned to *Skolithos annulatus*, they display a helicoidal morphology revealing affinities with *Gyrolithes*, which occurs in the same beds. All field photos

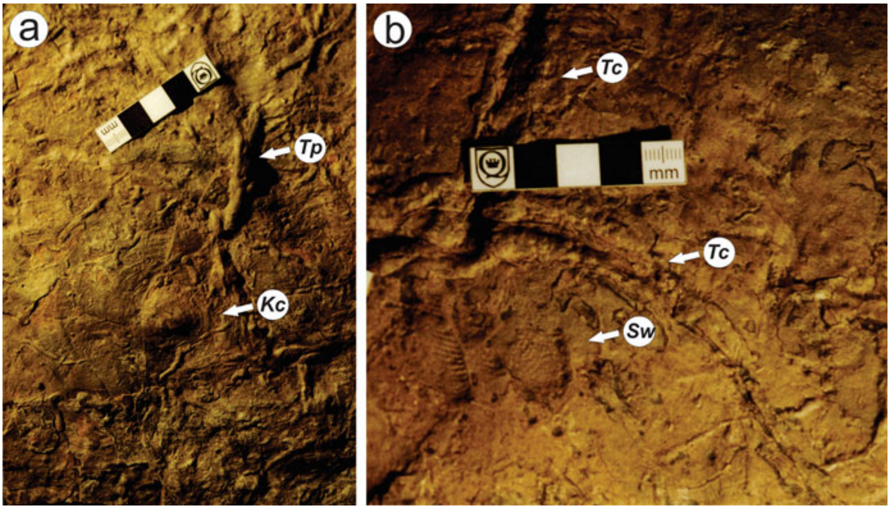

**Fig. 3.28** Ediacaran-type structures associated with typical Cambrian trace fossils, lower Cambrian Uratanna Formation at Angepensa syncline, Flinders Ranges, southern Australia. Specimens housed at the South Australia Museum (see Jensen et al. 1998 for a detailed discussion). (**a**) *Treptichnus pedum* (*Tp*) on the same bedding plane as the circular structure *Kullingia concentrica* (*Kc*); (**b**) The trail typically assigned to *Taphrhelminthopsis circularis* (*Tc*) associated with *Swarpuntia*-like (*Sw*) body fossils

those that typified emplacement in the modern mixed layer (Buatois et al. 2014). As discussed above (see 3.4), this is indicative of firmground conditions close or at the sediment surface, which is inconsistent with a well-established mixed layer (Droser et al. 2002a).

This dual nature of the Fortunian is also expressed by the preservation on the same bedding planes of typical Cambrian trace fossils, such as *Treptichnus pedum* and the trail usually referred to as *Taphrhelminthopsis circularis* (an ichnotaxon that awaits revision, but clearly shows affinities with *Psammichnites*) and structures similar to Ediacaran fronds, such as *Swartpuntia*-like fronds and *Kullingia concentrica* (Fig. 3.28a-b) (Jensen et al. 1998). Although the latter is now reinterpreted as formed by current or wave-induced rotation of an anchored tubular organism (Jensen et al. 2002), its preservation seems to be more consistent with Ediacaran-style substrates than typical Phanerozoic mixgrounds.

Finally, the combination of Ediacaran ecology and Cambrian innovation persisted in the deep sea for probably most, if not all, the Cambrian, as illustrated by the complex feeding patterns of *Oldhamia* in microbial mats (Buatois and Mángano 2003a). This fact demonstrates both the relict nature of Fortunian ecosystems and that colonization of the deep sea lagged behind that of shallow-water settings (see 3.5).

## 3.9 Conclusions

The trace fossil record provides a valuable insight to reconstruct the chronology of novelties and innovations related to the Cambrian explosion event. The early Cambrian displayed a dramatic increase in both global and alpha ichnodiversity and ichnodisparity, illustrating an independent way of calibrating the uniqueness of this evolutionary radiation. This sudden increase in ichnodiversity and ichnodisparity supports the Cambrian explosion scenario, but the fact that the main trace-fossil diversification event took place by the Fortunian allows for an approximately 20 Ma-long interval of phylogenetic fuse, considering that the rapid appearance of skeletonized body fossils occurred later in the early Cambrian (521–509 Ma). Whereas the Fortunian event marks the establishment of novel ways of interacting with the sediment resulting from the appearance of distinctive body plans and a wide repertoire of behavioral strategies, a second phase that took place during Cambrian Age 2 involves an evolutionary breakthrough in ecologic structuring. The appearance of deep-tier suspension feeders, in addition to the development of a more complex tiering structure consisting of multiple ichnoguilds, suggests good delivery from the water column into the sediment, and that bioturbation played a crucial role in nutrient recycling. Ichnologic information indicates that evolutionary innovations took place first in shallow-marine environments, although deep- and marginal-marine environments were already colonized during the Cambrian. The presence of trace fossils in Burgess Shale (BS) type deposits provides unquestionable evidence of an in situ benthic community. BS-type ichnofaunas reveal a complex interplay of taphonomic, ecologic, and evolutionary controls. Minute size, shallow penetration depth, and low diversity support a discontinuity redox surface very close to the sediment–water interface in BS-type settings.

**Acknowledgments** Financial support for this study was provided by Natural Sciences and Engineering Research Council (NSERC) Discovery Grants 311727-08/15 and 311726–13 awarded to Mángano and Buatois, respectively, as well as a University of Saskatchewan President Fund to Mángano. Anna Żylińska and Jean Vannier reviewed this chapters providing very useful feedback. Many colleagues guided us in Cambrian outcrops all over the world, including John Almond (South Africa, Namibia), Richard Bromley (Bornholm), Richard Callow (Newfoundland), Jean Bernard Caron (Canadian Rockies), Olaf Elicki (Jordan), Jim Gehling (Australia), Gerard Germs (Namibia), Liam Herringshaw (Newfoundland), Sören Jensen (Spain), Guy Narbonne (Australia, Newfoundland), Brian Pratt (Canadian Rockies), Rafie Shinaq (Jordan), Xiaoya Ma (China), Zhang Shishan (China), and Anna Żylińska (Poland). We thank LotharVallon for providing information on the *Diplocraterion* specimens from Norway. We also thank the curators and personnel of the Royal Ontario Museum (Toronto), Peabody Museum (Yale), Oxford Museum, Natural History Museum (London), Natural History Museum (Copenhagen), Berlin Museum of Natural History, Museum of the Faculty of Geology of the University of Warsaw, Geologisches Institut of Tübingen University, Australian Museum (Sydney), South Australia Museum (Adelaide), Geological Survey of South Africa (Cape Town), Yunnan Kunyan Phosphate Mine, Burke Museum (Seattle), Museo Egidio Feruglio (Trelew), and Instituto Miguel Lillo (Tucumán).

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# Chapter 4
# The Great Ordovician Biodiversification Event

**M. Gabriela Mángano, Luis A. Buatois, Mark Wilson, and Mary Droser**

## 4.1 Introduction

The Great Ordovician Biodiversification Event (GOBE) was undoubtedly one of the most significant evolutionary radiations in the history of the marine biosphere. The Ordovician Period witnessed a global three- to fourfold increase in the number of marine animal families and genera (Sepkoski 1995, 1997; Miller 1997). In terms of Sepkoski's evolutionary faunas, the GOBE represents a turnover from dominance of members of the Cambrian evolutionary fauna to those of the Paleozoic and Modern faunas (Sepkoski 1981; Miller and Connolly 2001). In particular, the Paleozoic evolutionary fauna was dominated by articulate brachiopods, rugose and tabulate corals, and crinoids (Sepkoski 1981). Stenolaemate bryozoans, graptolites, and cephalopods were common also (Sepkoski 1981). A diversification in deposit feeders, detritus feeders, suspension feeders, and grazers took place in the benthos, while suspension feeders and predators diversified in the pelagic setting (Bambach 1983; Sheehan 2001; Servais et al. 2008, 2010). The plankton started its diversification by the end of the Cambrian, continuing into the Ordovician in the so-called "Ordovician Plankton Revolution" (Nowak et al. 2015; Servais et al. in press). As a result, the ecological structure of marine communities became more complex. The GOBE resulted in an increase in the number of modes of life utilized by skeletal

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M.G. Mángano, L.A. Buatois (eds.), *The Trace-Fossil Record of Major Evolutionary Events*, Topics in Geobiology 39,
DOI 10.1007/978-94-017-9600-2_4

organisms to a total of 30 by the Late Ordovician (Bambach et al. 2007). Of the 20 potential Bambachian megaguilds (sensu Droser et al. 1997; i.e., adaptive strategies of Bambach 1983), 14 were filled by the Paleozoic fauna (Sheehan 2001). In addition, these profound biotic changes occurred parallel to a number of chemical and physical changes, such as sea-level changes, fluctuations in atmospheric oxygen and carbon dioxide content, and an overall decrease in temperatures (Munnecke et al. 2010; Rasmussen et al. 2016).

As in the case of all evolutionary events, most of our knowledge of the Ordovician radiation emerges from the study of the body-fossil record (e.g., Sepkoski 1995; Miller and Foote 1996; Miller 1997; Sheehan 2001; Droser and Finnegan 2003; Webby et al. 2004; Harper 2006; Servais et al. 2008, 2010). More recently, some studies have attempted to evaluate what the trace-fossil record can tell us about this evolutionary event (Mángano and Droser 2004). Particularly when combined with solid paleoenvironmental frameworks, the trace-fossil record can illuminate our understanding of the paleoecologic breakthroughs of the GOBE in terms of the unpreserved soft-bodied component, animal behavior and the expansion of the infaunal habitat, onshore–offshore patterns, increase in depth and extent of bioturbation, and colonization trends within specific sedimentary environments (e.g., Droser and Bottjer 1989; Orr 2001; Mángano and Droser 2004; Buatois et al. 2009; Mángano and Buatois 2011). In this chapter, we review the Ordovician trace-fossil record from the perspective of evolutionary paleoecology to evaluate patterns and processes involved in this biodiversification event.

## 4.2 Patterns of Environmental Colonization

Because trace fossils represent in situ responses to dynamic environmental conditions, they are ideally suited to evaluate adaptations of benthic faunas along a depositional profile. In this section, we address the ichnologic expression of the Ordovician radiation in various environmental settings. The colonization of continental and marginal-marine environments is addressed elsewhere (see Chap. 5).

### *4.2.1 Shallow-Marine Siliciclastic Environments*

#### 4.2.1.1 Conservative Nature of Infaunal Communities in High-Energy Nearshore Settings

As in younger parts of the geologic column, Ordovician shallow-marine siliciclastic deposits display two well-defined archetypal associations referred to as the *Skolithos* and *Cruziana* Ichnofacies. The former is dominated by vertical, cylindrical, simple or U-shaped (with or without spreite) dwelling burrows of sessile suspension feeders and passive predators, forming suites of low ichnodiversity and variable abundance in fine- to coarse-grained sandstone units. *Skolithos* (Fig. 4.1a), *Arenicolites*,

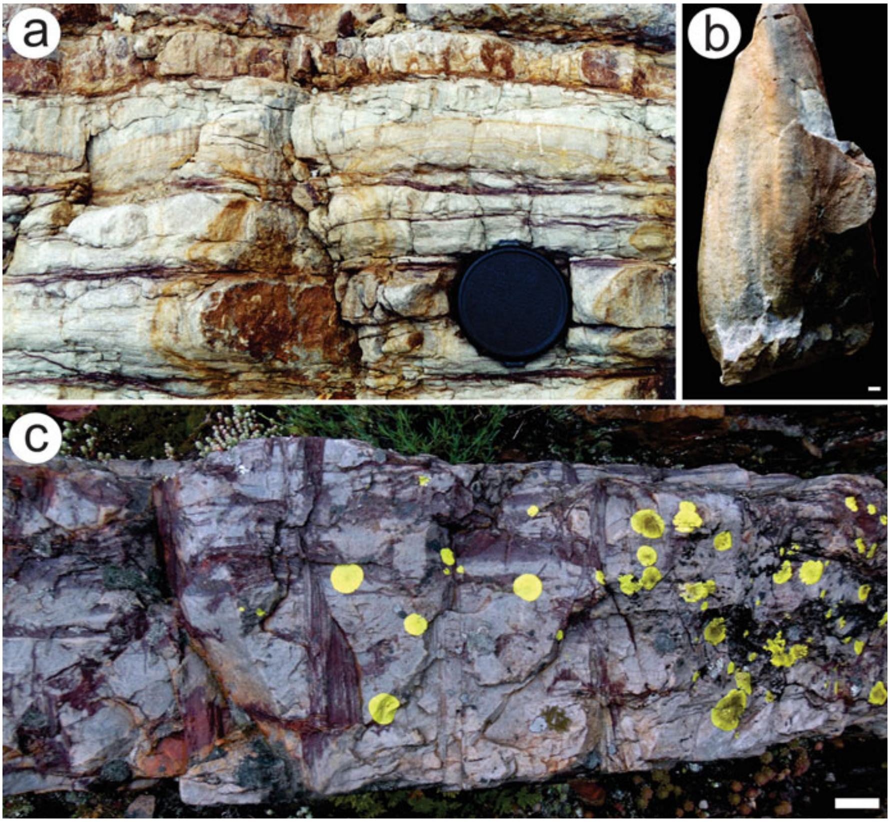

**Fig. 4.1** Typical Ordovician nearshore trace fossils. (**a**) *Skolithos* pipe rock in storm deposits. Tremadocian, Alfarcito Member, Santa Rosita Formation, Quebrada de Casa Colorada, northwest Argentina. Lens cover is 5.5 cm wide; (**b**) *Daedalus desglandi*. Floian–Darriwilian, north of Muscat, Oman. Scale bar is 1 cm. (**c**) General view of a storm bed showing colonization by *Daedalus halli*. Floian, Armoricain Quartzite, Penha Garcia, Portugal. Scale bar is 1 cm

and *Diplocraterion* are typical components of this facies in Phanerozoic strata (e.g. Mángano et al. 2005).

This association of vertical burrows occurs in well-oxygenated, relatively high-energy shallow-marine settings characterized by strong erosion, shifting sandy substrates, and high abundance of organic particles that are kept in suspension in the water column by waves and currents (Frey and Pemberton 1984; Pemberton et al. 1992; Buatois and Mángano 2011). In terms of specific depositional environments, it is typical of foreshore to upper- and middle-shoreface environments in wave-dominated shorelines and of lower-intertidal sand flats and subtidal sandbodies in tide-dominated systems (Buatois and Mángano 2011). The composition of the *Skolithos* Ichnofacies remained nearly unchanged throughout all the Paleozoic since its appearance in Cambrian Age 2. The conservative nature of this association is unsurprising, because the unstable nearshore settings of benthic communities tend to be dominated by opportunistic organisms (e.g. Mángano and Buatois 2003).

#### 4.2.1.2 Behavioral Innovations and Faunal Turnovers in High-Energy Nearshore Settings

Despite the overall conservative nature of nearshore ichnofaunas, some behavioral innovations are noted for the Ordovician. The spreite J-shaped burrow *Daedalus* (Fig. 4.1b) seems to have a much more restricted stratigraphic range than other components of this association, occurring only in Ordovician–Silurian rocks (Seilacher 2000), being a product of the Ordovician radiation rather than the Cambrian explosion. The ethological significance of this ichnogenus is far from clear. The complex spreite of *Daedalus* argues against a predation of suspension-feeding mode, but a deposit-feeding strategy is hard to reconcile with its presence in very clean quartzite (de Carvalho 2004; Seilacher 2007).

In addition, it has been shown that ichnofabrics consisting of stacked *Rosselia*, one of the most characteristic ichnofabrics of post-Paleozoic shallow-marine settings having relatively high rates of sedimentation, were already present by the Middle to Upper Ordovician (Fig. 4.2a and b) (Buatois et al. 2016a). This ichnofabric reflects the ability of the whole infaunal community to coordinately move upwards in order to avoid burial due to episodic sedimentation. Although *Rosselia* is known from the Cambrian (e.g., Desjardins et al. 2010; Hofmann et al. 2012), no examples of synchronous upward movement have been recorded in the Cambrian, suggesting that this behavior may have been attained during the GOBE (Buatois et al. 2016a).

Although nearshore trace-fossil associations remained relatively stable through the Paleozoic, some specific ichnofabrics display temporal changes. For

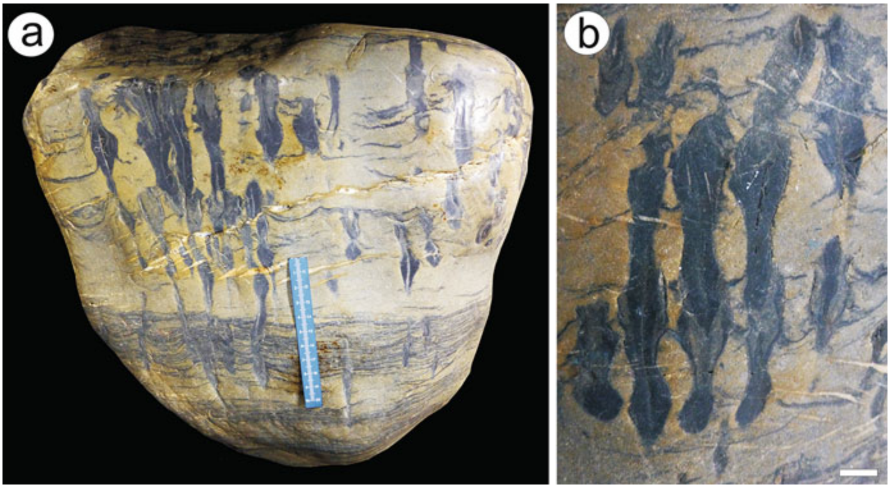

**Fig. 4.2** Crowded synchronous *Rosselia* ichnofabrics from the Middle to Upper Ordovician Castro Formation of Cabo de Peñas, Asturias, Spain. (**a**) General view in cross section; (**b**) close-up showing several stacked specimens. Scale bar is 1 cm

example, dense concentrations of *Skolithos* forming piperock became less common after the Ordovician (Droser 1991). The reasons for such a decline are still unclear, but radiations of predators (McIlroy and Garton 2004) and greater spatial competition for the infaunal ecospace as a result of the Ordovician biodiversification (Desjardins et al. 2010) may have negatively impacted on the *Skolithos* tracemakers. Ultimately, the overall composition of this association dramatically changed during the early Mesozoic, when decapod crustaceans became the dominant bioturbators in nearshore settings, producing a wide variety of burrow systems, such as *Ophiomorpha* and *Thalassinoides* (Droser and Bottjer 1993; Carmona et al. 2004; see Chap. 9).

#### 4.2.1.3 Faunal Turnovers in the *Cruziana* Ichnofacies

The *Cruziana* Ichnofacies reflects much more variability, and its comparative analysis through the Ordovician reveals substantial compositional turnovers (Mángano and Droser 2004). This association is dominated by horizontal trace fossils and subordinate presence of vertical and inclined structures. A wide variety of ethologic categories (e.g., locomotion, feeding, resting, dwelling, grazing) and trophic types (e.g., deposit, detritus and suspension feeding, predation) are represented, mostly reflecting the activity of a mobile fauna, forming suites of high ichnodiversity and abundance in heterolithic deposits. Locomotion behavior is illustrated by both trails, such as *Cruziana*, *Didymaulichnus*, *Protovirgularia*, and *Gyrochorte*, and trackways, such as *Diplichnites*, *Dimorphichnus*, *Monomorphichnus*, and *Allocotichnus*. Resting traces are represented by *Rusophycus*, *Asteriacites*, *Bergaueria*, and *Lockeia*. Feeding structures include *Phycodes*, *Heimdallia*, *Arthrophycus*, *Teichichnus*, *Trichophycus*, *Parataenidium*, *Alcyonidiopsis* (= *Tomaculum*), and *Asterosoma*. Dwelling burrows are mostly represented by the horizontal burrow *Palaeophycus* and by vertical structures, such as *Rosselia* and *Cylindrichnus*. Grazing trails include *Gordia* and *Archaeonassa*. This trace-fossil association occurs in moderate- to low-energy marine settings characterized by the accumulation of organic detritus in the associated heterolithic sediment under relatively stable conditions (Buatois and Mángano 2011). In wave-dominated systems, this trace-fossil association typifies areas slightly above fair-weather wave base to the storm-wave base (i.e., lower shoreface to lower offshore). In tide-dominated shorelines, this association may occur subtidally along the margins of sand sheets, compound dune fields and tidal sand-ridges, but it also may occur in shallower water, being present between the high- and low-tide lines (Buatois and Mángano 2011; Desjardins et al. 2012a).

Ichnofaunal changes in lower-shoreface and offshore siliciclastic deposits through the Ordovician reveal faunal turnovers resulting from the evolutionary radiation. Lower to Middle Ordovician deposits interpreted as representing the *Cruziana* Ichnofacies tend to contain abundant trilobite-produced trace fossils, most commonly *Cruziana*, *Rusophycus*, *Dimorphichnus* and *Monomorphichnus*, with examples recorded from almost all paleocontinents (e.g., Bergström 1976; Baldwin 1977; Webby 1983; Pickerill et al. 1984; El-Khayal and Romano 1988; Seilacher 1992; Mángano and Buatois 2003; Knaust 2004; Mángano et al. 2005).

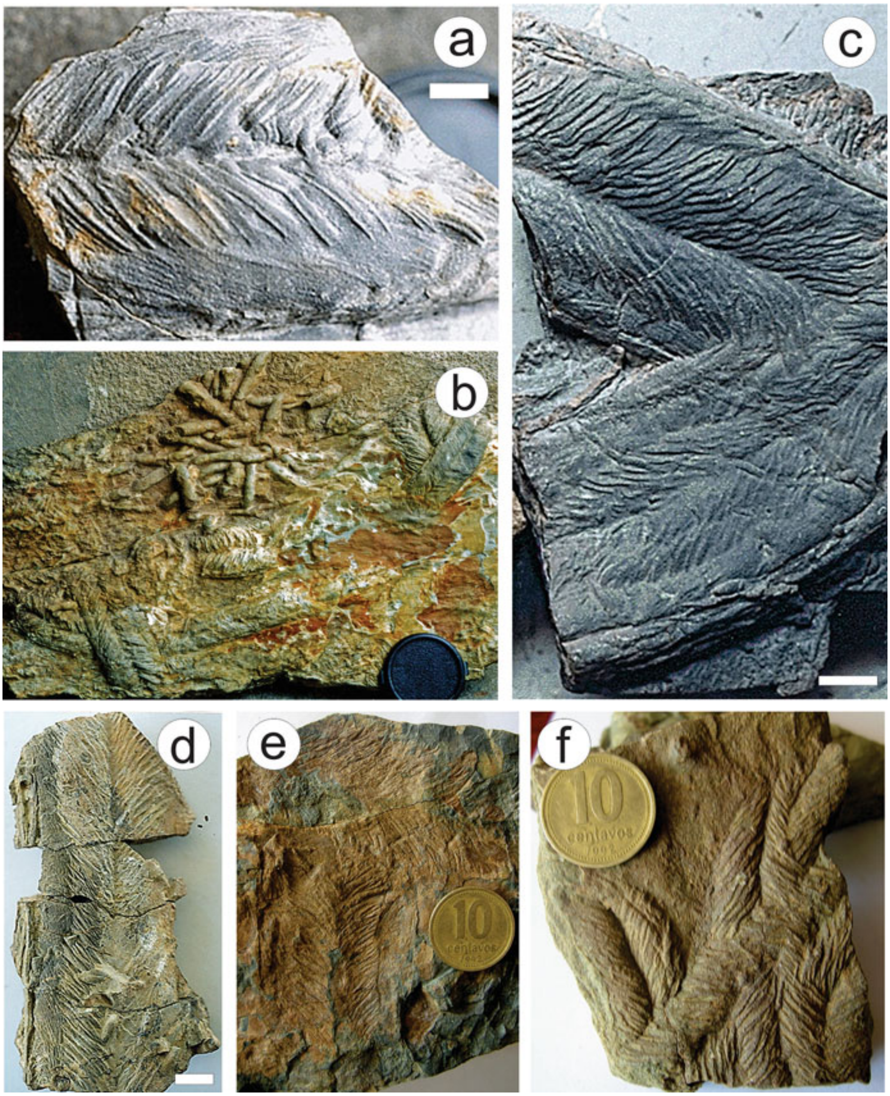

**Fig. 4.3** Examples of the Furongian–Tremadocian *Cruziana semiplicata*. (**a**) Furongian, Olenus Beds, Wiśniówka Quarry, Holy Cross Mountains, Poland; (**b**) several specimens cross cut by *Phycodes* isp. and *Palaeophycus tubularis*. Furongian, Festiniog Beds, Lingula Flags, North Wales. Lens cap diameter is 5.5 cm; (**c**) two overlapping specimens displaying the typical morphology of *C. semiplicata*. Furongian–Tremadocian, Bell Island Group, Bell Island, eastern Newfoundland, Canada. Scale bar is 1 cm; (**d**) specimen displaying marginal furrows, exopodal external lobes with delicate scratch marks oriented subparallel to the axis, and endopodal lobes with scratch marks at an acute angle with respect to axis. Tremadocian, Guayoc Chico Group, Angosto del Moreno, northwest Argentina. Scale bar is 1 cm; (**e**) epichnial preservation. Furongian, Lampazar Formation, Sierra de Cajas, northwest Argentina. Coin diameter 1.8 cm; (**f**) overlapping specimens. Furongian, Lampazar Formation, Sierra de Cajas, northwest Argentina. Coin diameter 1.8 cm

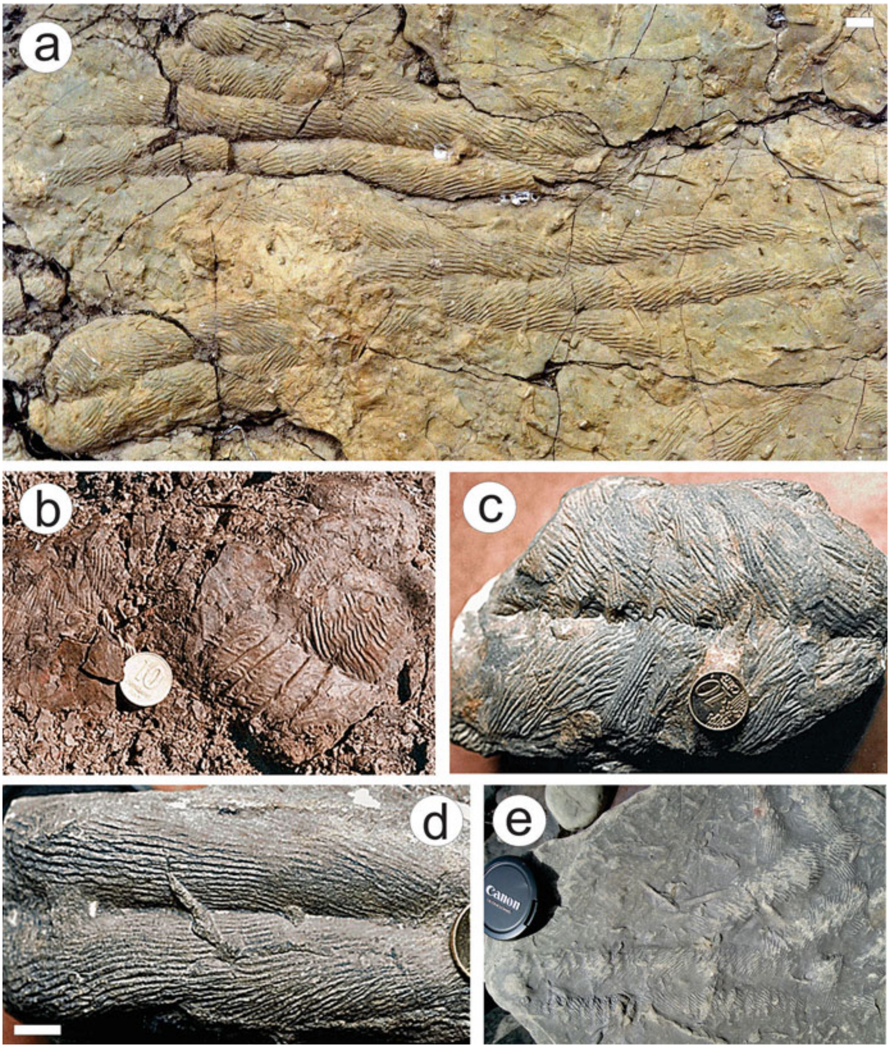

**Fig. 4.4** Examples of the Floian–Darriwilian *Cruziana rugosa* group. (**a**) *Cruziana rugosa furcifera* showing sharp, regular scratch marks forming a highly variable V-angle. Floian–Darriwilian, Mojotoro Formation, Quebrada del Gallinato, northwest Argentina. Scale bar is 1 cm; (**b**) highly asymmetrical specimen of *Cruziana rugosa rugosa* exhibiting strong transversal ridges on left lobe. Floian–Darriwilian, Mojotoro Formation, Quebrada del Gallinato, northwest Argentina. Coin diameter 1.8 cm; (**c**) *Cruziana rugosa rugosa*, displaying sets of sharp scratch marks. Floian–Darriwilian, Afghanistan. Coin diameter 1.9 cm; (**d**) *Cruziana rugosa goldfussi* showing well-developed internal lobes covered by fine scratch marks forming an acute angle, in places tending to be parallel towards the axis. Floian–Darriwilian, Khabour Quartzite, Ora, Irak. Scale bar is 1 cm; (**e**) Overlapping specimens of *Cruziana rugosa rugosa.* Floian, Powers Steps Formation, Greb Nest, Bell Island, eastern Newfoundland, Canada. Lens cap diameter is 5.5 cm

In order to quantify the relative contribution of trilobite trace fossils to alpha ichnodiversity, a systematic database of Ordovician ichnofaunas was constructed. Of a total of ten case studies for the Tremadocian documenting individual trace-fossil assemblages, an average of 41.5 % of the alpha ichnodiversity at ichnospecies level was due to trilobite-produced trace fossils. Similarly, based on a compilation of 20 case studies for the Floian–Dapingian–Darriwilian, trilobite trace fossils contributed to an average of 30.6 % of the alpha ichnodiversity at ichnospecies level.

During the Early Ordovician, there was a significant turnover of trilobite trace fossils, which has been recorded in peri-Gondwanan settings. Elements of the *Cruziana semiplicata* group (Fig. 4.3a–f) (Furongian–Tremadocian) were replaced by elements of the *Cruziana rugosa* group (Fig. 4.4a–e) (typically Floian–Darriwilian) (Crimes 1975; Seilacher 1992) with overlapping assemblages occurring in the late Tremadocian (Baldwin 1975, 1977; Mángano and Buatois 2003). This faunal turnover may have been related to intraclade taxonomic changes in the components of a community, reflecting onshore–offshore evolutionary trends, such as the retreat of olenids to deeper-water settings during the Early Ordovician (Fortey and Owens 1990), where preservation of trace fossils is negatively impacted by the scarcity of sandstone–mudstone interbeds.

Upper Ordovician lower-shoreface to offshore ichnofaunas suggest more varied behavioral patterns (Mángano and Droser 2004). Trilobite-produced trace fossils (Fig. 4.5a–e) are rarely the dominant components in these deposits, particularly in Upper Ordovician assemblages. A compilation of 23 case studies for the Sandbian–Katian–Hirnantian revealed that trilobite trace fossils only contributed to an average of 12.1 % of the alpha ichnodiversity.

The dominant architectural designs (see Buatois and Mángano 2013 and Chaps. 1 and 16) include horizontal burrows with horizontal to vertical branches (e.g., *Arthrophycus*, *Phycodes*), actively filled (meniscate) horizontal burrows, such as *Nereites*, *Taenidium* and *Parataenidium* (Fig. 4.6a), branched burrow mazes and boxworks (e.g., *Thalassinoides*), dumbbell-shaped trace fossils (e.g., *Arthraria*), radial branching structures, (e.g. *Volkichnium, Cladichnus*), horizontal, branched concentrically filled burrows (e.g., *Asterosoma*), horizontal burrows with serial chambers (e.g., *Halimedides*), burrows having a shaft or bunch with downwards radiating probes (e.g., *Chondrites*), almond-shaped burrows (e.g., *Lockeia*, Fig. 4.6b and c), and chevronate trails (e.g., *Protovirgularia*, Fig. 4.6c). The vast majority of these architectural designs and ichnotaxa were present since the Cambrian (see Chap. 3), but they generally were subordinate in abundance and diversity to trilobite-produced trace fossils. Examples of ichnofaunas reflecting this diversity of morphological patterns are known worldwide (Osgood 1970; Hofmann 1979; Mikuláš 1988, 1992, 1998; Stanistreet 1989; Stanley and Pickerill 1998; Mángano and Buatois 2003).

This biotic turnover may be due to the replacement of the trilobite-dominated Cambrian evolutionary fauna by the more diverse Paleozoic evolutionary fauna and/or a taphonomic overprint reflecting the full development of the mixed layer. In the first scenario, the observed pattern is simply the ichnologic record of a trend inferred from the analysis of body fossils, which indicates a decline in the diversity

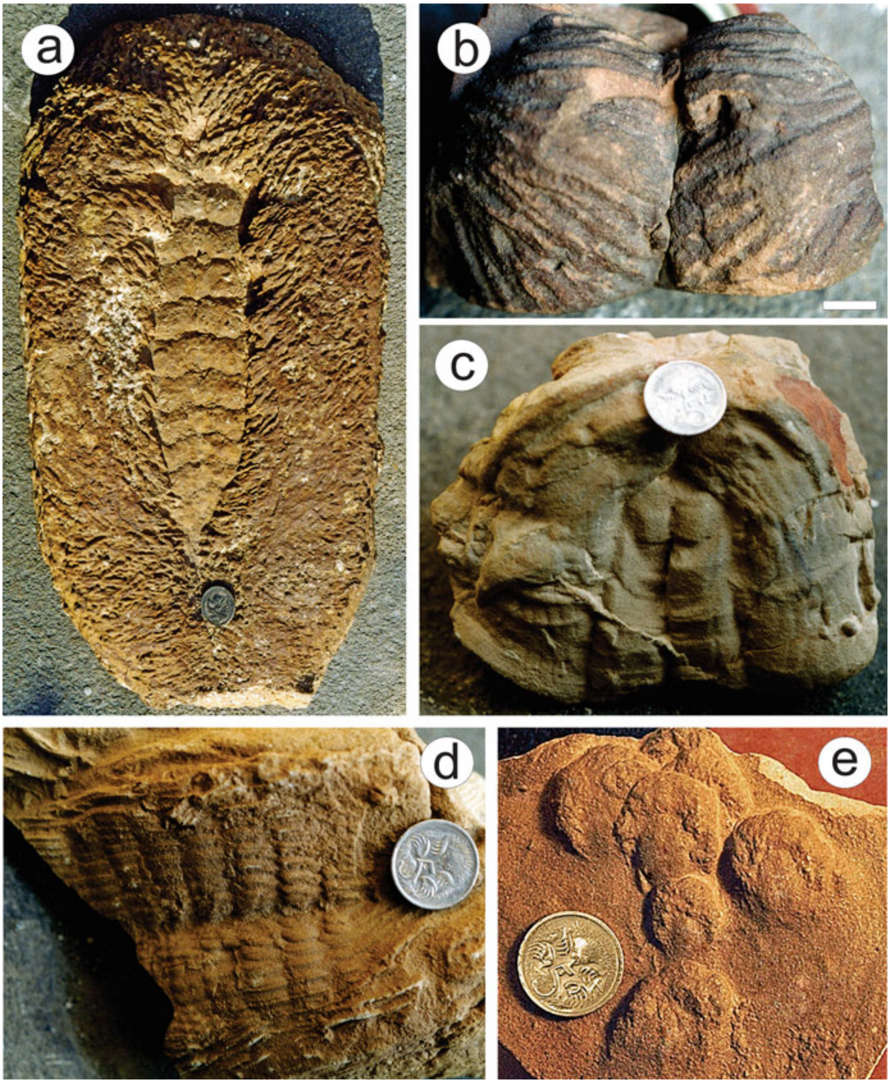

**Fig. 4.5** Examples of Sandbian–Hirnantian trilobite trace fossils. (**a**) *Rusophycus radialis* characterized by large size, radial scratch pattern, and well-developed coxal impressions. Upper Ordovician, Mithaka Formation, Toko Range, Queensland, Australia. Coin diameter 1.9 cm; (**b**) *Cruziana petraea* with rounded and subequal scratch marks. Upper Ordovician, Sabellarifex Sandstone, Sahl-el Karim, Jordan. Scale bar is 1 cm; (**c**) *Rusophycus almadenensis* characterized by a deep head shield impression. Upper Ordovician, Sabellarifex Sandstone, Sahl-el Karim, Jordan. Coin diameter 1.9 cm; (**d**) *Cruziana flammosa* with flame-like front leg scratch marks. Upper Ordovician, Sabellarifex Sandstone, Sahl- el Karim, Jordan. Coin diameter 1.9 cm; (**e**) *Rusophycus perucca* (= *Cruziana perucca*) showing typical deep wig-like structures as a result of leg action. Upper Ordovician, Conularia Sandstone, northwest of Mudawwara, Jordan. Coin diameter 1.9 cm

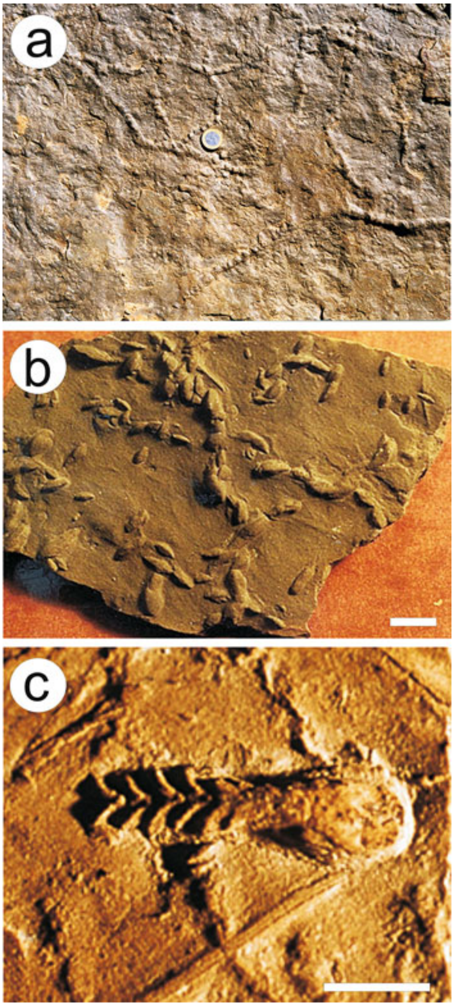

**Fig. 4.6** Examples of morphologic variability of Middle–Upper Ordovician trace fossils. (**a**) *Parataenidium monoliformis*. Darriwilian-Katian, First Bani Group, Jbel Gaiz succession, Morocco. Coin diameter is 2.1 cm; (**b**) *Lockeia siliquaria*, Katian, Cincinnati, Ohio, USA. Scale bar is 1 cm; (**c**) *Protovirgularia rugosa* intergrading with *Lockeia siliquaria*, Katian, Maysville Beds, Cincinnati, Ohio, USA. Scale bar is 1 cm

and abundance of trilobites with the onset of the Paleozoic evolutionary fauna (Sepkoski 1995, 1997; Finnegan and Droser 2008). However, further studies have noted that the actual pattern is far more complex, with the Ibex trilobite fauna actually decreasing in diversity and the Whiterock trilobite fauna increasing its diversity through the Ordovician (Adrain et al. 1998; Westrop and Adrain 1998). In any case, the appearance of newly radiating groups that typify the Paleozoic evolutionary fauna may have contributed to the dilution of trilobite faunas (Westrop et al. 1995), a pattern consisting with the trace-fossil record.

According to the second scenario, the Ordovician trace-fossil record may reflect a preservational bias. Cambrian to Middle Ordovician shallow-marine deposits tend to be dominated by biogenic structures that are thought to indicate firm bottom substrates (Droser et al. 2002a, b, 2004; Dornbos et al. 2004, 2005; Jensen et al. 2006; Tarhan et al. 2012; Mángano et al. 2013). In particular, trilobite trace fossils, such as *Cruziana* and *Rusophycus* with well-preserved bioglyphs, have been regarded as evidence of firmground conditions (Goldring 1995; Droser et al. 2002b). The presence of widespread firmgrounds close to or at the sediment-water interface may have resulted from limited extent and depth of bioturbation in the virtual absence of a biologically mixed layer in the sediment (Droser et al. 2002a, b, 2004). The establishment of the mixed layer during the early Paleozoic, may have been detrimental to the preservation of shallower-tier trilobite trace fossils (Tarhan et al. 2012). This view raises certain issues with respect to the substrate affinities of the *Cruziana* Ichnofacies, which is often cited as one of the typical examples of the Softground Marine Ichnofacies. In fact, the *Cruziana* Ichnofacies reflects an evolutionary control, with classic lower Paleozoic occurrences dominated by trilobite trails and trackways produced on firm substrates and younger ones representing the typical softground examples (Mángano et al. 2013). Finally, it should be stressed that both explanations, dilution of trilobite faunas and formation of the mixed layer, are actually complementary. Further work on the precise timing and environmental controls on these evolutionary innovations is necessary.

## *4.2.2 Shallow-Marine Carbonate Environments*

### 4.2.2.1 Peculiarities of Carbonate Ichnology

Carbonates have certain peculiarities (e.g., role of early cementation, influence of organisms on early diagenesis, common absence of color contrast, heterogeneity in sediment composition and texture) that impact on production and preservation of biogenic structures (Kennedy 1975; Ekdale et al. 1984; Curran 1994, 2007). Although this is not always the case (Droser and Bottjer 1989), some of these factors negatively affect trace-fossil preservation. For example, textural contrasts between trace fossils and the host sediment are rare in carbonates, and color contrasts commonly are induced secondarily, complicating visualization of biogenic sedimentary structures (Curran 1994, 2007; Buatois and Mángano 2011). Interestingly, carbonates with high textural and compositional contrasts tend to favor preservation of discrete trace fossils (Archer 1984; Maples and Archer 1986). In general, mixed carbonate-siliciclastic systems have higher preserved ichnodiversity than pure carbonate deposits.

### 4.2.2.2 The *Thalassinoides* Conondrum

Ichnofaunas in Ordovician shallow-marine carbonate are generally of low to moderate diversity. These ichnofaunas occur in two different contexts: soft (to firm) substrates and hard substrates, represented by bioturbation and bioerosion structures, respectively. The main architectural designs in the first case are branched burrow mazes and boxworks (e.g., *Thalassinoides*), passively filled horizontal burrows (e.g., *Palaeophycus*), actively filled (massive) horizontal burrows (e.g., *Planolites*),

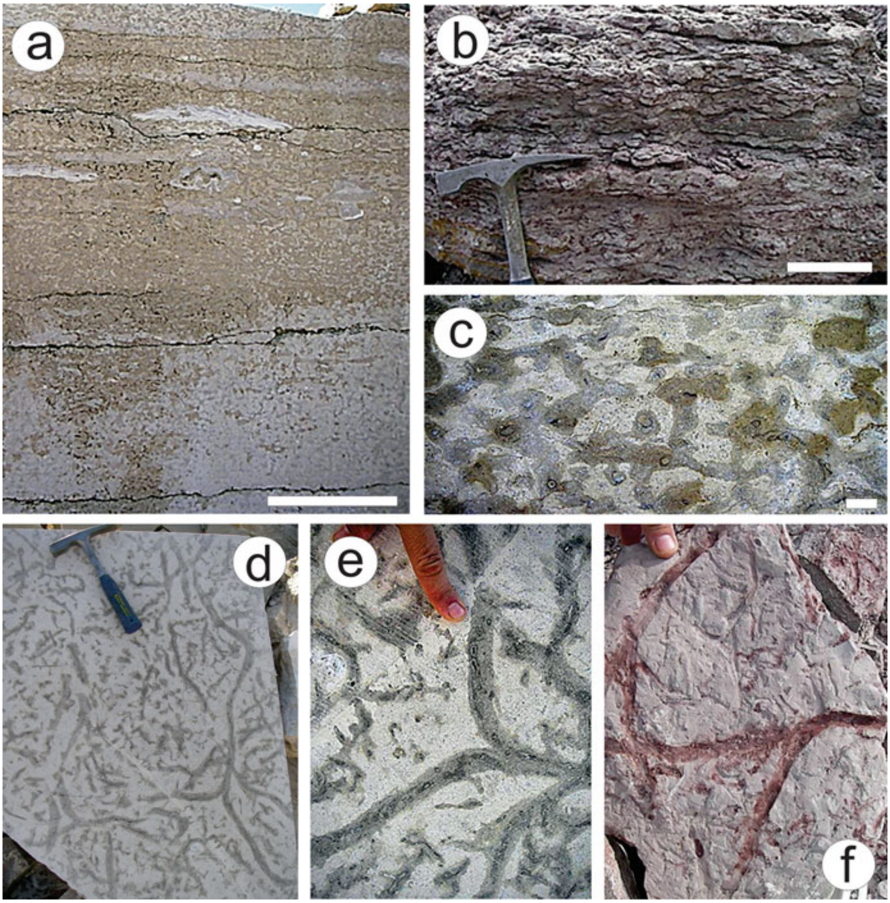

**Fig. 4.7** *Thalassinoides*-like ichnofabrics in Upper Ordovician carbonates. (**a**) Katian, Selkirk Member, Red River Formation, Gillis Quarries, Garson, Manitoba, Canada. Scale bar is 40 cm; (**b**) Katian, Gunton Member, Stony Mountain Formation, Stony Mountain Quarries, Stony Mountain, Manitoba, Canada. Scale bar is 10 cm; (**c**) Katian, Selkirk Member, Red River Formation, Gillis Quarries, Garson, Manitoba, Canada. Scale bar is 1 cm; (**d**) Katian, Selkirk Member, Red River Formation, Gillis Quarries, Garson, Manitoba, Canada. Length of hammer is 33.5 cm; (**e**) Katian, Selkirk Member, Red River Formation, Gillis Quarries, Garson, Manitoba, Canada; (**f**) Katian, Gunton Member, Stony Mountain Formation, Stony Mountain Quarries, Stony Mountain, Manitoba, Canada

dichotomically branching burrows (e.g., *Chondrites*), burrows with vertical spreiten (e.g., *Teichichnus*), burrows with horizontal spreiten (e.g., *Zoophycos*), and vertical U-shaped burrows (e.g., *Arenicolites*).

In particular, *Thalassinoides* is quite common in Ordovician carbonates, typically representing an elite trace fossil (sensu Bromley 1990, 1996). During the Late Ordovician, massive-bedded *Thalassinoides* ichnofabrics were common on carbonate platforms along the paleoequator of Laurentia (Fig. 4.7a–f) (Jin et al. 2012). The identity of the producers of these burrow systems has been strongly debated

(Sheehan and Schiefelbein 1984; Myrow 1995; Ekdale and Bromley 2003; Carmona et al. 2004; Cherns et al. 2006). Ordovician *Thalassinoides* seems to display box-work architecture. However, re-use of burrows (i.e. secondary successive branching) rather than simultaneous branching seems to be a distinctive feature (Figs. 4.7d–f). Unquestioned scratch trace (bioglyph) ornamentation has not been documented (Carmona et al. 2004). These Ordovician examples largely predate the first occurrence of decapod crustacean body fossils in the Devonian (Schram et al. 1978). Accordingly, it has been suggested that these burrow systems were most likely produced by other malacostracans (e.g., phyllocarids) or unrelated clades (e.g., enteropneusts), reflecting behavioral convergence (Carmona et al. 2004). The presence of trilobite body fossils within *Thalassinoides* galleries has been invoked as evidence of tunneling behavior by these animals as well (Cherns et al. 2006). However, it is not uncommon for fossils to be trapped inside burrow galleries, therefore establishing a genetic link between the burrow system and the preserved body fossil may be quite problematic (Buatois and Mángano 2011).

A very similar ichnofabrics to that of *Thalassinoides* in carbonate has been recorded in the Middle Ordovician limestone of Russia and attributed to *Balanoglossites* (Knaust and Dronov 2013). The *Balanoglossites* ichnofabric apparently develops not only in softground and firmground but also in hardground, in cases delineating omission surfaces. These structures were attributed by these authors to eunicid polychaetes having the ability to both bioerode and burrow. According to this study many of the burrow systems in Ordovician limestone currently attributed to *Thalassinoides* may actually belong in *Balanoglossites*.

#### 4.2.2.3 The Ordovician Bioerosion Revolution

During the Ordovician Bioerosion Revolution, macroboring organisms display significant evolutionary innovation and diversification in shallow-water hardgrounds and other carbonate substrates (Fig. 4.8a–e) (Wilson and Palmer 2006). Cambrian macroborings are limited to only two ichnogenera: *Trypanites* (a simple tubular boring penetrating roughly perpendicular to the substrate; see James et al. 1977) and *Oichnus* (a circular hole often attributed to predators and found from the Ediacaran to today; Bengtson and Zhao 1992). During the Ordovician nine additional macroboring ichnogenera appear: *Palaeosabella* (a cylindrical boring with an expanded distal end; Fig. 4.8c; Tapanila and Copper 2002), *Petroxestes* (a slot-shaped boring produced by bivalves; Fig. 4.8d; Wilson and Palmer 1988), *Ropalonaria* (an etching made by ctenostome bryozoans; Fig. 4.8e; Pohowsky 1978), *Sanctum* (an irregular boring inside the endozone of trepostome bryozoan zoaria; Erickson and Bouchard 2003), *Cicatricula* (a radiating boring apparently made by sponges; Palmer and Palmer 1977), *Podichnus* (a cluster of pits associated with pedicle attachments; Santos et al. 2014), *Caedichnus* (a trace associated with the predatory "peeling" of a shell aperture; Stafford et al. 2015), *Tremichnus* (a boring in echinoderm ossicles associated with reactive skeletal tissue; Vinn and Wilson 2015), and *Gastrochaenolites* (a flask-shaped boring, which has been made by bivalves from the later Paleozoic

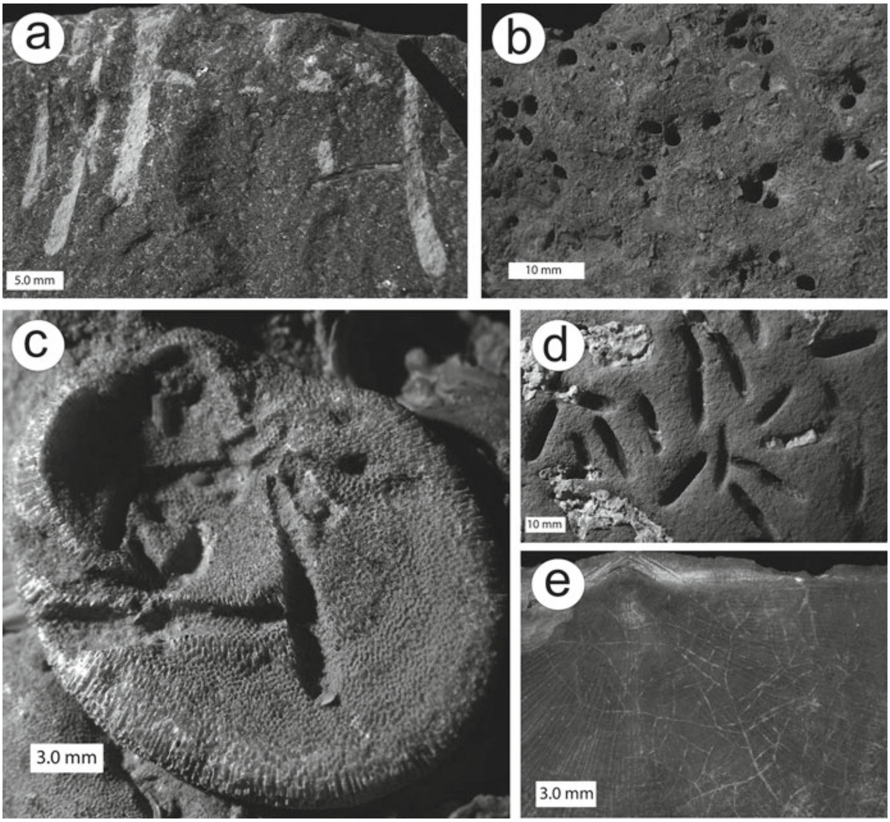

**Fig. 4.8** Upper Ordovician bioerosion structures. (**a**) *Trypanites weisi* (*cross-sectional view*) in a carbonate hardground. Katian, Grant Lake Limestone, near Washington, Kentucky, USA; (**b**) *Trypanites weisi* (*bedding-plane view*) in a carbonate hardground. Katian, Grant Lake Limestone, near Manchester, Ohio, USA; (**c**) *Palaeosabella* isp. in a trepostome bryozoan. Katian, Whitewater Formation, near Richmond, Indiana, USA; (**d**) *Petroxestes pera*. Katian, Whitewater Formation, Caesar Creek Lake emergency spillway, near Waynesville, Ohio, USA; (**e**) *Ropalonaria venosa* in a strophomenid brachiopod. Katian, Liberty Formation near Brookville, Indiana, USA

until today, but in the Ordovician was likely produced by some other taxon; Ekdale and Bromley 2001; Ekdale et al. 2002; Benner et al. 2004, 2008).

Along with the macroboring ichnodiversity increase in the Ordovician is a significant rise in the rate of bioerosion in carbonate substrates. Although rates are difficult to quantify because the length of the colonization windows is not known, Ordovician carbonate substrates are often thoroughly riddled with borings, most from deeply penetrating *Trypanites* and *Palaeosabella* (Taylor and Wilson 2003; Wilson 2007).

The macroboring ichnogenera in Lower Ordovician rocks are rare, represented primarily by *Trypanites*, *Gastrochaenolites* and *Podichnus*. By the Middle Ordovician macroborings became abundant, now also including *Palaeosabella*, *Cicatricula*, *Caedichnus* and *Tremichnus*. Boring activity and diversity appears to have peaked during the Late Ordovician with the addition of *Sanctum* and *Ropalonaria* to the ichnofaunas (Taylor and Wilson 2003; Wilson 2007). The increase in numbers of macroborings may be correlated with the increase in carbonate hardgrounds and heavy calcitic skeletons associated with Calcite Sea geochemistry (Palmer and Wilson 2004).

Ordovician microborings have only recently been studied in detail. Vogel and Brett (2009) examined microborings in skeletal substrates from the Upper Ordovician of the Cincinnati region. Because many of the microborers presumably were photosynthesizers, the first occurrences of ten ichnospecies were sorted into distinctive facies related to light penetration. Much more work needs to be done to place this study in chronological context, but we can at least conclude that by the Late Ordovician diverse microboring communities of cyanobacteria, algae and fungi are fully in place.

### 4.2.3 Deep-Marine Environments

Because body fossils are uncommon in deep-marine deposits, trace fossils are an unparalleled source of information to address the evolution of deep-sea ecosystems. The Ordovician represents a pivotal point in the colonization of the deep sea, which is characterized by a significant turnover in infaunal diversity (Orr 2001; Uchman 2003, 2004; Mángano and Droser 2004; Buatois et al. 2009). Cambrian deep-marine ichnofaunas are dominated by surface-coverage branching burrows (*Oldhamia*), simple horizontal trails (e.g., *Helminthopsis* and *Helminthoidichnites*) and trackways (e.g., *Diplichnites*) (see Chap. 3). These strategies were for the most part linked to exploitation of microbial mats (Buatois and Mángano 2003).

This is in sharp contrast with Ordovician deep-sea ichnofaunas, which typically do not seem to be associated with microbial mats (Buatois et al. 2009). During the Ordovician, the main architectural designs that typify the modern *Nereites* Ichnofacies became established in the deep sea (Uchman 2003, 2004; Mángano and Droser 2004). These include regular networks (e.g., *Megagrapton*, *Protopaleodictyon*, *Paleodictyon*), delicate spiral burrows (e.g., *Spirorhaphe*), guided meandering graphoglyptids (e.g., *Cosmorhaphe*), uniramous meanders (e.g., *Belorhaphe*), and radial graphoglyptids (e.g., *Lorenzinia*, *Yakutatia*). The only exception is biramous meanders, which appeared by the Silurian, being represented by *Desmograpton* (Uchman 2003). In addition to ichnotaxa that later became common in deep-marine ichnofaunas, the ichnogenus *Dictyodora*, a peculiar meandering to spiral complex form, is restricted to the Paleozoic (Benton and Trewin 1980; Benton 1982). In particular, the ichnospecies *Dictyodora simplex* is recorded in the Cambrian and Ordovician, while *D. zimmermanni* is restricted to the Ordovician, and *D. scotica* and *D. tenuis* are Ordovician–Silurian (Mángano et al. 2012).

Some of these morphologic patterns (e.g., regular networks, guided meandering graphoglyptids) were already present in the Cambrian, but they occurred in shallow-water environments (e.g., Crimes and Anderson 1985; Crimes and Fedonkin 1994; Jensen and Mens 1999). This has been interpreted according to the tenets of the onshore–offshore model, as it has been suggested that these complex behaviors first evolved in shallow water, and migrated down toward the deep sea by the Ordovician

(Crimes and Anderson 1985). The explanation for this pattern is far from clear, but it has been postulated that increased competition for ecospace or resources (or both) in shallow-marine ecosystems drove benthic animals into deeper-water settings by the end of the Cambrian (Crimes et al. 1992; Crimes 2001; Orr 2001). However, the actual pattern seems to be much more complicated in some cases, and the timing of migration of some ichnotaxa is uncertain. For example, *Paleodictyon* has been recorded in Middle Cambrian slope deposits, arguing for an early migration to relatively deep waters (e.g., Pickerill and Keppie 1981; Jensen and Palacios 2006). In addition, *Paleodictyon* is present in Upper Ordovician middle- to outer-shelf deposits, suggesting an initial phase of expansion to the deep sea and then a post-Ordovician retreat (Stanley and Pickerill 1993, 1998). In any case, sporadic occurrences of *Paleodictyon* in shallow water are relatively common even in post-Paleozoic rocks (e.g., Fürsich et al. 2007). Regardless of the precise timing, ichnologic evidence indicates that the colonization of the deep sea was a protracted process spanning

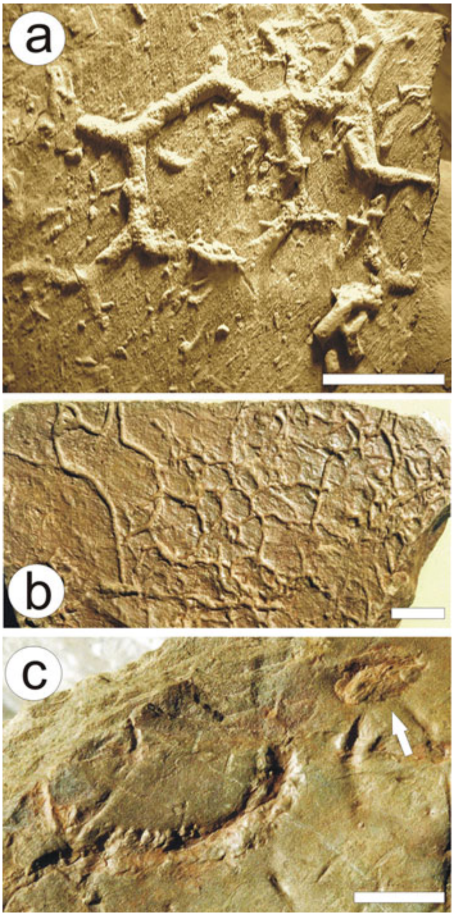

**Fig. 4.9** Deep-marine ichnofaunas, Tremadocian, Chiquero Formation, Susques, northwest Argentina. (**a**) *Paleodictyon* isp.; (**b**) *Multina magna*; (**c**) *Protovirgularia* isp. and *Lockeia* isp. (*arrow*). All scale bars are 1 cm long

much of the early Paleozoic, and lagging behind colonization of shallow-marine environments (Buatois et al. 2009; Buatois et al. 2016b).

By the late Tremadocian, the appearance of radial graphoglyptids and regular networks in deep-water turbidite systems indicates the arrival of novel trophic types (i.e., trapping of microorganisms and bacterial farming) to the deep sea (Buatois et al. 2009). In any case, graphoglyptids apparently were still quite rare, poorly diverse, and geometrically simpler during the Tremadocian (Fig. 4.9a). In contrast, graphoglyptids display much more varied morphologic patterns in the Floian (Crimes et al. 1992). Yet lower to middle Ordovician deep-sea ichnofaunas are dominated by feeding (Fig. 4.9b and c) and grazing trace fossils rather than graphoglyptids (Orr 1996, 2001; Uchman 2003). In contrast, by the Late Ordovician to Early Silurian, deep-marine communities graphoglyptids became more abundant (Orr 2001; Mángano and Droser 2004; Uchman 2004). These complex structures were particularly common in low-energy turbidite frontal splay and levee deposits, but the colonization of high-energy channelized and proximal-lobe areas of turbidite systems was relatively rare during the early Paleozoic (Buatois et al. 2009). These zones were colonized by the Late Jurassic, when *Ophiomorpha* attributed to crustacean galleries became common in thick-bedded sandy turbidites (Tchoumatchenco and Uchman 2001). An increase in ichnodiversity, trace-fossil size, intensity of bioturbation and burrowing depth has been recorded in Middle to Upper Ordovician pelagic radiolarian cherts in comparison with their older counterparts (Kakuwa and Webb 2010).

## 4.3 Trends in Ichnodiversity and Ichnodisparity

Conceptual issues of ichnodiversity and ichnodisparity are presented in Chap. 1 (see also Buatois and Mángano 2013; Buatois et al. 2016c) and will not be repeated here. After the dramatic increase in global diversity of bioturbation ichnogenera that took place during the early Cambrian (Mángano and Buatois 2014; see Chap. 3), ichnodiversity experienced a plateau during the middle to late Cambrian (Buatois et al. 2016b). Analysis of changes in global ichnodiversity throughout the Ordovician indicates a continuous increase in ichnogeneric diversity in both shallow- and deep-marine environments (Fig. 4.10) (Mángano and Buatois 2014; Buatois et al. 2016b). In the case of shallow-marine settings, the diversity of bioturbation structures displayed a 45 % increase from the Tremadocian (73 ichnogenera) to the Hirnantian (106 ichnogenera) (Buatois et al. 2016b). This increase parallels substantial changes in the nature of shell beds (Kidwell and Brenchley 1994; Droser and Li 2001) and compositional turnovers by the dominant bioturbators of shallow-water environments (Mángano and Droser 2004).

The ichnodiversity increase in deep-marine environments was 71 % (31 ichnogenera in the Tremadocian to 53 ichnogenera in the Hirnantian) (Buatois et al. 2016b). The earlier view that early Paleozoic deep-marine ichnofaunas are of low alpha diversity (Seilacher 1974, 1977) has been challenged by discoveries of moderately diverse ichnofaunas in Ordovician deep-marine successions (Chamberlain 1977; Pickerill 1980; McCann 1990; Crimes and Crossley 1991; Orr 1996; Orr and

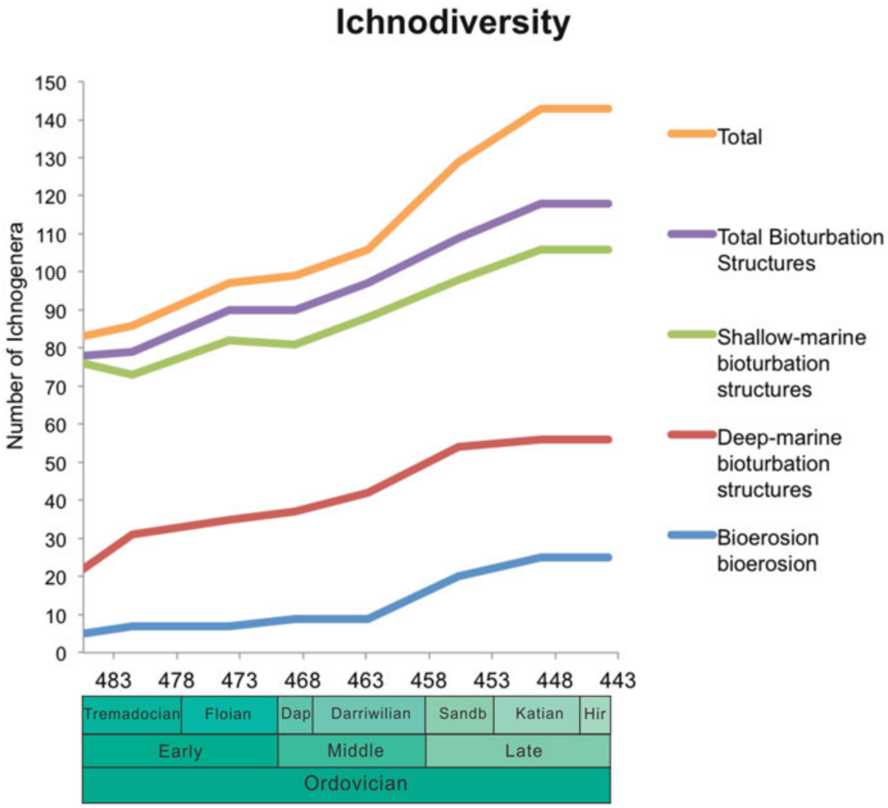

**Fig. 4.10** Trends in ichnodiversity of bioturbation and bioerosion structures through the Ordovician (after Buatois et al. 2016b)

Howe 1999). A systematic compilation by Uchman (2004) showed that 24 ichnogenera occur in the Middle Ordovician to lower Silurian Matapedia Group of Canada, indicating that maximum alpha ichnodiversity tripled with respect to lower Cambrian values (see Chap. 3). Also, one of the signatures of the GOBE in the deep sea is the increased beta ichnodiversity in comparison with Cambrian assemblages. Whereas Cambrian deep-marine trace-fossil assemblages essentially lack ichnogenera that were exclusive from these environments, this picture changed through the Ordovician with the establishment of graphoglyptids in the deep sea. Still, and in contrast to younger deep-marine ichnofaunas, graphoglyptids were not the dominant ichnotaxa in these settings. Uchman (2003, 2004) showed that the maximum proportion of graphoglyptids (13 % in the Matapedia Group) was still remarkably below that of Cenozoic assemblages (a maximum of 39 % recorded from Eocene deep-sea assemblages).

Interestingly, the increase in global ichnodiversity through the Ordovician is not paralleled by an increase in ichnodisparity of bioturbation structures (Fig. 4.11). In fact, whereas Ordovician global ichnodiversity doubled from Cambrian levels, Ordovician ichnodisparity of bioturbation structures is roughly similar to that of the

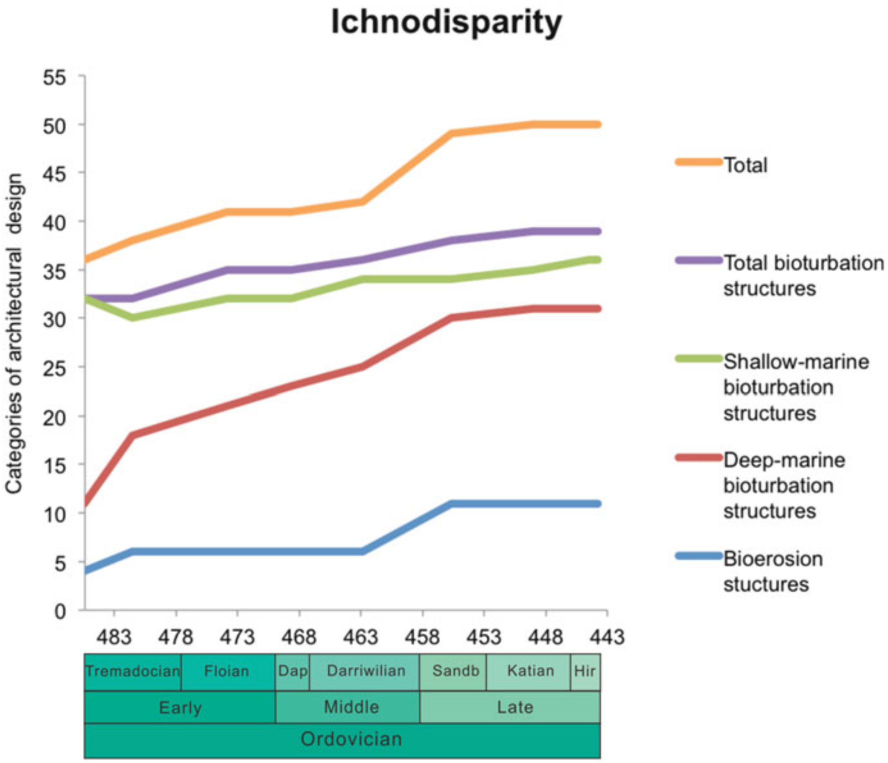

**Fig. 4.11** Trends in ichnodisparity of bioturbation and bioerosion structures through the Ordovician (after Buatois et al. 2016b)

Cambrian explosion (Buatois et al. 2016b). The different natures of the Cambrian and Ordovician radiations have long been recognized. Whereas the vast majority of body plans were established as a result of the Cambrian explosion, taxonomic increases during the Ordovician radiation were manifest at lower taxonomic levels (Droser and Finnegan 2003). The same trend is evident from the different trajectories exhibited by global ichnodiversity and ichnodisparity of bioturbation structures during the Cambrian and Ordovician (Buatois and Mángano 2013; Buatois et al. 2016b).

However, the picture for bioerosion structures is significantly different, with an increase in both ichnodiversity and ichnodisparity through the Ordovician (Figs. 4.9 and 4.10) (Buatois et al. 2016b). In particular, a rapid increase in diversity of bioerosion structures occurred during the Late Ordovician (178 % increase). This diversification of bioerosion structures is paralleled by an increase in ichnodisparity (83 % increase).

Comparative ichnologic analysis of the Cambrian explosion and the GOBE indicates that innovations in bioerosion lagged behind bioturbation for approximately 80 my (Buatois et al. 2016b). The underlying causes of this macroevolutionary lag are hard to decipher. Possible causes for this pattern include a Middle to Late Ordovician increase in available hard substrates for bioerosion, bioerosion driven by increased predation (with structures being in some case produced by predators and in others to escape from predators), and higher energetic costs involved in penetrating hard substrates (Buatois et al. 2016b).

## 4.4 Trends in Tiering Structure and Diachronism in Infaunalization

The ichnologic expression of the GOBE is not only reflected by an increase in ichnodiversity, but also by an increase in degree and depth of bioturbation, as well as of tiering complexity. In this regard, ichnologic information is consistent with the body-fossil record (Ausich and Bottjer 1982; Servais et al. 2010), representing an independent calibration of paleoecologic and macroevolutionary models. Under favorable environmental conditions (e.g., oxygenated bottom and interstitial waters, relatively low energy), high degrees of bioturbation and even complete reworking of the primary fabric was attained (e.g., Dorador et al. 2014).

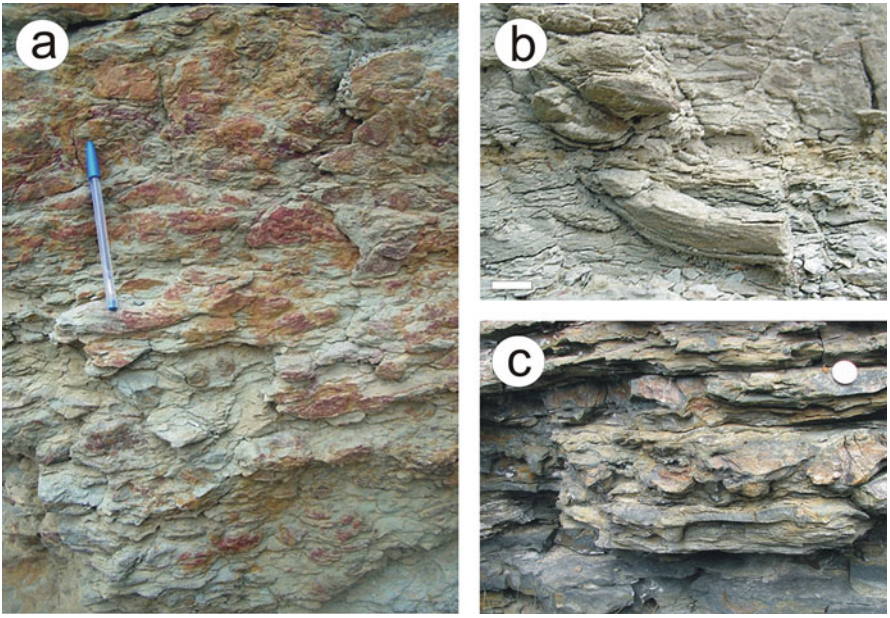

**Fig. 4.12** Lower Cambrian occurrences of the *Trichophycus* ichnofabrics in Baltica and Laurentia. (**a**) Cross-sectional view from the Lower Cambrian Norretorp Member, Bornholm, Denmark. Pencil is 14 cm long; (**b**) close-up showing the overall U-shaped morphology of *Trichophycus*. Lower Cambrian Norretorp Member, Bornholm, Denmark. Scale bar is 1 cm; (**c**) cross-sectional view from the Lower Cambrian Lake Louise Formation of the Gog Group, Canadian Rockies. Coin is 1.8 cm

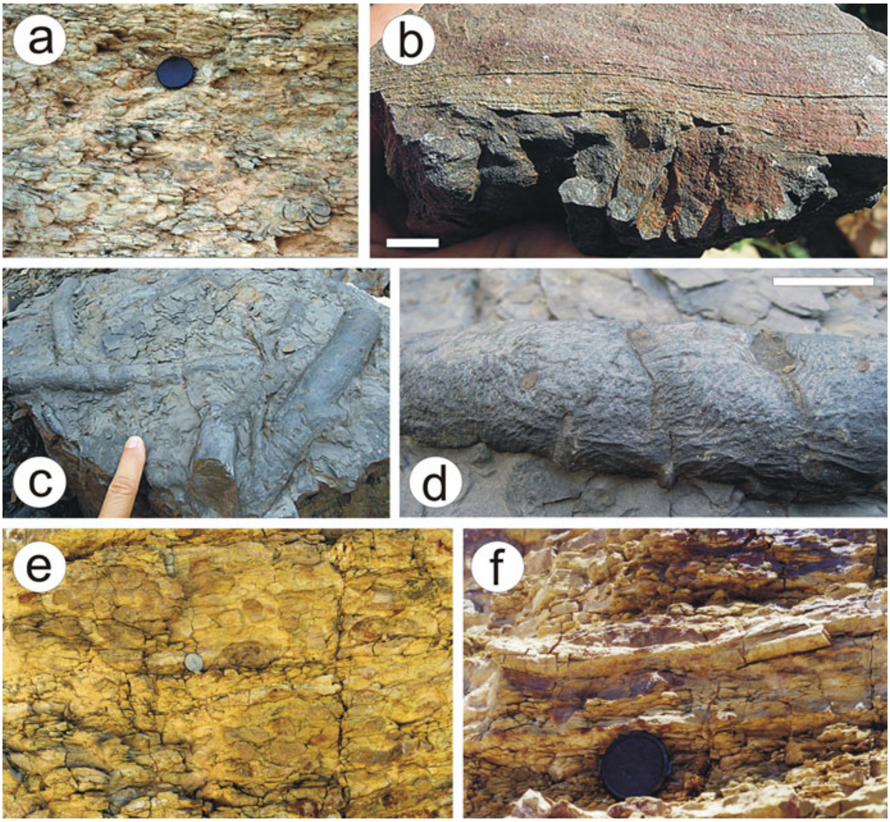

**Fig. 4.13** Upper Tremadocian–Floian occurrences of the *Trichophycus* ichnofabrics in Gondwana. (**a**) Intensely bioturbated deposits. Floian, Upper Fezouta Formation, Imini succession, Central High Atlas, Morocco. Lens cover is 5.5 cm; (**b**) Dense occurrence of *Trichophycus* at the base of a sandstone tempestite. Floian, Powers Steps Formation, Greb Nest, Bell Island, eastern Newfoundland, Canada. Scale bar is 1 cm; (**c**) bedding-plane view of robust *Trichophycus* specimens. Floian, Powers Steps Formation, Greb Nest, Bell Island, eastern Newfoundland, Canada; (**d**) close-up showing distinctive scratch marks. Floian, Powers Steps Formation, Greb Nest, Bell Island, eastern Newfoundland, Canada. Scale bar is 1 cm; (**e**) intensely bioturbated deposits. Upper Tremadocian, Rupasca Member, Santa Rosita Formation, Angosto de Chucalezna, Quebrada de Humahuaca, Argentina. Coin is 1.8 cm wide; (**f**) close-up showing U-shaped morphology of *Trichophycus*. Upper Tremadocian, Rupasca Member, Santa Rosita Formation, Angosto de Chucalezna, Quebrada de Humahuaca, Argentina. Lens cover is 5.5 cm wide

During the early Paleozoic, the tiering structure of ichnofaunas become more complex, as a result of both the addition of deeper tiers and of a wider variety of biogenic structures in previously occupied tiers. This increased complexity is particularly evident in low-energy offshore settings (Mángano and Droser 2004; Mángano and Buatois 2011; Buatois and Mángano 2011). A tendency to occupy slightly deeper tiers through the Ordovician is also evident in individual ichnogenera, such as *Arthrophycus* and *Phycodes* (Seilacher 2000; Mángano and Buatois 2011).

Interestingly, infaunalization by deposit feeders in offshore siliciclastic environments may have been diachronous, with the earlier establishment of a mid-tier infauna in Baltica (Fig. 4.12a and b) and Laurentia (Fig. 4.12c), and only subsequently in Gondwana (Fig. 4.13a–g) (Mángano and Buatois 2011). These authors noted that ichnofabrics containing the mid-tier ichnogenus *Trichophycus*, which crosscuts trace fossils emplaced by trilobites and worms in shallow depths, appeared in Gondwana by the early to late Tremadocian transition. However, identical ichnofabrics are present since the early Cambrian in shallow-marine units of Baltica and Laurentia (e.g., Jensen 1997; Mángano and Buatois 2011; Desjardins et al. 2012b). This indicates that infaunalization in offshore siliciclastics occurred in Laurentia and Baltica as part of the Cambrian radiation, while the delayed appearance of *Trichophycus* in Gondwana may reflect a later-stage dispersal and migration, or behavioral convergence by different producers during the Ordovician radiation (Mángano and Buatois 2011). Ichnologic evidence is consistent with body-fossil information, which suggests that both the timing of diversification and the accompanying ecologic changes during the early Paleozoic were diachronous across the different environments and paleocontinents (Webby et al. 2004; Harper 2006).

Pioneer work in carbonate rocks of the Great Basin documented an increase in the intensity and depth of bioturbation between the Middle and Late Ordovician, mostly resulting from an increase in the size of discrete structures and in the architecture of *Thalassinoides* from networks to mazes (Droser and Bottjer 1989). Up to 1 m deep and 4 cm wide *Thalassinoides* systems, displaying both classic T and Y branchings, are known in Upper Ordovician carbonates (Sheehan and Schiefelbein 1984). *Thalassinoides* is certainly present in Cambrian and Lower Ordovician strata, but burrows typically are less than 1 cm wide and architecturally simpler, forming two-dimensional networks rather than three-dimensional boxworks (Myrow 1995). In contrast, Upper Ordovician *Thalassinoides* display more similarities to modern structures produced by decapod crustaceans recording extensive reworking and intense obliteration of the primary fabric (Sheehan and Schiefelbein 1984; Droser and Bottjer 1989; Jin et al. 2012).

However, there are many departures to some of these trends. For example, Furongian to Tremadocian *Thalassinoides* from lagoonal carbonates in the Argentinean Precordillera shows unquestionable three-dimensional morphology, suggesting an earlier origin of boxwork burrow architecture (Cañas 1995; Mángano and Buatois 2003). In addition, deep-tier *Thalassinoides* mazes occur in lower Cambrian restricted carbonates of northern China, resulting in intense disruption of the primary fabric (Qi et al. 2015). As with siliciclastics, these examples of early infaunalization may underscore that significant diachronism may have been involved in the colonization of infaunal ecospace during the early Paleozoic. Reconstructing links between infaunalization patterns and paleogeography is still in its infancy, but growing evidence suggests that further analysis may unlock paleogeographic control in trace-fossils distribution (Mángano and Buatois 2011; Jensen et al. 2013).

Regardless of the precise timing of infaunalization, ichnofabric evidence also indicates an onshore–offshore pattern as extensive bioturbation first developed in nearshore settings and only later developed in more offshore settings (Droser and Bottjer 1989). The early appearance of boxwork burrows in restricted carbonates seems to be consistent with the pattern of onshore innovation and offshore expansion. Although depth of bioturbation and tiering complexity show a remarkable increase with respect to previous levels, they are still significantly below post-Paleozoic levels (Buatois and Mángano 2011; see Chap. 9).

In contrast to shallow-marine ichnofaunas, lower Paleozoic deep-marine examples typically represent the activity of shallow-tier organisms. However, up to 40 cm deep structures have been reported in levee deposits of a Cambrian-Early Ordovician turbidite system, suggesting colonization of the deeper infaunal ecospace in the deep sea (Pickerill and Williams 1989). Alternatively, these structures may have been produced by “doomed pioneers” (sensu Föllmi and Grimm 1990) transported from shallow-marine to deep-marine environments via turbidity currents (Waldron 1992; Allison and Briggs 1994). In any case, burrows reaching the same depth were also documented in Ordovician deep-marine deposits, and they have been interpreted as produced by a climax suite, rather than doomed pioneers or opportunistic colonizers (Orr 2003). These studies suggest that, although deep-marine trace fossils occupy for the most part shallow- to mid-tier positions, some organisms were able to colonize deep tiers.

## 4.5 Conclusions

Evaluation of the trace-fossil record provides valuable information to aid our understanding of the paleoecologic breakthroughs involved in the GOBE. A continuous increase in diversity of bioturbation structures occurs through the Ordovician in both shallow- and deep-marine environments. This increase in global ichnodiversity of bioturbation structures is not paralleled by an increase in ichnodisparity, because the number of architectural designs in the Ordovician is roughly similar to that resulting from the Cambrian explosion. However, both ichnodiversity and ichnodisparity of bioerosion structures increased during the Ordovician, resulting in the Ordovician Bioerosion Revolution. Lower Ordovician deposits tend to be dominated by abundant trilobite-produced trace fossils, whereas Middle to Upper Ordovician shallow-marine ichnofaunas tend to show more varied behavioral patterns, and trilobite trace fossils are rarely the dominant elements. During the early Paleozoic, the tiering structure of infaunal communities become more complex, as a result of both the addition of deeper tiers and of a wider variety of biogenic structures in previously occupied tiers. The establishment of a deep-marine ecosystem of modern aspect took place by the Late Ordovician. Infaunalization by deposit feeders in offshore siliciclastic environments was most likely diachronous, with the establishment of a mid-tier infauna first in Laurentia and Baltica, and only subsequently in Gondwana.

**Acknowledgments** Tony Ekdale and Thomas Servais provided very useful reviews of this chapter. We thank Laura Piñuela and Jose Carlos García Ramos for providing the photographs included in Fig. 4.2. Dolf Seilacher granted access to his impressive trace fossil collection. Financial support for this research was provided by the Natural Sciences and Engineering Research Council (NSERC) Discovery Grants 311727-05/08/13 and 311726-05/08/15 (to MGM and LAB, respectively).

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# Chapter 5
# The Prelude to Continental Invasion

**Nicholas J. Minter, Luis A. Buatois, M. Gabriela Mángano, Robert B. MacNaughton, Neil S. Davies, and Martin R. Gibling**

## 5.1 Introduction

The invasion of the land has been a protracted process that probably started relatively early in the history of life and continues until today (Buatois and Mángano 1993; Buatois et al. 1998a; Miller and Labandeira 2002; Kennedy et al. 2006). Phylogenetics and genomic timescales suggest a Hadean origin of life, prior to 4.1 Ga, and early colonization of land at 2.8–3.1 Ga (Battistuzzi et al. 2004). The earliest evidence for continental terrestrial ecosystems goes back to the Neoarchean, as documented by geochemical data that suggest the presence of organic matter probably representing remnants of microbial mats in 2.6-Ga-old paleosols (Watanabe et al. 2000). Information from relaxed molecular clocks suggests that cyanobacteria may have originated in continental freshwater environments and subsequently migrated into

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M.G. Mángano, L.A. Buatois (eds.), *The Trace-Fossil Record of Major Evolutionary Events*, Topics in Geobiology 39,
DOI 10.1007/978-94-017-9600-2_5

the ocean by the beginning of the Proterozoic (Blank and Sánchez-Baracaldo 2010; Blank 2013). Microbially induced sedimentary structures have been documented in Paleoproterozoic eolian interdune and playa deposits (Simpson et al. 2013) and late Mesoproterozoic to early Neoproterozoic fluvial and lake-margin deposits (Prave 2002; Callow et al. 2011; Fedorchuk et al. 2016). The timing of the first appearance of land plants is debated, but bryophytes (Strother et al. 2004) may have been present by the Cambrian and geochemical data point to the presence of mycorrhizal fungi on land by this time (Horodyskyj et al. 2012). The earliest evidence of embryophytes comes from the Middle Ordovician (Rubinstein et al. 2010). An increase in clay mineral deposition proposed to have taken place during the Neoproterozoic was linked by Kennedy et al. (2006) to an initial expansion of a terrestrial biota that may have enhanced production of pedogenic clay minerals. Carbon isotopic data has been also put forward to suggest a Neoproterozoic explosion of photosynthesizing communities and greening of the land (Knauth and Kennedy 2009). The most direct biologic evidence is represented by terrestrial microfossils preserved in late Mesoproterozoic and early Neoproterozoic paleokarst surfaces (Horodyski and Knauth 1994) and lacustrine deposits (Strother et al. 2011; Battison and Brasier 2012). This increasingly documented diversity of nonmarine microfossils in later Proterozoic strata suggests that terrestrial habitats may even have been relatively biologically diverse during the interval of 1.8–0.8 Ga, often termed the "boring billion" in the marine record (Wellman and Strother 2015). In short, the available evidence points to the presence of a primitive land biota during the Precambrian, most likely of microbial type. Microbially induced sedimentary structures have an extensive history, but are not specifically considered in our study (see Davies et al. 2016 for further details). We restrict our attention to biogenic sedimentary structures that are the result of behavioral interactions between animals and sediments.

The timing of invasion of the land by animals has been debated and interpretations of the nature of specific deposits are questionable (e.g., Retallack and Feakes 1987; Retallack 2001, 2011a, b, 2012a, b, 2013a, b, 2014; Davies and Gibling 2010, 2012; Davies et al. 2010, 2011a, b; Kennedy and Droser 2011, 2012; McIlroy 2012; Jago et al. 2012; Callow et al. 2013; Xiao and Knauth 2013; Xiao et al. 2013, 2014; Mángano et al. 2014). There is increasing congruence between molecular clock and fossil data for the origins of many clades. Molecular clocks for ecdysozoan evolution have recovered an Ediacaran origin for all major lineages (587–543 Ma) and indicate a Cambro-Ordovician (510–471 Ma) colonization of land by different arthropod groups (Rota-Stabelli et al. 2013). Another analysis has identified a late Cambrian (Furongian) (491 Ma) split between the Xiphosura and Arachnida, and radiation of crown group arachnids during the Early Ordovician (475 Ma); such timing of arachnid origins is consistent with Cambro-Ordovician estimates for terrestrialization (Garwood et al. 2014).

Trace fossils provide direct, in situ evidence for the presence of animals in specific sedimentary environments. They can also predate the oldest body fossils of their inferred progenitors (MacNaughton et al. 2002). Integration of ichnologic and sedimentologic information is of paramount importance in tracking the invasion of the land. To critically evaluate colonization trends, it is important to differentiate between brackish-water ichnofaunas, periodic excursions of amphibious animals onto the land, and true terrestrial ichnofaunas (Buatois et al. 1998a, 2005; Davies et al. 2011b; Mángano et al. 2014). Additionally, to avoid circularity in contentious cases, it is imperative that salinity conditions are established independently of ichnofaunal composition—a task that is not simple to achieve, and which may not even be possible in many successions. Equally important is careful documentation of the relative timing of tracemaker activity and subaerial exposure. For example, close association between trackways and desiccation cracks may record subaerial exposure of a surface that was underwater when an animal moved across it. Similarly, trackways on a wind-marked surface could be undertracks, formed as an animal walked across a slightly younger, subaqueous sediment surface. Careful study of sedimentology and trackway morphology is essential if misinterpretation is to be avoided in such examples. In this chapter, we review the trace-fossil evidence of the initial colonization of the continents. To do so, we focus our analysis on the early evidence of landward migration of animals during the Ediacaran to Ordovician, an event that represents the prelude to the establishment of continental ecosystems later in the Paleozoic (see Chap. 6).

## 5.2 Environmental Framework

Trace fossils provide an advantage in examining changes in occupied ecospace at the community level and across environments because they are generally preserved in situ in precise environmental contexts, and record the activities of both less commonly preserved soft-bodied animals and those with more readily preserved, mineralized hard parts. In our analysis, three main environmental settings have been considered: coastal, alluvial and lacustrine. In turn, each of these settings has been subdivided into three categories in order to reflect an environmental/ecologic gradient from permanently subaqueous to subaerially exposed settings (Fig. 5.1). This generates both a seaward-to-landward gradient and a further gradient based upon the availability of water. The latter is a prime factor responsible for controlling the distribution of trace fossils (Gierlowski-Kordesch 1991; Buatois and Mángano 2002; Minter et al. 2007). Many continental invertebrates are opportunistic r-selected animals and their periods of activity are often associated with wet phases and confined to short-periods of time (Gierlowski-Kordesch 1991; Minter et al. 2007). The availability of water, in terms of moist sediment, also enhances the survivorship and preservation potential of trace fossils (Davis et al. 2007). This framework is regarded as the most appropriate to address routes to land and the colonization of ecospace. In the following text, “transitional” is used to denote settings that were variably subaqueous to subaerial within a limited stratigraphic interval.

The three categories included within coastal settings (subaqueous, transitional, and subaerial) can be understood as reflecting an environmental gradient along a coastal plain. The first two categories reflect for the most part the activity of brackish-water faunas. Fjord areas affected by strong freshwater discharge and tidal flats

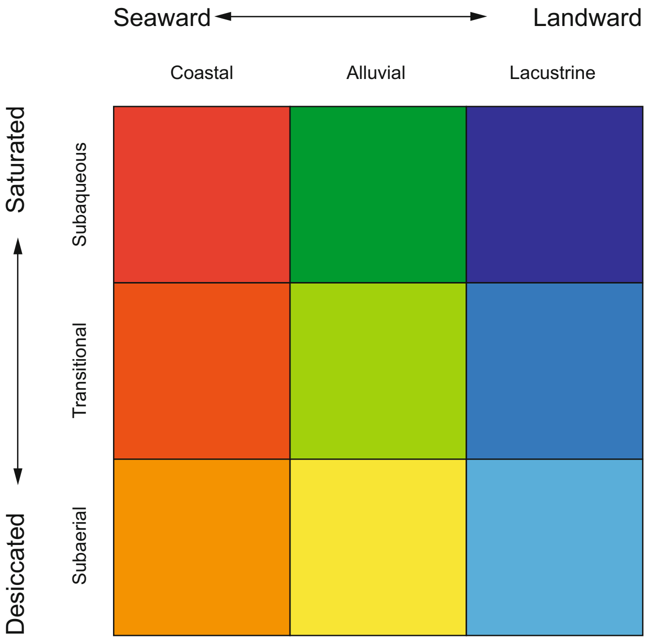

**Fig. 5.1** Environmental framework for analysis of depositional settings

formed in the innermost zones of estuarine systems, between the maximum landward limit of tidal influence and the maximum landward limit of the marine saline wedge, represent a departure from typical marginal-marine conditions because they host freshwater faunas (Buatois et al. 1997; Buatois and Mángano 2007). The subaerial category reflects the activity of terrestrial biotas. The three categories included within alluvial settings (subaqueous, transitional, and subaerial) also illustrate a gradient from active channels to riparian overbank settings and ultimately zones affected by eolian processes. This is more an ecologic gradient rather than an environmental gradient because eolian depositional systems are not necessarily associated with riverine systems. A terrestrial end member along an alluvial continuum is better represented by paleosols (see Chap. 14). The subaqueous category reflects the activity of freshwater biotas, while the transitional one accommodates the work of freshwater to terrestrial faunas. The subaerial category reflects the work of terrestrial animals. The three categories included within lacustrine settings (subaqueous, marginal, and ephemeral) illustrate an ecologic gradient, from fully subaqueous settings to lake margins affected by a fluctuating water table and ultimately to ephemeral water bodies that experienced longer periods of subaerial exposure. While the first two categories reflect environments adjacent in a depositional system, the latter typically illustrates arid to semiarid conditions that occur in connection with eolian or ephemeral fluvial systems. Placing of the different trace fossils in these categories was based on information provided in the literature. In some cases, original environmental interpretations have been adjusted based on information in additional papers dealing with sedimentologic aspects of the unit involved. For each of these environmental categories, we apply the methodology introduced in Chap. 1 to analyze modes of life, ecospace occupation, and ecosystem engineering through time; and also to compare patterns of ichnodiversity and ichnodisparity.

The completeness of the geological record may bias literal reading of the fossil record and results of meta-analytical studies (Benton and Simms 1995; Smith and McGowan 2007; Kalmar and Currie 2010; Mannion et al. 2011). Quantification of the volume of sedimentary rock for sub-Periods for the Phanerozoic reveals an increase in the Ordovician compared to that from the Cambrian. However, the percentages corresponding to terrestrial clastic deposits are uniformly low (2.7–4.2 %) for the early Paleozoic (Ronov et al. 1980) and equate to volumes of $0.5–1.9 \times 10^6$ $km^3$. It is therefore unlikely that there will be any effect of the volume of preserved rock on the patterns observed in the trace fossil record during this time span of the prelude to the colonization of land. A number of well-studied Cambro-Ordovician units corresponding to alluvial sedimentary environments have not yielded any trace fossils other than in intercalated marine units (Davies et al. 2011a). Lacustrine deposits are represented notably also in the Precambrian and preserve microbially induced sedimentary structures (Prave 2002; Callow et al. 2011), but not biogenic sedimentary structures from the activities of animals. As such, a variety of continental environments are represented in the Ediacaran and early Paleozoic, but do not preserve any trace fossils. We can therefore have confidence that the observed distribution of trace fossils for the prelude to the invasion of land is not simply an artifact of unrepresented or unsampled environments.

## 5.3 Ediacaran

Ediacaran ichnofaunas essentially represent the activity of marine biota under normal-salinity conditions (Chap. 2). However, in a few cases, trace fossils and problematica have been mentioned from terminal Ediacaran marginal-marine deposits that formed under subaqueous and transitional conditions.

### *5.3.1 Ediacaran Trace-Fossil Assemblages*

#### 5.3.1.1 Coastal Settings

A limited number of trace-fossil assemblages are currently known from coastal settings in the Ediacaran. These are the Serra dos Lanceiros and Pedra do Segredo formations of Brazil (Netto et al. 1992; Martini da Rosa 1999; Netto and Martini da Rosa 2001a, b; Netto 2012) and the Chapel Island Formation of Canada (Crimes and Anderson 1985; Narbonne et al. 1987; Landing et al. 1988; Gehling et al. 2001).

### Coastal—Subaqueous

The Serra dos Lanceiros and Pedra do Segredo formations of southern Brazil were reported to contain passively filled horizontal to oblique burrows (*Palaeophycus*) and the plug-shaped burrow *Bergaueria*, together with the problematic structure *Intrites* (Netto et al. 1992; Martini da Rosa 1999; Netto and Martini da Rosa 2001a, b; Netto 2012). *Intrites* is now considered to be a body fossil (Gehling et al. 2000) and almost all Ediacaran occurrences of *Bergaueria* have been called into question as dubiofossils or body fossils (Seilacher et al. 2005; Jensen et al. 2006; see Chap. 2). A few additional ichnogenera have been listed for these units but further work is necessary to document the ichnotaxonomic composition of these assemblages. Material identified as the actively filled (massive) horizontal to oblique burrow *Planolites* (Netto et al. 1992; Martini da Rosa 1999; Netto and Martini da Rosa 2001a, b; Netto 2012) is also most likely to be *Palaeophycus*. The structures appear to be present in a coastal-plain succession dominated by channel-fill and overbank deposits, and are thought to have been emplaced under brackish-water conditions during transgression. This very low diversity Ediacaran biota probably inhabited the seaward margin of fluvio-deltaic distributaries, reflecting an early attempt to colonize marginal-marine settings.

Another example comes from Member 1 of the Chapel Island Formation of Newfoundland (Crimes and Anderson 1985; Narbonne et al. 1987; Landing et al. 1988; Gehling et al. 2001). Crimes and Anderson (1985) reported this lowermost member as containing *Planolites*, the simple horizontal trail *Gordia*, *Buthotrephis*, and *Harlaniella*. These latter two are problematic. Uchman (1995) suggested the synonymy of *Buthotrephis* with *Chondrites*, whilst placing *B. palmatus* in *Phycodes*. Crimes and Anderson (1985) do not figure any of their material ascribed to *Buthotrephis* and so it cannot be evaluated. *Harlaniella* has subsequently been identified as a body fossil (Jensen 2003; Seilacher et al. 2005). *Gordia* was recorded to occur together with *Planolites* from a facies association that consists of grey-black laminated siltstones and shales with minor, thin-medium bedded, lenticular grey-green sandstones, and syneresis cracks (Crimes and Anderson 1985; Landing et al. 1988). This facies association is interpreted to have formed mostly under subaqueous conditions in an enclosed embayment or semi-restricted nearshore setting with channels (Landing et al. 1988). However, Ediacaran examples of *Gordia* and *Planolites* have not been illustrated for these deposits, and this occurrence needs to be checked in more detail.

### Coastal—Transitional

A second facies association within Member 1 of the Chapel Island Formation also contains *Planolites* in addition to horizontal burrows with horizontal to vertical branches (*Treptichnus* isp. but not *T. pedum*) (Landing et al. 1988; Gehling et al. 2001). Whereas convincing illustrations of *Treptichnus* are available, examples of *Planolites* have not been figured. This facies association comprises red and green sandstones, siltstones and mudstones with desiccation and syneresis cracks, current ripples, mud-chip conglomerates, and erosion surfaces. It has been interpreted as representing a tidally influenced intertidal to supratidal environment (Landing et al. 1988). In addition, Landing et al. (1988) reported the body fossil *Intrites* from this facies association.

### *5.3.2 Ediacaran Ecospace Occupation and Ecosystem Engineering*

In terms of the establishment of continental ecosystems, occupied ecospace in the Ediacaran is at best limited to the colonization of subaqueous and transitional marginal-marine coastal environments, essentially by the end of this period (Figs. 5.2 and 5.3). In subaqueous and transitional coastal environments, maximum bioturbation depth is limited to the shallow infaunal and semi-infaunal tiers

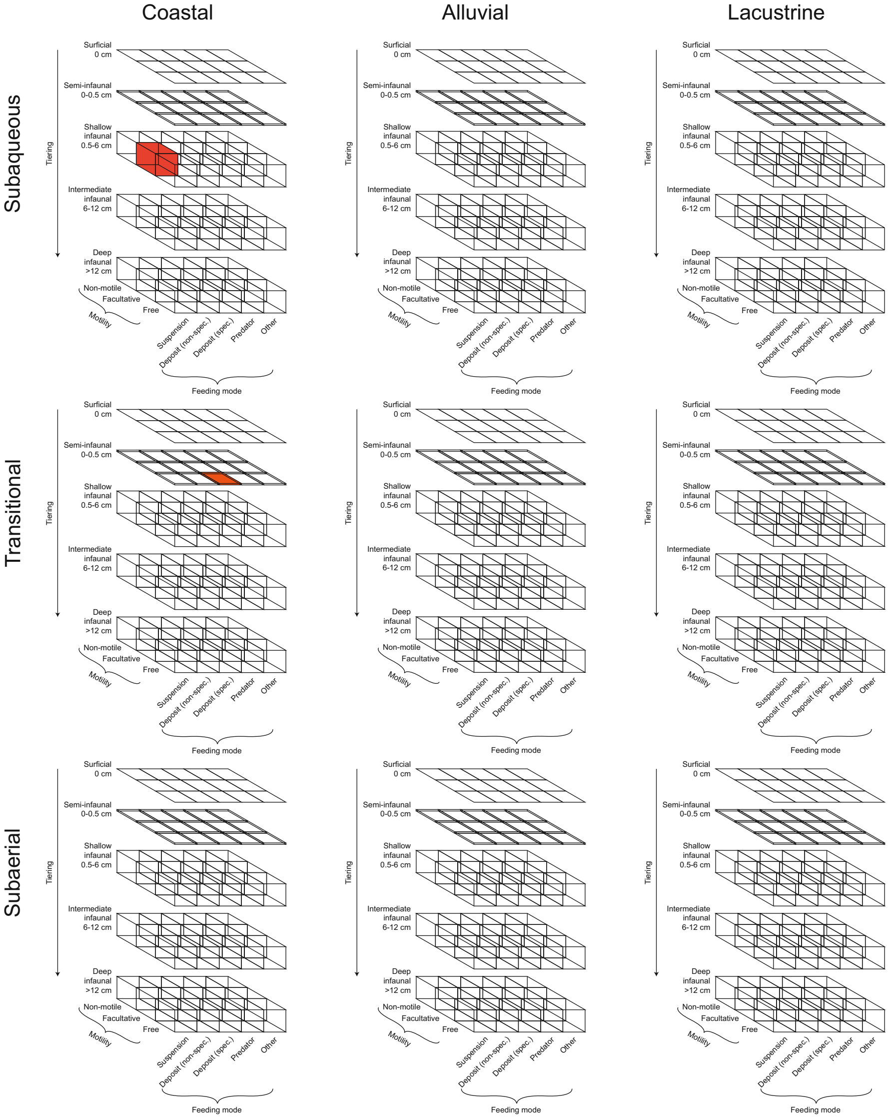

**Fig. 5.2** Ediacaran ecospace occupation

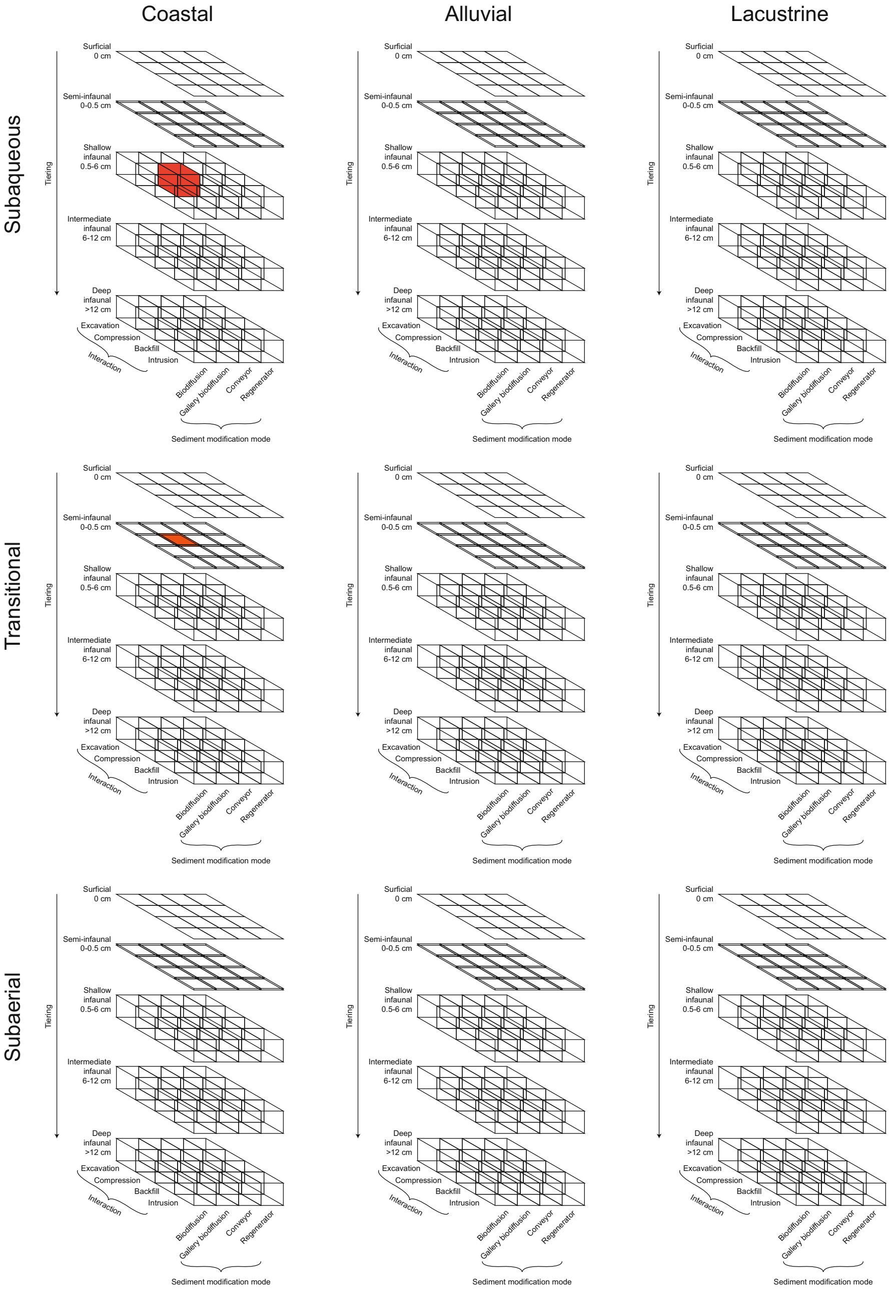

**Fig. 5.3** Ediacaran ecosystem engineering

respectively. In subaqueous coastal environments, facultatively mobile suspension feeders created open horizontal to oblique burrows by compression, generating gallery biodiffusive structures that extended down to the shallow infaunal tier. In transitional coastal settings, freely mobile but specialized deposit feeders created horizontal burrows with horizontal to vertical branches by compression in the semi-infaunal tier, also generating gallery biodiffusive structures. Reported occurrences of *Planolites* and *Gordia* in coastal deposits of this age are either not verifiable at present due to lack of figured material or, in the case of *Planolites* from Brazil, most likely represent *Palaeophycus*. Pending further study of this significant period in Earth history, a conservative estimate of the influence of bioturbating animals on the environment suggests that it was limited to the production of gallery biodiffusive structures by facultatively mobile, shallow infaunal tier suspension feeders (*Palaeophycus*) and freely mobile semi-infaunal deposit feeders (*Treptichnus*).

In addition to reworking sediment, indirect evidence from microfossils, biomarkers and evidence for ocean chemistry demonstrate the fundamental importance of primitive suspension-feeders in reducing the prevailing, ubiquitous global-ocean stratification and promoting alternative clear-water conditions for subsequent utilization (Butterfield 2011). Although the record is limited, Ediacaran marine trace fossils may have recorded the earliest incipient instances of metazoans as ecosystem engineers in fully marine environments, a novel ecological capacity that was to be an intrinsic component of the impending Paleozoic establishment of continental ecosystems.

## 5.4 Cambrian

Animals began their first forays on to land during the early Cambrian. The trace-fossil record of these earliest movements is found in marginal-marine paralic settings and intertidal and coastal-dune environments of North and South America, Europe, Africa, the Middle East, and Asia. Ichnologic evidence suggests that marine animals colonized very shallow-water settings and in some instances were able to tolerate brackish-water conditions or make amphibious excursions onto land. However, truly terrestrial or freshwater ichnofaunas seem to have been absent.

### *5.4.1 Early Cambrian Trace-Fossil Assemblages*

#### 5.4.1.1 Coastal Settings

A greater number of trace-fossil assemblages are known from coastal settings during the early Cambrian compared to the Ediacaran. These occur from the Fortunian Rosenhof Member of the Nama Group of Namibia (Geyer and Uchman 1995) and Kalk Gat Formation of the Vanrhynsdorp Group in South Africa (Buatois et al. 2007; Almond et al. 2008; Buatois et al. 2013); Fortunian to Cambrian Stage 2

Backbone Ranges Formation of Canada (MacNaughton et al. 1997; MacNaughton and Narbonne 1999); Cambrian Stage 2 Zhongyicum Member of China (Crimes and Jiang 1986); Terraneuvian to Cambrian Series 2 Wood Canyon Formation (Hogan et al. 2011; Kennedy and Droser 2011) and Tapeats Sandstone (Hagadorn et al. 2011a) of the USA; Cambrian Stage 2–3 Herrería Sandstone and Cándana Quartzite of Spain (Crimes et al. 1977), and Lake Oesa Member of the Gog Group of Canada (Desjardins et al. 2010, 2012a); Cambrian Stage 3–4 Rome Formation of the USA (Mángano et al. 2014); and Cambrian Stage 4 to Series 3 Campanario Formation of Argentina (Mángano and Buatois 2003, 2004). Other assemblages in deposits whose ages are not constrained beyond early Cambrian occur in the Paseky Shale (Mikuláš 1995) and in the subsurface (Vavrdová et al. 2003) of the Czech Republic, and in olistoliths encased within the Middle Ordovician Los Sombreros Formation of Argentina (Astini et al. 2000).

Integration of sedimentologic and ichnologic data indicates that only marginal-marine environments, rather than true continental settings, were colonized by animals in the early Cambrian. These settings can be categorized under three principal contexts: subaqueous coastal conditions within braid-delta settings, estuaries or bays, and transitional conditions associated with tidal flats (see Mángano and Buatois 2015, for a review). In this analysis, the latter category is reserved for clear examples with sedimentologic evidence of tidal processes and subaerial exposure (e.g., truncated ripple crests, desiccation cracks) and sound sequence-stratigraphic contexts for intertidal positions (e.g., presence in fining-upward parasequences resulting from progradation in tide-dominated shorelines).

### Coastal—Subaqueous

The Wood Canyon Formation of Death Valley, California contains simple (*Skolithos*) and single U-shaped (*Arenicolites*) vertical burrows, and complex actively filled (meniscate/pelletoidal) horizontal burrows (*Psammichnites*). In a high-profile paper, these were suggested to indicate an early metazoan invasion of the freshwater realm (Kennedy and Droser 2011, 2012). However, previous work had described metazoan traces from the same interval within a holistic sedimentologic and regional geologic study, suggesting that they were likely indicators of marine incursions onto distal fluvial/braid delta sands (Fedo and Cooper 2001). The fluvial origin of the trace fossil-bearing strata was questioned also on ichnologic and sedimentologic grounds by McIlroy (2012) and Davies and Gibling (2012) and is contrary to the most recent stratigraphic and paleoenvironmental frameworks for the Death Valley region (Hogan et al. 2011).

The Wood Canyon Formation succession comprises three facies: a basal massive and trough cross-bedded, poorly sorted cobble conglomerate that fills erosionally based amalgamated channels; parallel-laminated red mudstone; and channelized coarse-grained sandstone and arkosic pebble-conglomerate (Kennedy and Droser 2011). Trace fossil occurrences are limited to situations where the mudstone facies overlies the channelized facies and were attributed to the tops of fluvial channels.

However, in a separate study Davies et al. (2011b) attributed these facies to a distal braid-delta setting. Kennedy and Droser (2012) argued against these deposits being marine on the grounds that they are texturally submature and arkosic, although Davies and Gibling (2012) noted that there are records of cross-bedded conglomerates and arkosic sheet sandstones from marine environments. They also stressed the difficulty of separating marine from nonmarine facies at this time in Earth history due to the lack of vegetation, pointing out that mudstone facies are particularly rare in Cambrian alluvial deposits and that those from the Wood Canyon Formation most likely represent marine offshore fines derived from wind processes from the land (Davies and Gibling 2012). Finally, all other well-documented occurrences of *Psammichnites* are marine to marginal marine, with no examples documented from continental settings (Mángano et al. 2002). Accordingly, the most parsimonious interpretation is of a brackish-water rather than freshwater fauna, with bioturbation in brackish-water, marine-influenced channels.

The Tapeats Sandstone of Arizona and Nevada contains two facies suites with trace fossils (Hagadorn et al. 2011a). The first consists of trough cross-bedded, ribbon- or flaser-bedded, planar laminated or tabular subarkosic to arenitic sandstone with minor mudstone. Herringbone cross-bedding and reactivation surfaces are also present. The deposits are interpreted to have formed in intertidal to shallow subtidal settings with brackish or variable salinity, within a braided fluvial or estuarine setting. Monotaxic assemblages comprising *Arenicolites* are present, whereas *Planolites* and *Skolithos* occur locally (Hagadorn et al. 2011a). *Aulichnites*, a junior synonym of *Psammichnites* (Mángano et al. 2002), is noted as being rare but was not illustrated and cannot be evaluated. As such, the ichnofauna is similar to that of the Wood Canyon Formation. Trackways (*Diplichnites*), "worm" trails and vertical tubes are also recorded in this facies suite. The lack of "typical" marine trace fossils was used to suggest that some of this facies suite may have been deposited under continental conditions (Hagadorn et al. 2011a), but the presence of assemblages dominated by *Arenicolites* is consistent with brackish-water conditions, and *Psammichnites* is only known from marine and marginal-marine settings (Mángano et al. 2002). Therefore, a continental environment is unsupported by ichnologic evidence. The second suite comprises interbedded sandstones and shales interpreted as an intertidal transition zone from continental-coastal marine to exclusively marine conditions (Hagadorn et al. 2011a). The ichnofauna comprises *Skolithos*, *Arenicolites*, vertical single U-shaped burrows (?*Diplocraterion*), *Planolites*, *Treptichnus*, *Psammichnites* (*Aulichnites* in original publication), bilaterally symmetrical short, scratched burrows (*Rusophycus*), bilobate trails and paired grooves (*Cruziana*), *Diplichnites*, scratch trace fossils (*Monomorphichnus*), and horizontal burrows with vertical spreiten (*Teichichnus*).

The Herrería Sandstone of Spain contains trace-fossil assemblages from subaqueous and transitional settings. Near Porma Dam, it preserves high-angle and herringbone cross-stratified arkosic sandstones and granule conglomerates interbedded with thin shales that are interpreted as fluvially influenced tidal channels (Crimes et al. 1977). These deposits represent a similar context to that of the Wood Canyon Formation, and they contain *Diplocraterion* and *Rusophycus* (Crimes et al. 1977).

Early Cambrian brackish-water marine embayments and estuaries typically host low-diversity ichnofaunas. The Paseky Shale of the Czech Republic contains *Diplichnites*, several ichnospecies of *Monomorphichnus* and a further scratch trace (*Dimorphichnus*), as well as coprolites and possible specimens of *Rusophycus* and *Bergaueria* (Mikuláš 1995). The same deposits contain a well-preserved arthropod biota (Chlupáč 1995). The environmental setting of this unit is a restricted, brackish-water bay (Chlupáč 1995; Geyer et al. 2008). Similarly aged marginal-marine deposits in the subsurface of the Czech Republic contain *Skolithos*, *Planolites*, and *Diplocraterion* (Vavrdová et al. 2003). These may have accumulated in nearshore areas in the distal regions of a braidplain system. The Lake Oesa Member of the Gog Group in the Canadian Rocky Mountains includes trace-fossil assemblages that can be attributed to exclusively subaqueous or transitional coastal settings. In the case of the former, planar, trough, and herringbone cross-stratified sandstones with mudchips and reactivation surfaces are interpreted as subtidal sand sheets and contain *Skolithos* (Desjardins et al. 2010, 2012a). The Rome Formation of Tennessee records landward incursions of trilobites, with trace fossils from subtidal and intertidal settings (Mángano et al. 2014). Thick-bedded sandstones and dolostones interpreted as forming under subtidal conditions yield *Rusophycus*, *Bergaueria*, and horizontal burrows with horizontal to vertical branches (*Phycodes*). The Backbone Ranges Formation of northwestern Canada includes interdistributary bay, lagoon, and abandoned distributary facies (MacNaughton et al. 1997). These strata contain a moderate diversity ichnofauna that is dominated by abundant *Planolites* but also contains simple horizontal trails (*Helminthoidichnites*), *Palaeophycus*, *Rusophycus*, *Teichichnus*, *Treptichnus*, and undescribed, graphoglyptid-like traces (MacNaughton and Narbonne 1999). Unnamed simple horizontal burrows are also locally common in tidally influenced sandstones (MacNaughton and Narbonne 1999). The deposits contain herringbone cross-stratification but evidence of subaerial exposure was not reported, suggesting deposition in tidally influenced interdistributary bays or abandoned distributaries (MacNaughton et al. 1997).

### Coastal—Transitional

The earliest Cambrian examples of tidal-flat ichnofaunas with evidence of subaerial exposure are from the Nama-Vanrhynsdorp Basin in Namibia and South Africa. *Treptichnus pedum* is associated with desiccation cracks in tidal-flat deposits of the Rosenhof Member of the Nama Group in Namibia (Geyer and Uchman 1995). The same ichnospecies (Fig. 5.4a) occurs in a similar context in the Kalk Gat Formation of the Vanrhynsdorp Group in South Africa (Buatois et al. 2007, 2013; Almond et al. 2008). Here it is found within flaser- and wavy-bedded heterolithic strata with wave- and current-ripple cross-lamination, parallel lamination, and parting lineation. Truncated ripples indicate exposure and possible tidal conditions (Tanner 1958), supported by the presence of double mudstone drapes. Buatois et al. (2013) interpreted the facies as representing shallow subtidal sandbars, lower intertidal sandflats, and middle intertidal mixed flats, with trace fossils more common in the lower intertidal sandflats.

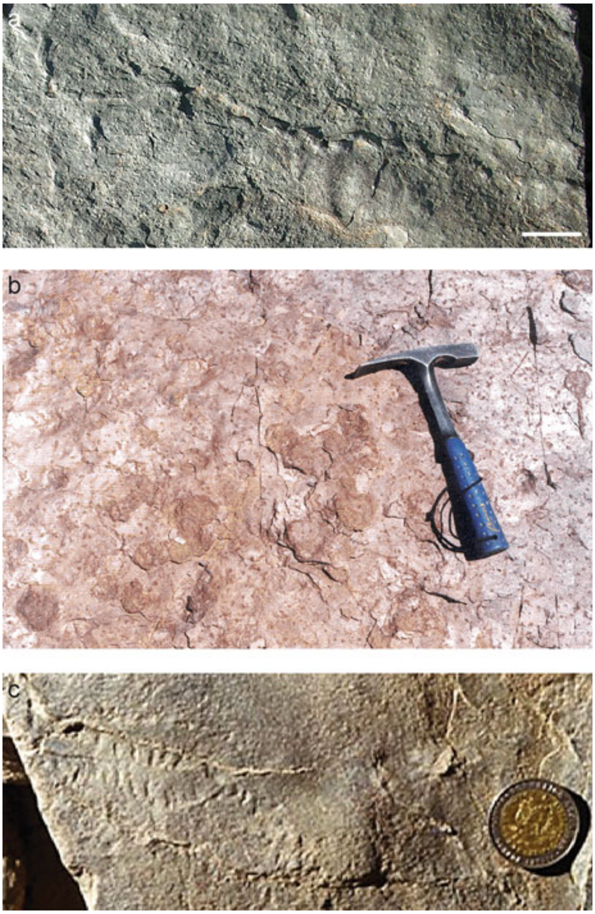

**Fig. 5.4** Selected Cambrian trace fossils from transitional settings within coastal environments. (**a**) *Treptichnus pedum* from Fortunian tidal-flat deposits of the Kalk Gat Formation, Vanrhynsdorp Group, South Africa. Scale bar is 10 mm; (**b**) Bedding plane view (*top*) of a concentration of *Rusophycus leifeirikssoni* in mixed-flat deposits of the lower to middle Cambrian, Campanario Formation, Mesón Group, NW Argentina. Hammer is 335 mm long; (**c**) *Diplichnites* isp. from upper Cambrian middle estuarine tidal rhythmites, of the Pico de Halcón Member, Santa Rosita Formation, NW Argentina. Coin is 22 mm in diameter

The Rubia Beds of the Cándana Quartzite of Spain contain fining-upward successions of herringbone cross-stratified granule to medium-grained quartzite with erosional bases and mudchips, interbedded with mudcracked sandstone and shale with flaser and lenticular bedding (Crimes et al. 1977). The quartzites are interpreted as having formed in tidal channels and the heterolithic strata as deposited on intertidal sand and mud flats. *Arenicolites* and *Rusophycus* are found within and at the tops of quartzite beds, whereas *Skolithos* occurs within the heterolithics and *Diplocraterion* is present throughout quartzite and heterolithic facies (Crimes et al. 1977). At Meishucun in China, a 0.3 m unit of grey, thin bedded, oolitic or pseudo-oolitic dolomitic phosphorite of the Zhongyicun Member may represent intertidal conditions and contains the trace fossils *Cruziana*, *Rusophycus*, *Monomorphichnus*, and bilobate trails and paired grooves (*Didymaulichnus*) (Crimes and Zhiwen 1986).

The Herrería Sandstone, in its shale-dominated lower part between Los Barros de Luna and Irede, contains discontinuous quartzites interbedded with trilobite-bearing, mudcracked heterolithics that are interpreted as tidal channel and intertidal mudflat deposits (Crimes et al. 1977). *Planolites*, *Skolithos*, *Arenicolites*, *Diplocraterion*, *Rusophycus*, and *Cruziana* are present. The upper part contains the same facies in addition to low-angle cross-stratified and parallel-laminated quartzites interpreted as beach deposits (Crimes et al. 1977). The trace-fossil assemblage comprises *Skolithos* and other vertical simple burrows (*Monocraterion*), *Planolites*, *Arenicolites*, *Diplocraterion*, *Rusophycus*, *Monomorphichnus*, *Diplichnites*, *Bergaueria*, and other plug-shaped burrows (*Astropolichnus*; *Astropolithon* in original publication). The type material of *Monocraterion* from the Mickwitzia Sandstone belongs to the architectural design of radial to rosette burrows (see Chap. 16); although the majority of material that has been identified as *Monocraterion* around the world represents vertical simple burrows. Near Porma Dam, heterolithic deposits with herringbone cross-stratified quartzites are interpreted as formed in tidal channels and intertidal flats and contain *Planolites*, *Skolithos*, *Arenicolites*, *Diplocraterion*, *Cruziana*, *Rusophycus*, and *Diplichnites*. The same trace fossils, together with *Phycodes*, *Teichichnus*, and *Psammichnites* (*Plagiogmus* in the original study), occur within interbedded herringbone cross-stratified quartzites and shales interpreted as intertidal and shallow subtidal flat deposits (Crimes et al. 1977).

In addition to subtidal sand-sheet deposits, the Lake Oesa Member of the Gog Group also includes lenticular- and flaser-bedded heterolithic deposits that contain a low-diversity suite of trace fossils that comprises *Rusophycus*, *Dimorphichnus*, *Diplichnites*, *Helminthoidichnites*, and other simple horizontal trails (*Helminthopsis*). Associated wrinkle marks, interference ripples and mudcracks indicate that the trace fossils were emplaced in very shallow water and that the tracemakers may have been matground grazers (Desjardins et al. 2010, 2012a). Similarly, the Rome Formation also includes heterolithic deposits with desiccation cracks that represent middle to upper intertidal flats and contain *Cruziana*, *Rusophycus*, *Monomorphichnus*, *Dimorphichnus*, and trackways (*Petalichnus*), together with *Planolites*, *Palaeophycus*, and *Skolithos* (Mángano et al. 2014). Tidal-flat deposits, mostly sand to mixed-flat facies, of the Campanario Formation of northwestern Argentina contain abundant *Rusophycus* (Fig. 5.4b), *Helminthoidichnites*, *Palaeophycus*, *Skolithos* and three-dimensional spreiten traces (*Syringomorpha*) (Mángano and Buatois 2003, 2004). Elsewhere in Argentina, *Cruziana* and *Rusophycus* have been documented from tidal flat deposits with desiccation cracks and structures indicative of very shallow-water conditions (e.g., truncated ripples). These deposits occur in lower Cambrian olistoliths encased within the Middle Ordovician Los Sombreros Formation in the Precordillera region (Astini et al. 2000).

## *5.4.2 Middle to Late Cambrian Trace-Fossil Assemblages*

### 5.4.2.1 Coastal Settings

As in the case of lower Cambrian examples, younger Cambrian ichnofaunas have been recorded from marginal-marine paralic environments (e.g., estuaries and deltas) and intertidal settings. In connection with the latter, there is substantial evidence from North America for animals beginning to make excursions onto the land in coastal settings. Trace-fossil assemblages from transitional coastal settings are known from the Cambrian Series 3 Oville (Legg 1985) and Furongian to Lower Ordovician (Floian) Cabos (Baldwin 1977) formations of Spain; and Furongian Pico de Halcón Member of the Santa Rosita Formation of Argentina (Buatois and Mángano 2003; Mángano and Buatois 2003; Buatois et al. 2006). Abundant evidence for animals making forays onto the land comes from the middle Cambrian to Furongian Elk Mound Group of the USA (Driese et al. 1981; Hagadorn et al. 2002; Getty and Hagadorn 2008, 2009; Hagadorn and Seilacher 2009; Collette and Hagadorn 2010; Collette et al. 2010), the Potsdam Group of the USA and Canada (MacNaughton et al. 2002; Getty and Hagadorn 2008, 2009; Hagadorn and Belt 2008; Collette and Hagadorn 2010; Collette et al. 2010; Hagadorn et al. 2011b), and the Lamotte Sandstone and Gasconade formations of the USA (Getty and Hagadorn 2008, 2009).

Data for animals in middle to late Cambrian (Furongian) subaqueous coastal settings are more limited and extend to: the middle Cambrian Bright Angel Shale of the USA (Baldwin et al. 2004); and middle Cambrian (Series 3) Hanneh Member of the Burj Formation and the overlying upper Cambrian (Furongian) Umm Ishrin Formation of Jordan (Selley 1970; Amireh et al. 1994; Hofmann et al. 2012; Mángano et al. 2013).

### Coastal—Subaqueous

The Tapeats Sandstone of Arizona is overlain by the Bright Angel Shale, attributed to an unincised, low-relief estuary (Baldwin et al. 2004) and containing a moderate-diversity ichnofauna of *Skolithos*, *Diplocraterion*, *Monomorphichnus*, *Cruziana*, *Rusophycus*, *Planolites*, *Palaeophycus*, and *Teichichnus*. The late Cambrian to Ordovician rocks of Jordan contain a number of ichnofaunas dominated by *Cruziana*, *Rusophycus*, *Diplichnites* and other trackways (*Merostomichnites*) together with *Skolithos* and *Didymaulichnus* (Selley 1970; Amireh et al. 1994). These deposits were originally interpreted as fluvial and deltaic by Selley (1970). More recently, detailed studies of the Hanneh Member of the Burj Formation and the overlying Umm Ishrin Formation documented *Rusophycus*, *Cruziana*, *Skolithos*, and escape trace fossils from proximal to distal delta-front facies (Hofmann et al. 2012; Mángano et al. 2013).

### Coastal—Transitional

Within the Burj and Umm Ishrin formations, *Cruziana*, *Rusophycus*, *Diplichnites*, and *Dimorphichnus* were identified also in tidal-flat and proximal delta-front deposits within a braidplain delta complex (Hofmann et al. 2012; Mángano et al. 2013), with *Diplichnites* and *Dimorphichnus* specifically associated with wrinkle marks, suggesting stabilization of the substrate by microbial mats (Makhlouf and Abed 1991; Mángano et al. 2013).

A tidal-flat trace-fossil assemblage is present in the Oville Formation of Spain (Legg 1985). Evidence of lower intertidal sandflat to middle intertidal mixed flat and tidal channel conditions comes from wavy and lenticular heterolithics, herringbone cross-stratification, wave- and current-ripple cross-lamination, parallel lamination, and desiccation cracks. Trace fossils comprise *Skolithos*, *Arenicolites*, *Diplocraterion*, *Treptichnus*, *Teichichnus*, *Cruziana*, *Rusophycus*, *Monomorphichnus*, and *Diplichnites* (Legg 1985). A further, partly contemporaneous trace-fossil assemblage from Spain occurs within the Cabos Series (Baldwin 1977). Trace fossil-bearing deposits here consist of flaser, wavy and lenticular heterolithics with current- and wave-ripple cross-lamination, and desiccation cracks. These are interpreted as middle intertidal mixed flats to upper intertidal mudflats and tidal channels and contain *Skolithos*, *Diplocraterion* (*Corophioides* in the original study), *Cruziana*, *Rusophycus*, *Monomorphichnus*, *Dimorphichnus*, and *Didymaulichnus* (*Fraena* in original publication). However, further sedimentologic work in these units is needed to test the tidal origin of these successions.

Ichnofaunas associated with estuarine valleys occur in Furongian peri-Gondwanic successions. The Pico de Halcón Member of the Santa Rosita Formation in northwest Argentina contains two trace-fossil assemblages: the first comprising *Cruziana*, *Rusophycus*, *Diplichnites*, *Monomorphichnus*, *Palaeophycus*, *Planolites*, *Teichichnus*, *Diplocraterion*, *Skolithos*, and plug-shaped burrows (*Conostichus*); and the second comprising *Diplichnites* (Fig. 5.4c), *Skolithos* and *Palaeophycus* (Buatois and Mángano 2003; Mángano and Buatois 2003; Buatois et al. 2006). Both assemblages represent lower intertidal sand flats to shallow subtidal flats but the first was formed in the outer region of a tide-dominated estuary whereas the second was formed in middle-estuarine tidal rhythmites. Trace fossils are significantly absent in more proximal facies, such as inner estuarine channel and bar deposits, which may have represented the landward limit to colonization due to extreme brackish-water conditions (Buatois and Mángano 2003; Mángano and Buatois 2003; Buatois et al. 2006).

In the Elk Mound Group of Wisconsin, Driese et al. (1981) identified tidal-flat deposits with *Cruziana*, *Rusophycus*, and *Planolites*. Additionally, *Diplichnites*, other trackways (*Protichnites*), trails with undulating transverse bars and furrows (*Climactichnites*), oval-shaped impressions (*Musculopodus*), *Monomorphichnus*, *Gordia*, and rope-like trace fossils have been identified (Hagadorn et al. 2002; Getty and Hagadorn 2008, 2009; Hagadorn and Seilacher 2009; Collette and Hagadorn 2010; Collette et al. 2010). Material identified as *Helminthoida* has been reported as well (Hagadorn et al. 2002), but this ichnogenus is not considered a valid ichnotaxon (Uchman 1995). The material has not been figured, and so we are unable to reassign it to any valid ichnotaxon. *Cruziana*, *Rusophycus*, and the rope-like trace fossils are associated with phyllocarid crustaceans (Collette and Hagadorn 2010; Collette et al. 2010). The trace-fossil assemblage from the Potsdam Group resembles that from the Elk Mound Group, with reports of *Climactichnites*, *Diplichnites*, *Protichnites*, *Didymaulichnus*-like bilobate trails, *Musculopodus*, and *Cruziana* from tidal-flat deposits (Getty and Hagadorn 2008, 2009; Hagadorn and Belt 2008; Collette and Hagadorn 2010; Collette et al. 2010). The *Cruziana* and *Didymaulichnus*-

like trace fossils preserve euthycarcinoids at their terminations (Collette et al. 2010). This suite from intertidal deposits of the Elk Mound and Potsdam groups is associated with mudcracks and raindrop imprints, suggesting at least intermittent subaerial exposure (Collette et al. 2010). *Climactichnites* and *Musculopodus* have been also reported from tidal-flat deposits of the Lamotte Sandstone and Gasconade formations (Getty and Hagadorn 2008, 2009).

Tidal-channel deposits identified in the Elk Mound Group contain *Skolithos* and *Arenicolites* (Driese et al. 1981). In addition, Collette and Hagadorn (2010) noted the presence of *Skolithos* and *Arenicolites* in the Potsdam Group. No detailed information is given on this occurrence, but it is probably similar to the scenario in the Elk Mound Group where these ichnogenera occur in tidal channels adjacent to the tidal flat. Shallowly dipping cross-beds in the Ausable-Covey Hill Formation of the Potsdam Group contain *Arenicolites* together with *Diplichnites* and *Protichnites*, and these traces were emplaced on and within the bottomsets of seaward migrating coastal dunes (Hagadorn et al. 2011b).

### Coastal—Subaerial

MacNaughton et al. (2002) reported an occurrence of arthropod-produced trackways in large-scale cross-stratified quartz sandstones in southeastern Ontario (Fig. 5.5). These strata were interpreted as eolian based on the scale and style of the cross-beds, and on the presence of wind ripples, adhesion marks, and inverse grading produced by climbing wind ripples (Fig. 5.5b). Local lenses of quartz-pebble conglomerate were interpreted as ephemeral-stream deposits. No sedimentary evidence for marine conditions was found. Trackways are robust and abundant, occurring on at least 11 bedding surfaces. At least two varieties of *Protichnites* (Fig. 5.5c) and one of *Diplichnites* (Fig. 5.5d) are present. They are interpreted to have been produced by euthycarcinoids, and MacNaughton et al. (2002) inferred a marginal-marine dunefield setting, based in part on the in-phase gait displayed by the trackways, which suggested that the animals were amphibious rather than fully adapted to life on land. This occurrence was considered to be within the Nepean Formation (Potsdam Group) and at that time could not be constrained more narrowly in age than Furongian to Darriwilian. Subsequent work has suggested that the Nepean Formation is unlikely to be younger than Furongian (Dix et al. 2004). More recently, this locality was reassigned to the middle Cambrian (Cambrian Series 3) Hannawa Falls Member of the Covey Hills Formation (Sanford and Arnott 2010). The Hannawa Falls Member was considered to be entirely of nonmarine origin and it was suggested that the trackmakers had "… migrated a long distance from the nearest seaway and hence had become adapted to continental conditions" (Sanford and Arnott 2010, p. 45). If this interpretation is correct, then these trackways are highly anomalous in the Cambrian. Although the eolian origin of the beds at the trackway site is not controversial, the work of Sanford and Arnott (2010) was a regional study of stratigraphy and tectonics, and a detailed sedimentologic analysis of Cambrian outcrops around the trackway site probably is needed. The revised stratigraphic

**Fig. 5.5** Cambrian arthropod trackways from subaerial coastal environments. (**a**) Locality in the middle Cambrian (Cambrian Series 3) Hannawa Falls Member of the Covey Hills Formation, Ontario, Canada. Note large-scale foresets well exposed at *right* of photograph. *Top* of outcrop is a major bounding surface. Trackways are abundant on bedding surfaces in outcrop and float; (**b**) Quarried slab from trackway locality, showing well developed adhesion ripples. Lens cap for scale; (**c**) *Protichnites* from a quarried block at the Kingston trackway locality. Compass is 10 cm long; (**d**) *Diplichnites* from another quarried block at the locality. Note the "back-push" mounds, providing evidence for subaerial production by an animal going uphill. Compass is 10 cm long

assignment suggests that these trackways are of similar age to reports of *Diplichnites*, *Protichnites*, and paired grooves (cf. *Diplopodichnus*) by Hagadorn et al. (2011b) from interfingering eolian dunes and marine deposits of the Ausable-Covey Hill Formation in northern New York State—a setting much like that inferred originally for the Ontario trackways (MacNaughton et al. 2002).

### 5.4.3 Cambrian Ecospace Occupation and Ecosystem Engineering

Integration of ichnologic information within a sedimentologic framework suggests that no true terrestrial animals were established during the Cambrian. Instead, the emerging picture is one of relatively low-diversity communities in marginal-marine settings, such as tidal flats, estuaries and bays (Buatois et al. 2005). Ichnofaunas from these restricted settings reflect the establishment of brackish-water communities rather than freshwater or terrestrial biotas. Notably, some of these animals may have been able to survive intermittent periods of desiccation and even to foray into subaerial settings, as illustrated by trackways in coastal-dune deposits of eastern North America (MacNaughton et al. 2002; Hagadorn et al. 2011b). This ichnologic evidence indicates the initial stages of routes to the land.

As in the Ediacaran, Cambrian coastal subaqueous settings play host to animals filling shallow infaunal tier roles of facultatively mobile suspension feeders and possible predators. However, ichnodiversity, ichnodisparity, ecospace occupation, and ecosystem engineering in coastal Cambrian subaqueous and transitional settings show a marked increase from those in the Ediacaran (Figs. 5.6 and 5.7). Cambrian subaqueous coastal settings record a global total of 20 ichnogenera, corresponding to 14 architectural designs, 15 modes of life, and ten impacts upon the sediment. Ichnodiversity and ichnodisparity are greater in coastal transitional settings, with a global total of 27 ichnogenera that represent 15 architectural designs, 14 modes of life, and 11 methods of modifying the sediment. Many ichnogenera are shared amongst the two settings. All of those present in subaqueous coastal settings, except *Merostomichnites*, a graphoglyptid-like trace fossil, and escape trace fossils, are found within coastal transitional settings. Coastal Cambrian trace-fossil assemblages that formed under subaerial conditions are limited and of very low ichnodiversity and ichnodisparity, comprising a global total of just three ichnogenera, corresponding to two architectural designs. These represent two modes of life that have a single type of impact upon the sediment.

Occupied ecospace in both subaqueous and transitional coastal settings during the Cambrian was similar to a large extent. All except one of the modes of life recorded in subaqueous settings are represented in transitional settings. This mode is represented by a graphoglyptid-like trace fossil reported from the Backbone Ranges Formation of Canada (MacNaughton and Narbonne 1999). Graphoglyptids are complex patterned trace fossils that are typically interpreted to represent farming behavior of freely mobile animals in the semi-infaunal tier. Such trace fossils would

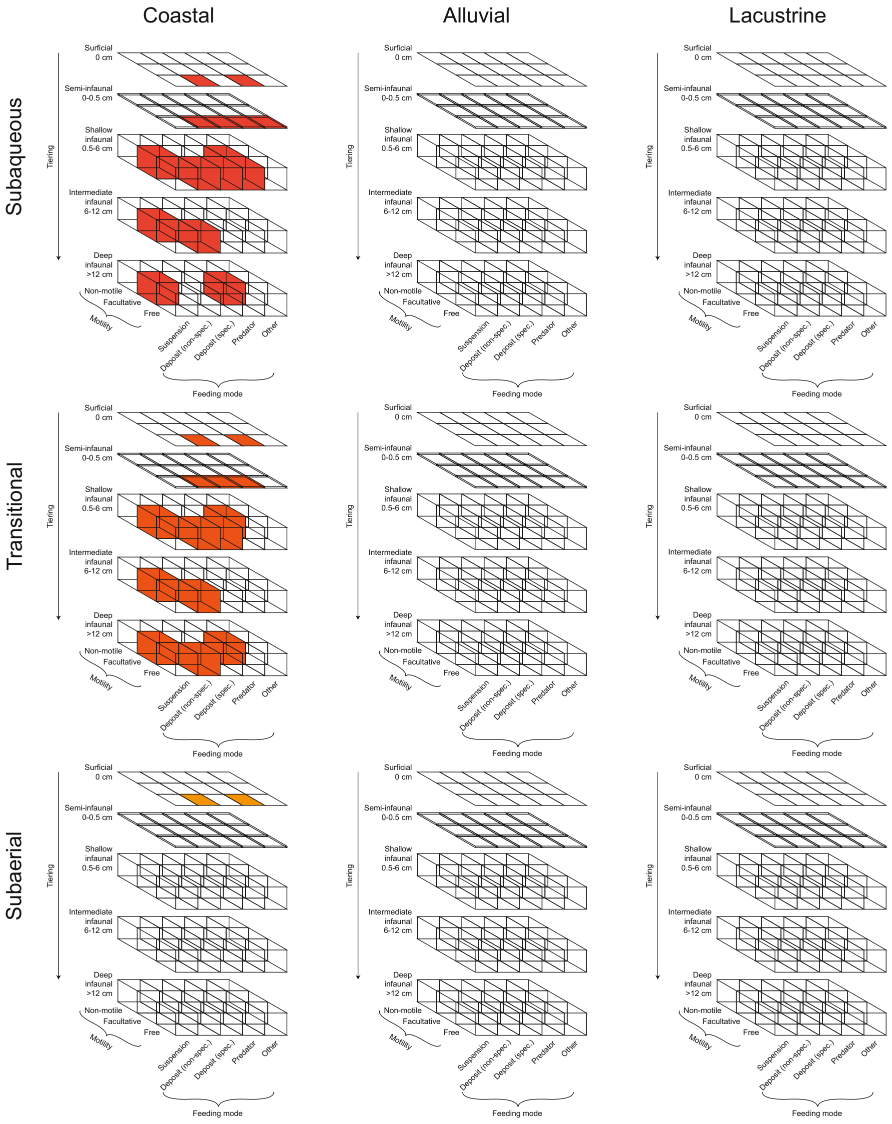

**Fig. 5.6** Cambrian ecospace occupation

have been produced by compression and acted as gallery biodiffusive structures. Escape trace fossils of shallow infaunal tier, freely mobile, non-specialized deposit feeders or possible predators are present in subaqueous but absent in transitional coastal settings. The latter possible mode of life is also not represented by other trace fossils from transitional coastal settings. Such escape trace fossils were produced by intrusion through the sediment, resulting in biodiffusion of sediment particles.

Both subaqueous and transitional coastal settings contained facultatively mobile suspension feeders that inhabited shallow to deep infaunal tiers, as well as freely

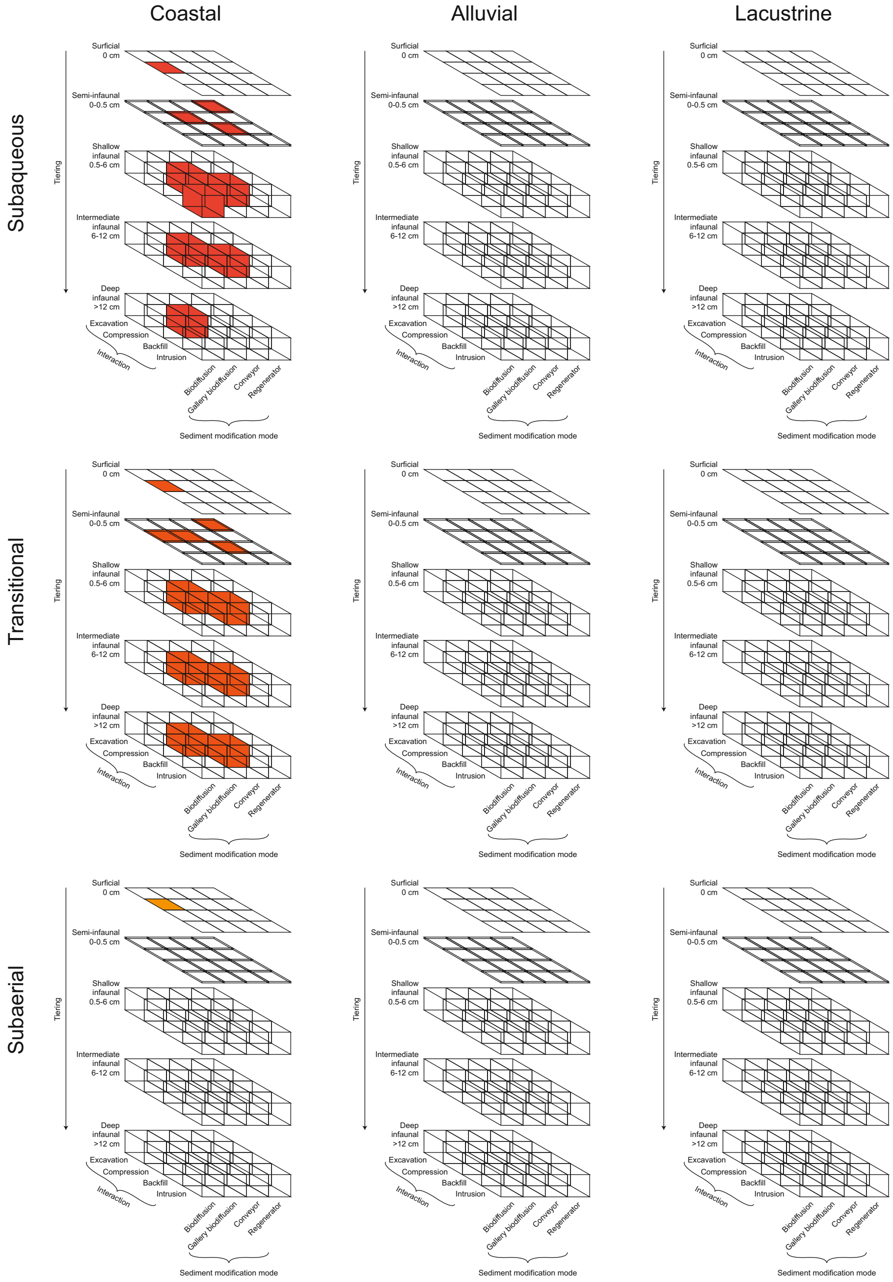

**Fig. 5.7** Cambrian ecosystem engineering

mobile non-specialized deposit feeders that occupied the surficial to intermediate infaunal tiers. Some of these animals may have been predators. Freely mobile specialized deposit feeders also occupied the shallow and semi-infaunal tiers. Taken as a whole, the suspension-feeding animals were responsible for producing a variety of gallery biodiffusive structures by compression. These comprised deep and intermediate tier vertical single U- and Y-shaped burrows, deep tier vertical simple burrows, and plug-shaped and passively filled horizontal to oblique burrows in the shallow infaunal tier. Furthermore, specialized deposit feeders produced complex actively filled (meniscate/pelletoidal) horizontal burrows in the shallow infaunal tier, with the producer moving through the substrate by backfilling and acting as a sediment conveyor. In the semi-infaunal tier, other freely mobile specialized deposit feeders produced horizontal burrows with horizontal to vertical branches by compression that acted as gallery biodiffusive structures. Infaunal non-specialized deposit feeders acted as sediment conveyors, moving through the sediment via backfilling to produce intermediate tier vertical burrows with spreite, and shallow tier simple, actively filled (massive) horizontal to oblique burrows. In the semi-infaunal tier, non-specialized deposit feeding vermiform animals and possible arthropods produced simple horizontal trails by backfilling and acted as sediment conveyors. Further in this tier, non-specialized deposit feeding and possible predatory arthropods were responsible for bilobate trails and paired grooves as well as bilaterally symmetrical short, scratched burrows. These animals excavated the substrate whilst plowing through it, which resulted in sediment regeneration. Additional non-specialized deposit feeding and possible predatory arthropods also occupied the surficial realm and produced a variety of trackways and scratch marks. Such animals would have had minimal impact on the substrate, with production of their compressive tracks causing small-scale biodiffusion of the sediment.

The above role includes the trackway *Merostomichnites*, which is present in coastal subaqueous settings but has not been recorded from transitional settings. Of the roles being performed in both subaqueous coastal and transitional settings during the Cambrian, a number are represented by additional ichnogenera in transitional settings compared to the number recorded in subaqueous settings. These include: the shallow tier plug-shaped burrows *Conostichus* and *Astropolichnus* produced by facultatively mobile suspension feeders; and the trackways *Protichnites* and *Petalichnus*, produced by arthropods and recording surficial, freely mobile, non-specialized deposit feeders, and possibly also predatory animals. This indicates a similar amount and range of ecospace being occupied but a greater number of animals fulfilling the same roles and occupying that ecospace.

In addition to *Cruziana* and *Rusophycus*, non-specialized deposit feeders that were freely mobile and inhabited the semi-infaunal tier are further represented by *Climactichnites* and *Musculopodus* in transitional settings. However, these trace fossils are attributed to molluscs as opposed to arthropods and constitute trails with undulating transverse bars and furrows, together with oval-shaped impressions that are produced by compression and have minimal biodiffusive impact on the substrate. This contrasts with *Cruziana* and *Rusophycus*, which are produced by excavation and result in regeneration of sediment.

The three-dimensional spreiten trace *Syringomorpha* is one architectural design present in transitional settings that is absent from Cambrian subaqueous coastal environments and it constitutes a different mode of life. *Syringomorpha* was produced by deep tier, freely mobile and non-specialized deposit feeders that moved through the sediment by backfilling and acted as sediment conveyors. The fact that *Syringomorpha* is typically present in clean sandstone devoid of organic detritus suggests possible alternative feeding strategies, such as exploitation of meiofauna or microbial films on sand grains (Mángano and Buatois 2004).

Evidence for animals inhabiting subaerial settings within coastal environments appears for the first time during the Cambrian. This is limited to the trackways *Diplichnites* and *Protichnites* and paired grooves *Diplopodichnus* produced by freely mobile surficial and non-specialized deposit feeding and possible predatory arthropods. The animals responsible had minimal impact upon the substrate, with their compressive tracks and trails causing small-scale disruption of sediment grains by biodiffusion. Of these ichnogenera, *Diplichnites* is shared with coastal subaqueous and transitional settings, and *Protichnites* with transitional settings. *Diplopodichnus* is exclusive to subaerial settings.

A number of phyla have macroscopic forms that have colonized the land and could potentially produce trace fossils: the Annelida, Arthropoda, Chordata, Cnidaria, Mollusca, Nematoda, Nemertea, Onychophora, Platyhelminthes, and Tardigrada. Cnidarians were probably responsible for shallow plug-shaped burrows found in subaqueous and transitional coastal settings. Of the remaining phyla, there is definitive trace fossil evidence that arthropods and molluscs had already begun to colonize at least intermittently exposed transitional coastal settings by the middle to late Cambrian (Furongian), as had possibly one or more of the annelids, nematodes, and nemerteans. The producers of semi-infaunal bilobate trails, paired grooves, and bilaterally symmetrical short, scratched burrows in subaqueous and transitional coastal settings were all likely trilobites. Trilobites were probably also responsible, together with other arthropods such as euthycarcinoids, aglaspidids, chasmataspidids, marellamorphs, and myriapod-like animals, for surficial trackways and scratch marks. Unusual examples of *Protichnites* with obliquely segmented medial impressions were, at one point, attributed to eurypterid-like stem arthropods carrying mollusc shells, in a mode analogous to hermit crabs, in order to reduce desiccation of the gills when out of water (Hagadorn and Seilacher 2009). However, this interpretation was abandoned in favor of a euthycarcinoid producer (Collette et al. 2012). Microbial sedimentary structures occur in association with such trace fossils, and microbial mats could have provided a food source for these animals. Mortichnial associations between arthropod body fossils and their locomotion, feeding, and resting or sheltering traces may point to strategies for avoiding desiccation in the intertidal zone by sheltering under algal mats or being shallowly buried (Collette et al. 2010). Further surficial trace fossils, consisting of trails with undulating transverse bars and furrows, plus oval impressions, associated with arthropod trackways in tidal-flat deposits, were probably produced by molluscs. Trackways and trails left behind in coastal dune deposits represent evidence of the first truly amphibious excursions of arthropods onto land. Such trackways were probably produced by euthycarcinoid or myriapod-like arthropods (MacNaughton et al. 2002; Hagadorn et al. 2011b). Producers of vertical simple burrows, single U- and Y-shaped burrows, horizontal burrows with vertical spreiten, passively and actively filled horizontal to oblique burrows, horizontal burrows with horizontal to vertical branches, and simple horizontal trails were probably made by worm-like animals or arthropods.

In short, integration of ichnologic and sedimentologic evidence within a sequence-stratigraphic framework indicates that the Cambrian explosion was not restricted to fully marine settings. On the contrary, there is solid evidence to suggest that key evolutionary innovations associated with this evolutionary event also took place in marginal-marine settings (Mángano and Buatois 2004, 2015; Mángano et al. 2014).

## 5.5 Ordovician

In the Ordovician, trace-fossil assemblages that record the movements of animals onto land have a global distribution, with reports from Antarctica, Africa, North America, and Europe. However, the majority of assemblages are still restricted to coastal settings. A few assemblages have been reported from alluvial settings but, in most instances, the environmental interpretations have been questioned or are in need of confirmation. One such instance is from the likely earliest Ordovician (Tremadocian) Grindstone Range Sandstone of Australia (Retallack 2009). This is purported as representing an alluvial setting with fluvial-overbank deposits containing *Diplichnites*, *Palaeophycus* and simple horizontal trails (*Cochlichnus*), whereas paleosols contain *Diplichnites*, *Cochlichnus*, *Planolites*, *Palaeophycus*, bilaterally symmetrical short, scratched burrows (*Crescentichnus*; see Romano and Whyte 2015), simple, actively filled (massive) horizontal to oblique burrows (*Torrowangea*), and irregular networks (*Myrowichnus*) (Retallack 2009). However, as with other purported paleosols from the Ediacaran and early Paleozoic (e.g., Retallack and Feakes 1987; Retallack 2001, 2011a, 2012a, b, 2013a, b, 2014; Davies and Gibling 2010, 2012; Davies et al. 2011a, b; Jago et al. 2012; Callow et al. 2013; Xiao and Knauth 2013; Xiao et al. 2013, 2014), the interpretations of the depositional settings for the Grindstone Range and the identity of some of the material as trace fossils are questionable.

### *5.5.1 Early Ordovician Trace-Fossil Assemblages*

#### 5.5.1.1 Coastal Settings

Early Ordovician trace-fossil assemblages in subaqueous and transitional coastal settings have been recorded in peri-Gondwanic settings from the Graafwater Formation of South Africa (Braddy and Almond 1999) and Blaiklock Glacier Group of Antarctica (Weber and Braddy 2004). Age constraint on these deposits is limited to being of the Early Ordovician. Early Ordovician coastal trace-fossil assemblages also occur from the Tremadocian to Floian Oville Formation of Spain (Baldwin 1977) and Bell Island and Wabana groups of Canada, although these latter two may extend back in age to the Furongian (Fillion and Pickerill 1990).

### Coastal—Subaqueous

The Graafwater Formation contains trace fossils from an estuarine or shallow-subtidal to tidal-flat setting (Braddy and Almond 1999). The trace-fossil assemblage comprises *Diplichnites*, *Merostomichnites*, *Petalichnus* and other trackways (*Palmichnium*), *Cruziana*, *Rusophycus*, *Monomorphichnus*, *Arenicolites*, large plug-shaped burrows (*Metaichna*), simple, actively filled (meniscate) horizontal to oblique burrows, and horizontal burrows with horizontal to vertical branches (*Arthrophycus*) (Braddy and Almond 1999).

### Coastal—Transitional

The Blaiklock Glacier Group of Antarctica contains a diverse trace-fossil assemblage in facies attributed to a high-energy intertidal to supratidal setting (Weber and Braddy 2004). The trace-fossil assemblage consists of *Diplichnites*, *Merostomichnites* and other trackways (*Asaphoidichnus*), *Monomorphichnus*, *Rusophycus*, *Crescentichnus* (*Selenichnites* in original publication), *Didymaulichnus* and other bilobate trails and paired grooves (*Taphrhelminthoides*), *Gordia*, *Planolites*, *Palaeophycus*, simple, actively filled (meniscate) horizontal to oblique burrows (*Beaconites*), and vertical simple burrows (?*Laevicyclus*) (Weber and Braddy 2004).

The Barrios Formation of Spain overlies the Cambrian Oville Formation (Baldwin 1977). Evidence for lower intertidal to upper intertidal and tidal channel environments comes in the form of flaser- and lenticular-bedded heterolithics and herringbone cross-stratification. It contains *Skolithos*, *Arenicolites*, *Diplocraterion* (*Corophioides* in original publication), *Planolites*, *Teichichnus*, *Arthrophycus*, *Rusophycus*, *Cruziana*, *Didymaulichnus* (*Fraena* in original publication), and *Monomorphichnus* (Baldwin 1977). Further sedimentologic analysis needs to be performed in order to confirm the tidal interpretation of the Barrios Formation.

The Bell Island and Wabana groups of Newfoundland contain interbedded shales, sandstones and siltstones variably interpreted as supratidal and upper, middle and lower tidal flats (Ranger 1979; Fillion and Pickerill 1990). According to Ranger (1979), tidal-flat deposits are present in most of the Beach and Ochre Cove formations, as well as in the upper interval of the Powers Steps Formation. The ichnofaunas of these units were analyzed by Fillion and Pickerill (1990), who documented diverse associations from the middle and lower intertidal flats. The lower intertidal flat ichnofauna consists of *Planolites*, *Palaeophycus*, *Skolithos* and other vertical simple burrows (*Laevicyclus*; *Calycraterion* in original publication), *Monocraterion*, *Arenicolites*, *Diplocraterion* and other vertical single U- and Y-shaped burrows (*Catenichnus*), *Cruziana*, *Rusophycus*, *Monomorphichnus*, *Diplichnites*, *Gordia*, *Helminthopsis*, *Phycodes*, *Psammichnites*, dumbbell- or arrow-shaped burrows (*Arthraria*), vertical concentrically filled burrows (*Rosselia*), and isolated and serial almond-shaped burrows (*Lockeia*). The middle intertidal flat ichnofauna comprises *Planolites* and other simple, actively filled (massive) horizontal to oblique burrows (*Furculosus*), *Palaeophycus*, *Skolithos*, *Monocraterion*, *Trichichnus*, *Arenicolites*, *Diplocraterion*, *Catenichnus*, *Cruziana*, *Rusophycus*, *Didymaulichnus*, *Monomorphichnus*, *Dimorphichnus*, *Diplichnites*, *Gordia*, *Helminthopsis*, *Phycodes*, *Bergaueria*, *Laevicyclus* (*Calycraterion* in original publication), *Teichichnus* and other horizontal burrows with vertical spreiten (*Trichophycus*), *Psammichnites* (*Aulichnites* in original publication) and other complex actively filled (meniscate/pelletoidal) horizontal burrows (*Nereites*; *Neonereites* in original publication), *Conostichnus*?, *Arthraria*, vertical helicoidal burrows (*Gyrolithes*), simple, actively filled (meniscate) horizontal to oblique burrows (*Imponoglyphus*), *Rosselia*, and circular trails (*Circulichnis*). The upper intertidal flat trace-fossil assemblage contains *Planolites*, *Skolithos*, and *Bergaueria* (Fillion and Pickerill 1990). The supratidal trace-fossil assemblage comprises *Palaeophycus*, *Skolithos*, and *Diplocraterion*. However, the environmental setting of these ichnofaunas requires further examination. Sedimentologic features of the upper interval of the Powers Steps Formation, including hummocky cross-stratification, wave ripples and combined-flow ripples, suggests deposition in wave-dominated offshore to shoreface environments rather than tidal flats (Buatois and Mángano, personal observations). Also, the Beach Formation has been recently reinterpreted as a wave-dominated shoreline affected by mud-rich density-driven flows (Harazim and McIlroy 2015). Fillion and Pickerill (1990) acknowledged that the reported occurrences of *Diplocraterion* and *Arenicolites* respectively in interpreted supratidal and lower intertidal facies were based on uncertain identifications; these two occurrences are not included in our analysis.

## *5.5.2 Middle Ordovician Trace-Fossil Assemblages*

### 5.5.2.1 Coastal Settings

Reports of trace-fossil assemblages from coastal settings during the Middle Ordovician are scarce. They comprise the Floian to Dapingian Grès Armoricain of France (Durand 1985); Floian to Darriwilian Mojotoro and Alto del Cóndor formations of Argentina (Mángano et al. 2001; Astini et al. 2004); ?Dapingian-Darriwilian Amdeh Formation of Oman, and Darriwilian Stairway Sandstone of Australia (Davies and Sansom 2009). The age of the Hudson River Shales of New York is not constrained beyond being late Middle to early Late Ordovician (Sharpe 1932).

Coastal—Subaqueous

The Hudson River Shales of New York contain *Palmichnium* in a reported coastal setting (Sharpe 1932), but additional information on the environmental occurrence is lacking. The Amdeh Formation of Oman, and Stairway Sandstone of Australia share similar ichnologic and sedimentologic motifs to those seen in the Anzaldo and Harding formations (see below; Davies and Sansom 2009) and likely represent subaqueous coastal settings. The Amdeh Formation contains *Cruziana*, *Rusophycus*, *Skolithos*, *Planolites*, *Teichichnus*, *Phycodes*, and three-dimensional spreiten traces

(*Daedalus*) (Davies et al. 2007); and the Stairway Sandstone contains *Skolithos, Monocraterion, Arenicolites, Diplocraterion, Arthrophycus, Didymaulichnus, Diplichnites,*?*Gordia, Lockeia, Monomorphichnus, Phycodes, Planolites,* six ichnospecies of *Cruziana* and *Rusophycus*, horizontal branched concentrically filled burrows (*Asterosoma*), and chevronate trails (*Protovirgularia*; *Uchirites* in the original study) (Gibb et al. 2009; Davies et al. 2011c). In Argentina, estuarine deposits of the Mojotoro and Alto del Cóndor formations (Floian to Darriwilian) contain *Skolithos* in subtidal-sandbar deposits (Mángano et al. 2001; Astini et al. 2004).

Coastal—Transitional

The Mojotoro and Alto del Cóndor formations also contain *Cruziana* and *Dimorphichnus* in intertidal-flat and interbar heterolithic deposits (Mángano et al. 2001; Astini et al. 2004). Tidal-flat deposits comprising heterolithics, herringbone cross-stratification, reactivation surfaces and wrinkle marks occur from the Grès Armoricain (Floian to Dapingian) of France (Durand 1985). These deposits contain *Cruziana*, *Monocraterion*, *Phycodes*, and *Daedalus*.

## *5.5.3 Late Ordovician Trace-Fossil Assemblages*

### 5.5.3.1 Coastal Settings

Well-dated Late Ordovician trace-fossil assemblages from coastal settings occur from the Harding (Mohawkian = late Sandbian to early Katian) (Fischer 1978; Allulee and Holland 2005) and Little East Lake (Ashgill = Katian to Hirnantian) (Pollock et al. 1994) formations of the USA, and the Ringgold Member of the Sequatchie Formation (Katian) of the USA (Rindsberg 1983; Martin and Rindsberg 1999). A further trace-fossil assemblage comes from the ?Sandbian Anzaldo Formation of Bolivia (Davies and Sansom 2009). The Tumblagooda Sandstone of Australia (Trewin and McNamara 1995) is well known for trace fossils but is poorly dated. Recently it has been consistently cited as Late Ordovician (see Mory et al. 2003; Evans et al. 2007) but this oft-repeated age is ultimately based on only loose lithostratigraphic correlation with successions from which paleomagnetic data were gathered in the 1980s, and which themselves were tentatively dated based on inductive interpretations of the paleomagnetic results (Schmidt and Hamilton 1990; Schmidt and Embleton 1990). McNamara (2014) presented a number of lines of evidence suggesting that a mid-Silurian age is most likely for the unit: (1) the conformably overlying Dirk Hartog Group contains conodonts of late Llandovery age; (2) the Tumblagooda Sandstone is unaffected by the 434 ± 16 Ma-aged Pb mineralisation of the adjacent Northampton Inlier, suggesting that it post-dates this; and (3) geochronological dating of the uplift of the southern terrains, from which the Tumblagooda sediments were sourced, indicates a mid-Silurian event (see Chap. 6).

### Coastal—Subaqueous

The environment of the Harding Formation of Colorado has been controversial, with authors favoring a marine (Spjeldnaes 1979) or estuarine (Fischer 1978) setting. The sole interpretation of freshwater fluvial facies (Graffin 1992) relied entirely on the sedimentologic misapprehension that "epsilon cross-bedding" (lateral accretion) was a diagnostically fluvial phenomenon, and has since been rejected. A more recent study by Allulee and Holland (2005) revealed that this unit is actually a complex facies mosaic, encompassing a wide variety of coastal to shallow-marine environments. Restricted central-basin deposits of a bay or lagoon contain unidentified actively filled horizontal burrows (?*Planolites*). Less intense bioturbation occurs in bayhead delta deposits. Trace fossils occur mostly from delta-front deposits and an open marine fauna is absent, suggesting that there may have been freshwater influx and that the structures were emplaced close to a river mouth (Allulee and Holland 2005). *Arenicolites* and *Teichichnus* were identified in these deposits (Allulee and Holland 2005). In addition, Fischer (1978) identified *Rusophycus*, *Cruziana*, *Merostomichnites*, and other trackways including some of dubious ichnotaxonomic assignment (*Homopodichnus*, *Stiaria* (*Paleohelcura* in original publication), *Arachnomorphichnus* and *Kouphichnium*), *Selenichnites* (*Kouphichnium* in part in original publication), oval-shaped impressions (*Corpusculichnus*), and problematic structures (*Caridoidichnus* and *Agnathichnus*). The Harding Formation is also remarkable for the articulated vertebrate (fish) fossil fauna that occurs in association with this nearshore ichnofauna. Similar Ordovician Gondwanan arandaspid habitats, as recorded in the Amdeh Formation of Oman (?Dapingian-Darriwilian), Stairway Sandstone of Australia (Darriwilian), and Anzaldo Formation of Bolivia (?Sandbian) share similar ichnologic and sedimentologic motifs to those seen in the Harding Formation (Davies and Sansom 2009). This suggests a global distribution of comparable coastal environments with common or analogous ecological components during the Middle to Late Ordovician. The Anzaldo Formation also contains the trace fossils *Skolithos*, *Monocraterion*, *Arenicolites*, *Planolites*, *Palaeophycus*, *Phycodes*, *Teichichnus*, five ichnospecies of *Cruziana* and *Rusophycus*, and trilobate flattened trails (*Curvolithus*) (Davies et al. 2007).

A number of trace-fossil assemblages of Late Ordovician age are interpreted as alluvial; however, several are most likely from marine-influenced environments. Conspicuous amongst these is the Juniata Formation of Pennsylvania. This unit was reported as consisting of paleosols on a well-drained floodplain that contained burrow systems and was considered to contain the earliest evidence of infaunalization in truly continental settings (Retallack and Feakes 1987; Retallack 2001). This material was originally identified as *Skolithos* and *Planolites* (Retallack 1985), but it was later suggested that the burrows were connected in a compound burrow system that was named *Scoyenia beerboweri* (Retallack 2001). However, such a form does not conform to the diagnosis of *Scoyenia* and it is unlikely to belong to this ichnogenus (Davies et al. 2010). Reexamination of the unit by Davies et al. (2010) identified *Skolithos*, *Circulichnis*, and possible *Palaeophycus*. These authors have also questioned the environmental interpretation, suggesting that a marginal-marine setting subject to sporadic exposure and pedogenic processes is more likely and that the burrows are unlikely to have been produced subaerially (Davies et al. 2010).

The environmental setting of the trace fossils in the Little East Lake Formation is described as ambiguous, lacking diagnostic sedimentary structures, but the strata are interpreted as a tidal flat with no evidence of subaerial exposure. The trace-fossil assemblage is of low ichnodiversity, comprising just *Planolites* and *Palaeophycus* (Pollock et al. 1994).

Coastal—Transitional

An upper intertidal mudflat trace-fossil assemblage has been found from the Ringgold Member of the Sequatchie Formation of Georgia and Tennessee. Here, siltstones and shales contain mudstone drapes and desiccation cracks together with *Petalichnus* and the simple, actively filled (meniscate) horizontal to oblique burrow *Taenidium* (Rindsberg 1983; Martin and Rindsberg 1999).

### 5.5.3.2 Alluvial Settings

A number of trace-fossil assemblages of Late Ordovician age are interpreted as being from alluvial settings; however, as discussed above, the environmental interpretations of the Grindstone Range and Juniata formations are questionable, and the Tumblagooda Sandstone is likely mid-Silurian in age (see Chap. 6). Late Ordovician trace-fossil assemblages from an interpreted alluvial setting occur within the Borrowdale Volcanic Group (Sandbian-Katian) of England (Johnson et al. 1994).

Alluvial—Transitional

The ichnofauna of the Borrowdale Volcanic Group is interpreted as having formed in a shallow, ephemeral water body (Johnson et al. 1994; classed here as alluvial transitional due to cross-bedding evidence of directed tractional sediment transport) and consists of *Diplichnites* and *Diplopodichnus* (Fig. 5.8). As these trace fossils are candidates for the oldest known fully nonmarine arthropod trackways, it is worth noting that there is some ambiguity to their environmental context. The primary indicators of nonmarine conditions for the deposition of the Borrowdale Volcanic Group were outlined by Branney (1988) and include the presence of subaerial volcaniclastic facies (pyroclastic surge deposits, welded lapilli tuffs, eroded ignimbrite surfaces, lahar deposits, and vesicular lavas) and the absence of marine fossils in associated siliciclastic facies. Branney (1988) also noted that there was micropaleontological (acritarch) evidence for at least one marine incursion during the emplacement and deposition of the Borrowdale Volcanic Group and that the "subaerial" interpretation is a general reflection of the depositional conditions for the stratigraphic unit as a whole. As the unit is up to 6 km-thick, is heavily faulted and

**Fig. 5.8** *Diplichnites* from transitional alluvial deposits of the Ordovician Borrowdale Volcanic Group, UK. Zx 296, British Geological Survey, Keyworth. Scale bar is 10 mm

folded, and crops out intermittently over a wide area, the precise environmental conditions of discrete outcrops must be considered on a case-by-case basis. For the two known trace fossil horizons, one (the River Lickle) occurs in the Dunnerdale Formation in an isolated stream exposure with no environmentally diagnostic primary sedimentary structures. Johnson et al. (1994) noted that the lower part of the Dunnerdale Formation was likely marine, but that the River Lickle locality could not accurately be positioned within the known stratigraphy of the Formation due to exposure constraints (local glacial till cover and faulting), stating that there was thus a chance the trace fossils could be from an emergent paralic setting. Trace fossils from the second locality (Sour Milk Gill) are known only from a single loose block. Johnson et al. (1994) used the following criteria as support for the trace fossils being produced on a drying emergent substrate: (1) the preservation style of the traces, with *Diplopodichnus* and *Diplichnites* intergrading; (2) mudcracks in in situ strata at Sour Milk Gill, close to where the loose block sample was discovered; and (3) the “average” subaerial conditions of the entire 6 km-thickness of the Borrowdale Volcanic Group (Branney 1988).

### *5.5.4 Ordovician Ecospace Occupation and Ecosystem Engineering*

The Borrowdale Volcanic Group ichnofauna demonstrates that animals may have expanded from coastal settings into alluvial settings during the Ordovician (Figs. 5.9 and 5.10). Ichnodiversity and ichnodisparity in coastal Ordovician subaqueous and

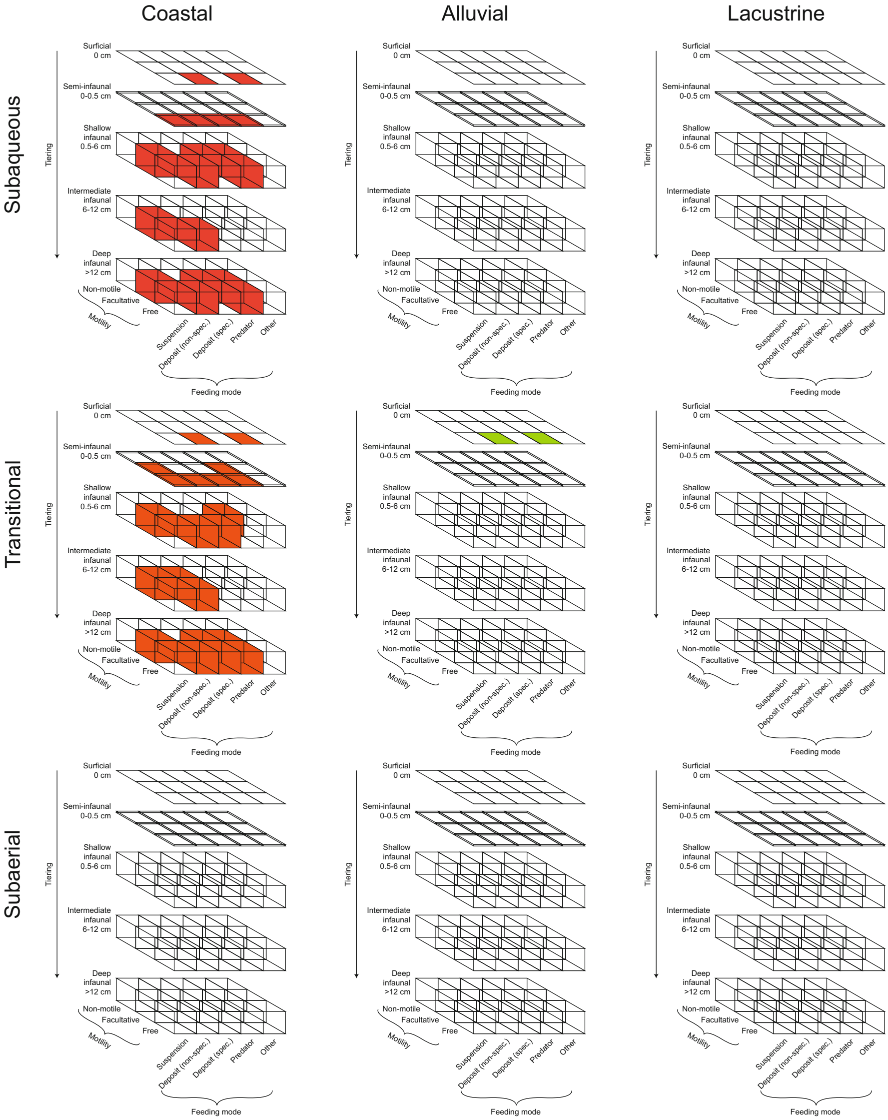

**Fig. 5.9** Ordovician ecospace occupation

transitional settings show further increases from those in the Ediacaran and Cambrian (Figs. 5.11 and 5.12). The global number of ichnogenera and architectural designs in Ordovician subaqueous coastal settings both approximately double from the Cambrian, with 32 ichnogenera and 18 architectural designs recorded worldwide. These represent 18 modes of life and 12 different impacts upon the sediment. The relative increase in ichnodiversity and ichnodisparity from the Cambrian is more modest in Ordovician transitional coastal settings, with 41 ichnogenera and 18 architectural designs; representing 21 modes of life and 13 methods of sediment

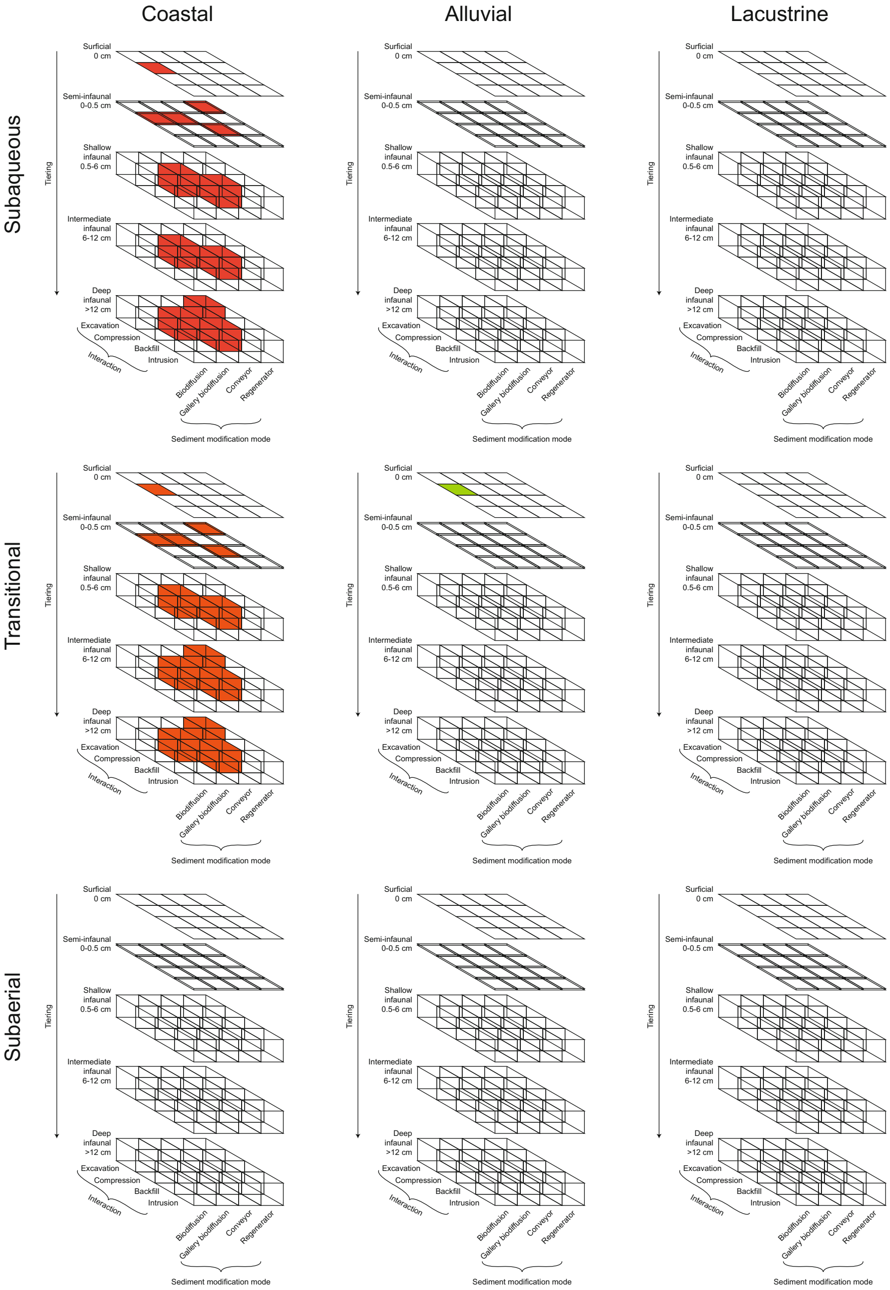

**Fig. 5.10** Ordovician ecosystem engineering

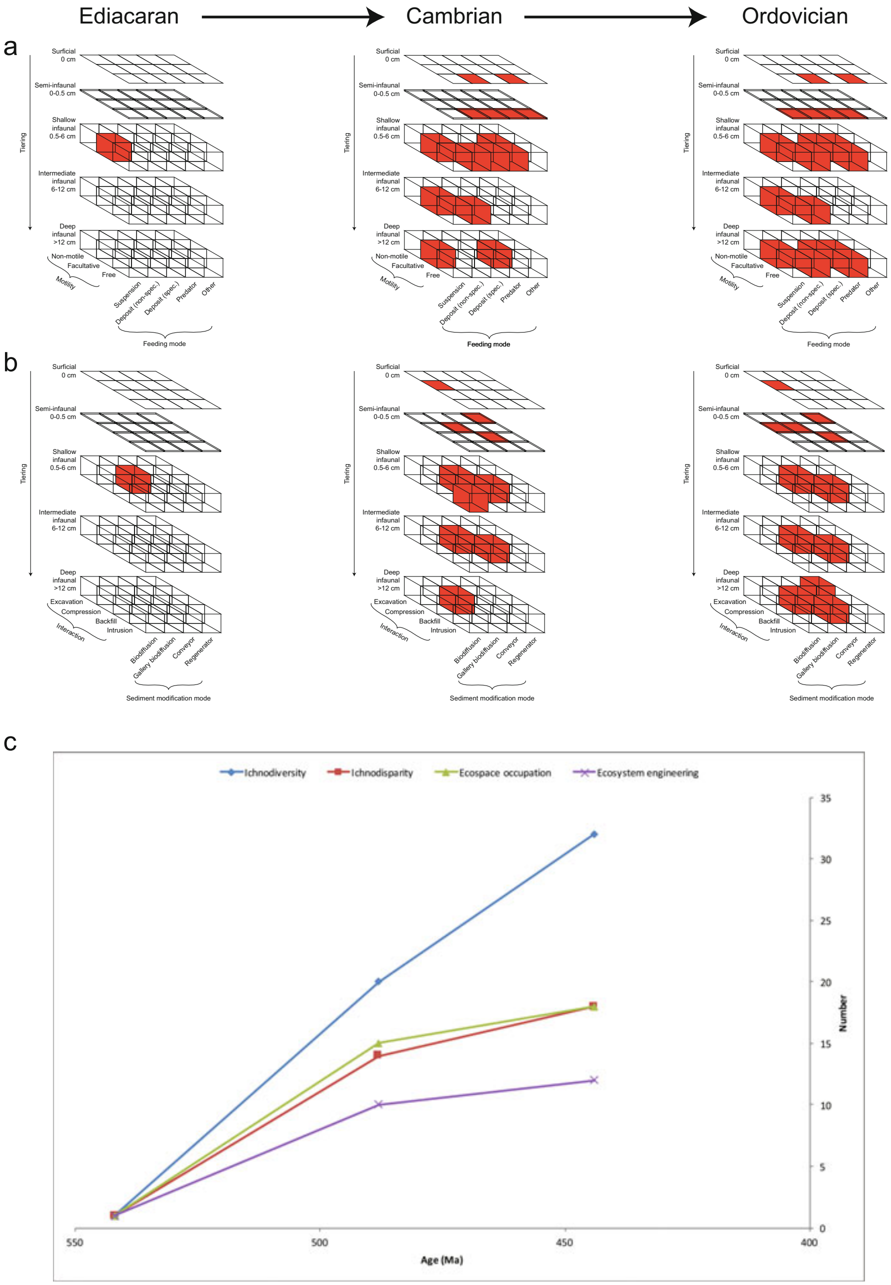

**Fig. 5.11** Colonization of subaqueous coastal environments. (**a**) Ecospace occupation; (**b**) ecosystem engineering; (**c**) plot of ichnodiversity, ichnodisparity, ecospace occupation in terms of number of modes of life, and ecosystem engineering in terms of number of modes of sediment modification for the Ediacaran to Ordovician

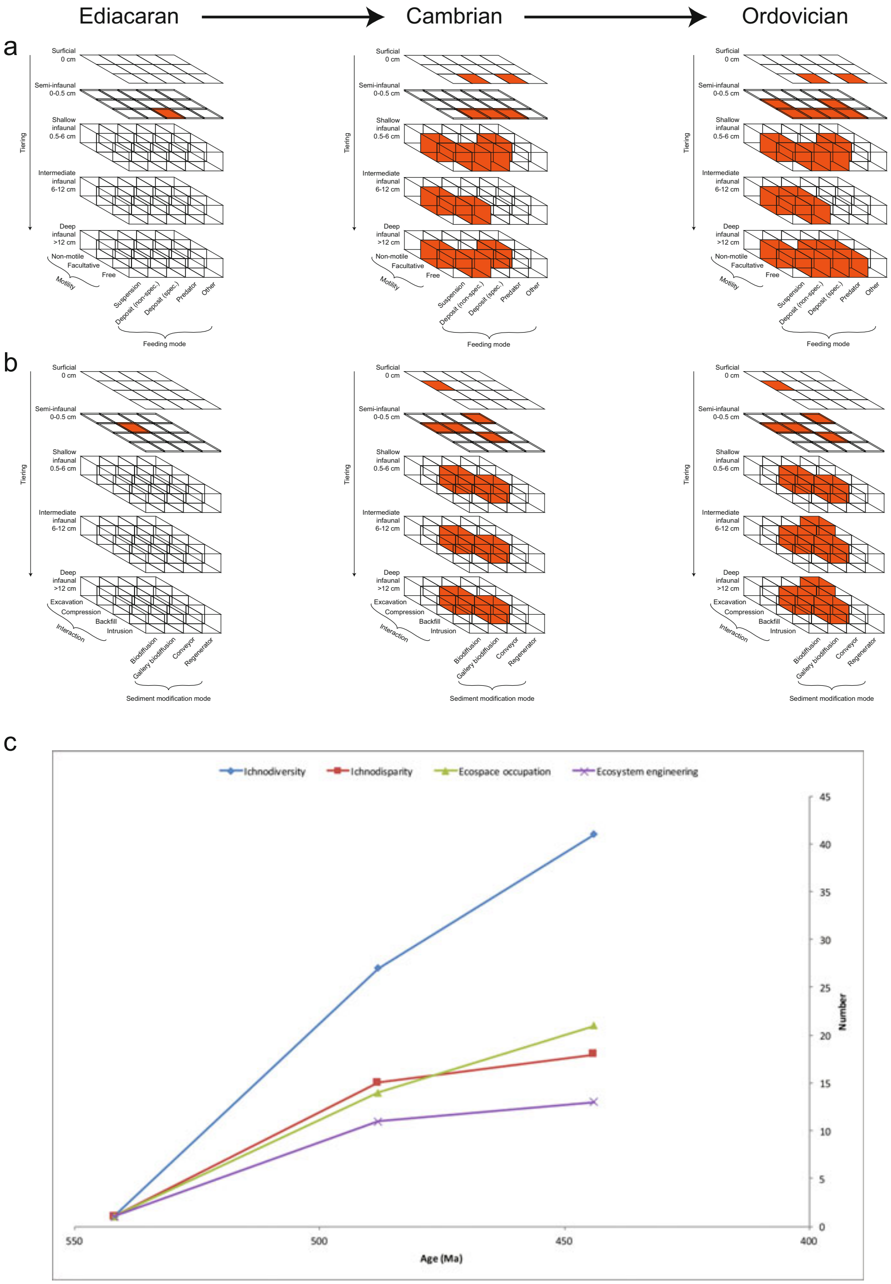

**Fig. 5.12** Colonization of transitional coastal environments. (**a**) Ecospace occupation; (**b**) ecosystem engineering; (**c**) plot of ichnodiversity, ichnodisparity, ecospace occupation in terms of number of modes of life, and ecosystem engineering in terms of number of modes of sediment modification for the Ediacaran to Ordovician

modification. The single potential Ordovician alluvial trace-fossil assemblage that formed under transitional conditions is of very low ichnodiversity, comprising *Diplichnites* and *Diplopodichnus*. This restricts transitional alluvial settings to hosting ichnogenera representing trackways and scratch marks, together with bilobate trails and paired grooves.

A large proportion of ichnogenera are shared amongst Ordovician subaqueous and transitional settings. Both settings played host to facultatively mobile suspension feeders that occupied the shallow to deep infaunal tiers, together with freely mobile non-specialized deposit feeders that inhabited the surficial tier to shallow infaunal tier. Some of these animals may also have been predators. Freely mobile specialized deposit feeders exploited the semi-infaunal tiers. Facultatively mobile suspension feeders produced a variety of forms of gallery biodiffusive structures by compression. These consist of shallow to deep infaunal tier vertical simple burrows, intermediate to deep infaunal tier vertical single U- and Y-shaped burrows, and shallow tier passively filled horizontal to oblique burrows. Specialized deposit feeders also created horizontal burrows with horizontal to vertical branches by compression within the semi-infaunal tier that could have acted as gallery biodiffusive structures. Non-specialized and specialized deposit feeders had a variety of impacts upon the sediment that were limited to shallow infaunal depths. These consisted of moving through the sediment by backfilling and acting as sediment conveyors in the production of shallow tier simple, actively filled (massive) horizontal to oblique burrows and simple, actively filled (meniscate) horizontal to oblique burrows, horizontal burrows with vertical spreiten, and horizontal burrows with horizontal to vertical branches. In the semi-infaunal tier, the same modes of life and mechanisms of sediment modification gave rise to simple horizontal and circular trails. Non-specialized deposit feeding and possible predatory arthropods living on the surficial tier created a variety of trackways and scratch marks but had minimal impact upon the substrate, their compressive tracks causing biodiffusion of sediment. Suspension feeding and non-specialized deposit feeding bivalves also had the same minor impact on the sediment in the semi-infaunal tier through the production of isolated and serial almond-shaped burrows. Other non-specialized deposit feeders and possible predatory arthropods were responsible for sediment regeneration when excavating and plowing through the substrate and producing bilobate trails and bilaterally symmetrical short, scratched burrows.

As with the Cambrian, more ichnogenera typically carried the same role and function in transitional settings than in subaqueous coastal settings. Additional morphologies of vertical simple burrows in transitional settings are represented by *Trichichnus* and ?*Laevicyclus,* whereas vertical single U- and Y-shaped burrows further include *Catenichnus*. Further actively filled burrows in transitional settings consist of the simple, actively filled (massive) horizontal to oblique burrow *Furculosus*, simple, actively filled (meniscate) horizontal to oblique burrows *Beaconites* and *Taenidium*, the complex actively filled (meniscate/pelletoidal) horizontal burrow *Nereites*, the horizontal burrow with vertical spreiten *Trichophycus*, and the simple horizontal trail *Helminthopsis*. Subaqueous coastal settings additionally contain the chevronate trail *Protovirgularia*. A number of trackway and scratch mark ichnogenera have their first appearances in subaqueous and transitional coastal settings during the Ordovician. *Stiaria*, *Homopodichnus*, *Arachnomorphichnus*, *Kouphichnium*, and *Palmichnium* are reported from various subaqueous coastal settings, whereas *Asaphoidichnus* and *Dimorphichnus* occur from transitional coastal settings.

In several cases, a particular architectural design is represented by different ichnogenera across subaqueous and transitional coastal settings. This indicates that the same modes of life and impacts on sediments were represented within these environments but were adopted and performed in part by different animals. Horizontal, branched concentrically filled burrows produced by mobile specialized deposit feeders are represented by *Asterosoma* in subaqueous coastal settings and *Imponoglyphus* in transitional coastal settings. The producers of these ichnotaxa were facultatively and freely mobile, respectively, and acted as sediment conveyors, moving through the substrate by backfilling. Plug-shaped burrows are represented also in subaqueous and transitional coastal settings. However, in the former case *Metaichna* is a deep-tier structure produced by excavation that resulted in sediment regeneration by a freely mobile non-specialized deposit feeder or predator. In contrast, in the latter case, suspension feeders produced *Bergaueria* in the shallow tier and *Conostichus* in the intermediate infaunal tier. These acted as gallery biodiffusive structures and were produced by compression.

Unique forms are found in both Ordovician subaqueous and transitional coastal settings. In subaqueous coastal settings, freely mobile non-specialized deposit feeders and possible predators produced semi-infaunal tier oval impressions and trilobate flattened trails. Both likely resulted in minimal biodiffusive sediment disruption by compression. In transitional settings, facultatively mobile suspension feeders and non-specialized deposit feeders created shallow tier dumbbell- or arrow-shaped gallery biodiffusive structures by compression, as well as intermediate tier vertical concentrically filled burrows that were produced also by compression and acted as gallery biodiffusive structures. Deep tier infaunal, freely mobile specialized deposit feeders acted as sediment regenerators in producing vertical helicoidal burrows by excavation. The surficial tier of transitional settings further contains trails with undulating transverse bars and furrows that caused minimal compressive biodiffusive disruption of the sediment and were produced by freely mobile non-specialized deposit feeding molluscs, equivalent to *Climactichnites* from the Cambrian.

Trace fossil producing animals in the surficial and semi-infaunal tier included arthropods, such as crustaceans, myriapod-like animals and eurypterids. These animals created bilobate trails and paired grooves, bilaterally symmetrical short, scratched burrows, and trackways and scratch marks. Molluscs were responsible for oval impressions, isolated and serial almond-shaped burrows, and trails with undulating transverse bars and furrows. Molluscs are also the likely producers of trilobate flattened trails, although vermiform platyhelminthes and nemerteans have been put forward also as possible trace makers (Buatois et al. 1998b). Vermiform animals were responsible for simple horizontal trails, circular trails, and horizontal burrows with horizontal to vertical branches. The latter were produced potentially also by arthropods. Producers of infaunal vertical simple burrows, vertical single U-, Y-shaped burrows, dumbbell- or arrow-shaped burrows, spreiten burrows, passively and actively filled horizontal to oblique burrows, and concentrically filled burrows were probably worm-like animals or arthropods. Cnidarians were probably responsible for the majority of shallow plug-shaped burrows. However, arthropods may have been responsible for *Metaichna*. Numerous Ordovician trace-fossil assemblages have been attributed to alluvial settings, but most of these inferences are a matter of debate. One potential nonmarine assemblage is from a shallow ephemeral water body. The producers of this trace-fossil assemblage were myriapod-like animals.

## 5.6 Discussion

The Ediacaran to Ordovician prelude to full-blown continental invasion represents a period of landward ecospace expansion and increasing diversity of trace-fossil producers, modes of life, and methods of sediment modification. Claims made for the first evidence of burrowing animals in freshwater fluvial environments or paleosols (Retallack 2001; Kennedy and Droser 2011), and for freshwater nektonic animals (Graffin 1992) need to gather significant evidence to enable rejection of the null hypothesis—that is, that they represent the activities of animals under fully marine or brackish-water conditions. To avoid circularity, it is imperative that environmental conditions are established independently from ideas on the environmental distributions of trace fossils by using detailed analysis of physical sedimentary structures, facies, and facies successions. For strata of any age, the notion that certain sedimentary structures are always unique to a given environment or can be conclusively diagnostic of a depositional setting is oversimplistic: such physical structures, viewed individually, are most commonly only indicative of depositional process rather than environment or water salinity. For example, hummocky cross-stratification remains a commonly cited structure seen as "diagnostic" of marine conditions (e.g., Retallack 2011b), despite the fact that such features have long been known to occur in modern freshwater settings when appropriate storm conditions prevail (Greenwood and Sherman 1986). As such, the context and content of surrounding sedimentary facies can be crucial in determining whether unfossiliferous siliciclastic sedimentary strata had a marine or continental origin and, even with detailed facies analysis, resultant interpretations cannot always be made with absolute certainty.

Furthermore, the assumption that there is a clear dividing line between marine and continental (fluvial) environments is also false, as both physical and ecological marine–freshwater interfaces are gradational in modern environments and can fluctuate significantly over time (e.g., Dalrymple and Choi 2007). In the key interval of the Cambro-Ordovician, the boundaries would have been even more blurred and are acutely problematic to interpret from the sedimentary record. Prior to the regulating effects on continental sedimentation imposed by abundant land plants, flashy progradation of unstable coastlines during flooding events and their subsequent marine reworking after the resumption of regular background conditions would likely have resulted in an unstable physical boundary between the marine and continental realms (Cotter 1983; Davies et al. 2011a). In the Cambro-Ordovician record such effects were even more pronounced because many preserved successions of this age were deposited in shallow epeiric seas.

Additionally, the nature of the freshwater–brackish–saltwater transition in these coastal zones remains unknown, but saltwater or brackish-water conditions may have extended considerable distances inland, particularly during periods of fluctuating sea-level or within those earliest Paleozoic successions that were deposited on low-gradient cratonic margins. Again, this is further compounded by the non-actualistic nature of the Cambro-Ordovician Earth, where tidal ranges were greater, and tidal frequency more closely spaced than today due to the closer proximity of the Moon (e.g., Williams 1989), resulting in the widespread abundance of tide-generated deposits (e.g., Desjardins et al. 2012b). In light of this, the relatively common intercalation of discrete, isolated trace fossil-bearing horizons within otherwise unfossiliferous Cambro-Ordovician sandstones interpreted as sheet-braided fluvial deposits (see examples in Davies et al. 2011a) should be expected, and does not necessarily require that these horizons record freshwater tracemaker communities. Rather, they may reflect tracemaker emplacement during sporadic marine incursions.

The above discussion demonstrates that the prerequisite sedimentary facies analysis needed to conclusively identify the oldest continental animals can be acutely problematic and often unresolvable. Future efforts to discover the oldest examples of trace fossils in continental environments should bear in mind these fundamental limitations and always be presented within a robust sedimentologic context. Ultimately, it is entirely plausible that the oldest examples of truly continental tracemakers occur within strata that lack any sedimentary signatures that would ever conclusively resolve a continental depositional environment. On the other hand, this fundamental uncertainty cannot be used to warrant claims for the oldest continental trace fossils solely because they occur in strata that lack diagnostic marine signatures. Whereas some of the suggestions of the first evidence of different animals in freshwater and continental environments cited in this chapter are attractive (Graffin 1992; Retallack 2001; Kennedy and Droser 2011), they have arguably not established sufficient independent evidence to irrefutably reject the null hypothesis and support their claims (Allulee and Holland 2005; Davies et al. 2010; Davies and Gibling 2012). As such, it is more parsimonious to conclude that they represent the activities of animals under marine or brackish-water conditions.

Increasing congruence of molecular clock estimates and the body fossil record points toward an Ediacaran emergence of bilaterian taxa (Peterson et al. 2008), although there is still a gap between the two records (Mángano and Buatois 2014). Relatively rapidly, following on from this origin, trace fossil evidence demonstrates that a number of animal phyla had already begun to colonize subaqueous and transitional brackish-water marginal marine environments by the end of the Ediacaran, although their range and modes of life were limited to the surface and shallow sediment tiers (Figs. 5.2 and 5.3). Shortly after initial colonization, during the Cambrian, deeper tiers were occupied in these environments and increased diversity is apparent in modes of life, trace-making animals, and the ways in which they modified the sediment (Figs. 5.6 and 5.7). Of the phyla to colonize the land, there is strong evidence that the Arthropoda and Mollusca, and one or more of the Annelida, Nematoda, and Nemertea had already begun to adapt to marginal settings during the Cambrian. Cnidarians were likely also present. The Chordata followed shortly thereafter, with body fossils of fish found from Ordovician coastal paralic settings, as well as evidence of possible Platyhelminthes. The amount of occupied ecospace and ways in which animals modified the sediment were remarkably similar between the Cambrian and Ordovician (Figs. 5.6, 5.7, and 5.9–5.12). However, the Ordovician marked an increase in the diversity of activities and trace-making animals, represented by concomitant increases in ichnodiversity and ichnodisparity (Figs. 5.11 and 5.12) within this already exploited ecospace. Some arthropods made amphibious excursions onto coastal dunes during the Cambrian, but this does not represent full terrestrialization (MacNaughton et al. 2002; Hagadorn et al. 2011b). The first evidence of animals in truly continental settings may occur in the Ordovician (Figs. 5.8 and 5.9), with arthropod trackways and trails preserved in an interpreted ephemeral lake-margin setting (Johnson et al. 1994).

Many trace fossils in emergent tidal settings are associated with sedimentary structures suggestive of microbial mats (Buatois and Mángano 2012). The presence of such microbial mats and evidence of grazing activity suggests that the search for food may have been the impetus for the earliest stages in the colonization of land. In addition to microbial mats, early land plants could potentially also have provided a source of nutrients for the pioneer continental metazoans. However, the oldest land plant macrofossils do not appear until the Silurian, although there is uncontroversial evidence for plant-dispersed microfossils in the rock record from the middle of the Ordovician (Rubinstein et al. 2010, 2015; Kenrick et al. 2012). Contentious microfossils and molecular clock estimates suggest even older origins (Steemans 2000; Clarke et al. 2011).

It has been suggested that early embryophytes played a fundamental role as continental ecosystem engineers, creating new physical habitats by modifying alluvial biogeomorphology from landscapes previously dominated by unconfined rivers with wide sand-beds and eolian tracts, and initiating a series of abiotic-biotic feedback loops that persist within present-day alluvial systems (e.g., Gibling and Davies 2012; Corenblit et al. 2015). Nonvascular embryophytes, such as the precursors to modern mosses, may have also played an important role (Lenton et al. 2012). The first appearance of uncontroversial cryptospores is stratigraphically correlative with a radiation in the sedimentary signatures and characteristics preserved in the global alluvial sedimentary record (Davies and Gibling 2010). In the latter half of the Ordovician, the global alluvial record exhibits a marked increase in mud content, particularly within distal alluvial successions, reflecting increased upland mud production, reduced eolian deflation, and the retention of fines through baffling and binding: together leading to the rise of new stable floodplain habitats available for animal and plant colonization (Davies and Gibling 2010; Davies et al. 2011a; Gibling and Davies 2012). Concomitantly, the "sheet-braided" style that had dominated earlier river systems gradually gave way to a "channelled-braided" style, suggesting an increase in stable, preservable alluvial channels. This increase in alluvial geomorphic and sedimentary diversity, apparently mediated by early plants, marked the beginning of a process of diversification of potential physical habitats in the continental realm that continued into the latest Paleozoic (Davies and Gibling 2013). The first appearance of apparently continental ichnofaunas is in close stratigraphic alliance with the increasing variety of continental landscapes, and it is possible that the increasing diversity of the latter opened up new colonization opportunities for pioneer tracemaker animals. Although it is currently impossible to conclusively identify causality between these trends in the sedimentary and ichnologic record, it is certainly true that the global Late Ordovician record of each represents incipient charges of diversity that, in both cases, began to fully explode during the Silurian (see Chap. 6).

## 5.7 Conclusions

We use trace fossil data to present a framework for analyzing ecospace expansion, ecosystem engineering, and the diversification of behavioral programs during the initial stage of the colonization of land. This initial stage began in the terminal Ediacaran and culminated with the first animals in alluvial environments, possibly by the end of the Ordovician. What followed was a significant explosion of diversity and expansion into new environments during the Silurian to Permian (see Chap. 6). Subaqueous and transitional coastal environments were colonized during the Ediacaran. However, ecospace occupation and ecosystem engineering were limited, extending to shallow and semi-infaunal tiers respectively in subaqueous and transitional coastal environments. The Cambrian shows evidence of expansion within brackish-water settings and animals capable of surviving temporary periods of desiccation and making excursions into subaerial coastal dune environments. In those environments that had begun to be colonized during the Ediacaran, the Cambrian saw a marked increase in ichnodiversity, the number of architectural designs, and an increase in ecospace exploitation to the deep infaunal tier. Rather than an increase in ecospace occupation, the Ordovician witnessed an increase of ichnodiversity and architectural designs within already exploited ecospace from the Cambrian. A pattern of ecospace exploitation emerges that consists of: (1) initial colonization of a new environment, (2) relatively rapid filling of available ecospace, (3) diversification of animals by establishing new behavioral programs represented by the creation of original architectural designs, and (4) proliferation of ichnogenera representing variation upon these established themes.

**Acknowledgments** We are grateful for the constructive comments of Godfrey Nowlan on an earlier version of this chapter, and for the thorough review from Russell Garwood. Paul Shepherd is thanked for facilitating access to specimens from the Borrowdale Volcanic Group at the British Geological Survey, Keyworth. The initial stages of this research were made possible thanks to a Government of Canada Postdoctoral Research Fellowship awarded to Minter under the Canadian Commonwealth Scholarship Programme. Financial support for this study was provided by Natural Sciences and Engineering Research Council (NSERC) Discovery Grants 311727-08/15 and 311726-08/13 awarded to Mángano and Buatois, respectively. Gibling also acknowledges funding from an NSERC Discovery Grant. This is Earth Sciences Sector Contribution 20140048.

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# Chapter 6
# The Establishment of Continental Ecosystems

**Nicholas J. Minter, Luis A. Buatois, M. Gabriela Mángano, Neil S. Davies, Martin R. Gibling, and Conrad Labandeira**

## 6.1 Introduction

While the Cambrian–Ordovician interval records the initial forays of benthic organisms into very shallow water and the first steps onto land (see Chap. 5), the remainder of the Paleozoic witnessed a dramatic change in continental landscapes and ecosystems. From the Silurian to the Permian, benthic biotas display a progressive expansion from coastal settings into rivers, floodplains, deserts, and lakes, as well as increasing colonization of the infaunal ecospace (Buatois and Mángano 1993a;

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M.G. Mángano, L.A. Buatois (eds.), *The Trace-Fossil Record of Major Evolutionary Events*, Topics in Geobiology 39,
DOI 10.1007/978-94-017-9600-2_6

Buatois et al. 1998a; Miller and Labandeira 2002). This evolutionary breakthrough parallels changes in vegetation and fluvial styles (Davies and Gibling 2010a, b; Davies et al. 2011; Gibling and Davies 2012) and the acquisition of major shifts in ecological roles among continental organisms in both freshwater (Park and Gierlowski-Kordesch 2007) and terrestrial (DiMichele and Hook 1992; Bateman et al. 1998; Labandeira 2007; Gensel 2008) habitats. The aims of this chapter are (1) to review the ichnologic record of Silurian to Permian continental environments, (2) to address paleoenvironmental expansion and ecospace utilization, and (3) to provide an evolutionary scenario for the establishment of continental ecosystems that integrates multiple lines of evidence.

Evolutionary radiations may be categorized into at least four distinctive types: (1) novelty events, whereby new morphological complexity is generated simultaneously in independent lineages but is not necessarily associated with increasing species diversity; (2) broad diversification events, in which many independent lineages diversify to create many new species in response to new ecological opportunities; (3) economic radiations involving a limited group of ecologically related clades that exploit a limited, new ecological opportunity; and (4) adaptive radiations that occur within a single clade, regardless of taxonomic level, and involve a rapid increase in diversity therein (Erwin 1992). In addition to an increase in species diversity, adaptive radiations also include an expansion in both the range of habitats occupied and breadth of novel morphological and functional adaptations used to exploit those habitats (Gavrilets and Losos 2009; Benton 2015).

It is important to distinguish between pattern and process in macroevolution. Analyses of patterns frequently focus upon the body-fossil record and the relationships between taxonomic diversity and morphological diversity (i.e., disparity). The null pattern is that diversity and disparity are coupled; as opposed to either the “disparity first” pattern whereby there is a rapid increase in disparity that exceeds initial taxonomic diversification rates, or the “diversity first” pattern whereby morphological disparity is constrained but is exceeded by taxonomic diversification (Foote 1993; Wesley-Hunt 2005; Erwin 2007; Benton 2015). Studies of patterns from the fossil record generally support the “disparity first” model, with an early burst producing maximal disparity early in the history of a clade (Labandeira 1997; Bateman et al. 1998; Erwin 2007; Hughes et al. 2013).

Three models for the underlying process responsible for adaptive radiations have been proposed: (1) the ecospace model where new species fill new or subdivide existing niches and variations in ecological opportunity control success; (2) the macromutation model where the origins of clades are the result of genomic or genetic revolutions; and (3) the developmental model where developmental patterning becomes increasingly constrained and resistant to modification over time (Benton 2015). However, these models are not necessarily mutually exclusive and could work synergistically (Erwin 2007). Rather than being limited to a single clade in the case of adaptive radiations, by contrast novelty events occur across lineages. In novelty events, there is an extrinsic control of available ecospace and an intrinsic control of genomic and developmental plasticity to enable novelty (Erwin 1992).

Broad diversification events also occur across independent lineages, but here morphological diversification is a consequence of taxonomic diversification, and so diversity and disparity are either coupled or the pattern is that of "diversity first" (Erwin 1992).

The methodology employed to analyze the trace-fossil record of ecospace occupation and ecosystem engineering during the establishment of continental ecosystems follows that laid out in Chap. 1. Initial studies of morphological disparity involved quantifying the numbers of higher taxonomic ranks (e.g., orders, classes, phyla) to compare with species diversity. The results of such studies were criticized as an artifact of taxonomy, but those same results have been borne out by studies using phylogenetic comparative methods (Erwin 2007). In addition to morphology, the phenotype of an organism includes its behavior. Trace fossils, in the form of ichnogenera and ichnospecies, provide a record of that behavioral or functional diversity employed by organisms. At a higher level, architectural designs (Buatois and Mángano 2013; Buatois et al. 2016) may be considered to represent broader-scale trace-fossil morphologies that result from organismal behavior and hence a measure of behavioral disparity. In an initial context, we therefore consider comparisons of the numbers of ichnogenera and architectural designs as a valid methodology for exploring patterns of behavioral diversification. At least implicit within traditional concepts of adaptive radiations is the existence of empty niches waiting to be occupied; however, ideas relating to ecosystem engineers and niche construction theory argue that the activities of organisms may modify their environment to create niches for themselves and can also influence the success of other organisms (Erwin 2008; Odling-Smee et al. 2013). We are appreciative that conceptually ecospace is not sitting there empty, waiting to be occupied. However, it is necessary to have an initial framework in which to conduct an analysis. The framework of ecospace occupation used here was established *a posteriori* from our current reference point in time and space, although it can theoretically extend beyond the margins of the ecospace cube. As in Chap. 5, the term "transitional," when used in an environmental context, denotes settings that were variably subaqueous to subaerial within a limited stratigraphic interval.

## 6.2 Silurian

Silurian coastal to continental trace-fossil assemblages have been reported from North America, Australia, South America, and Europe. Among the earliest is the Tumblagooda Sandstone of Australia, which has been consistently cited as Late Ordovician, although recent work has identified a number of lines of evidence that indicate a more likely early or middle Silurian age (McNamara 2014; see Chap. 5). The majority of Silurian assemblages occur in coastal settings. For terrestrial settings, coprolites from the Late Silurian provide the oldest evidence of trophic interactions between terrestrial macroscopic animals and plants (Edwards et al. 1995).

## 6.2.1 *Silurian Trace-Fossil Assemblages*

### 6.2.1.1 Coastal Settings

The Tumblagooda Sandstone of Australia contains a number of trace-fossil assemblages and is likely to be lower or middle Silurian in age (Trewin and McNamara 1995; McNamara 2014). Some facies associations have been interpreted as representing alluvial environments, but these are likely to have been in close proximity to marine settings and formed under a range of conditions within coastal environments. Trace fossils from coastal settings of late Silurian (Ludlow) age occur from the Leopold and Cape Storm formations of Arctic Canada (Narbonne et al. 1979; Narbonne 1984), Major Mitchell Sandstone of Australia (Gouramanis et al. 2003), and Sundvollen Formation of the Ringerike Group in Norway (Whitaker 1979; Davies et al. 2006). Younger late Silurian (Prídolí) coastal trace-fossil assemblages occur from the Holmestrand Formation of the Ringerike Group in Norway (Dam and Andreasen 1990; Davies et al. 2006) and Freshwater East Formation of Wales (Morrissey and Braddy 2004; Marriott et al. 2009). The trace-fossil assemblage from the Port Stephens Formation of the Falkland Islands ranges from the late Silurian to Early Devonian (Hunter and Lomas 2003).

#### Coastal—Subaqueous

Sheet-braided fluvial sandstones in the Tumblagooda Sandstone with large bar structures and high intensities of bioturbation are taken to represent transitional fluvial to marine deposits (Trewin and McNamara 1995; McNamara 2014). The associated trace-fossil assemblage consists of trackways and scratch marks (*Diplichnites*), vertical simple (*Skolithos*), and U- and Y-shaped (*Diplocraterion*) burrows, and complex, actively filled (meniscate/pelletoidal) horizontal burrows (*Psammichnites*; *Aulichnites* in the original publication) (Trewin and McNamara 1995; Fig. 6.1a–f). Other deposits interpreted as having formed in interdistributary bay, overbank, and distributary-channel environments contain *Skolithos*, *Diplocraterion*, three-dimensional spreiten traces (*Daedalus*), and vertical simple burrows with lunate cross-sections (*Lunatubichnus*) (Trewin and McNamara 1995; Evans et al. 2007; Fig. 6.1a–f).

The Leopold and Cape Storm formations of Arctic Canada yield trace-fossil assemblages from carbonate intertidal settings (Narbonne et al. 1979; Narbonne 1984). The trace-fossil assemblages from the two formations are very similar, with the Leopold Formation containing passively filled horizontal burrows (*Palaeophycus*), *Skolithos*, *Diplocraterion*, and other U- and Y-shaped burrows (*Arenicolites*, *Polarichnus*), dumbbell-shaped burrows (*Arthraria*), plug-shaped burrows (*Bergaueria*), simple horizontal trails (*Cochlichnus*, *Gordia*), bilobate trails and paired grooves (*Cruziana*), trackways and scratch marks (*Monomorphichnus*), horizontal helical burrows (*Helicodromites*), and burrows with a shaft or bunch with downwardly radiating probes (*Chondrites*). By contrast,

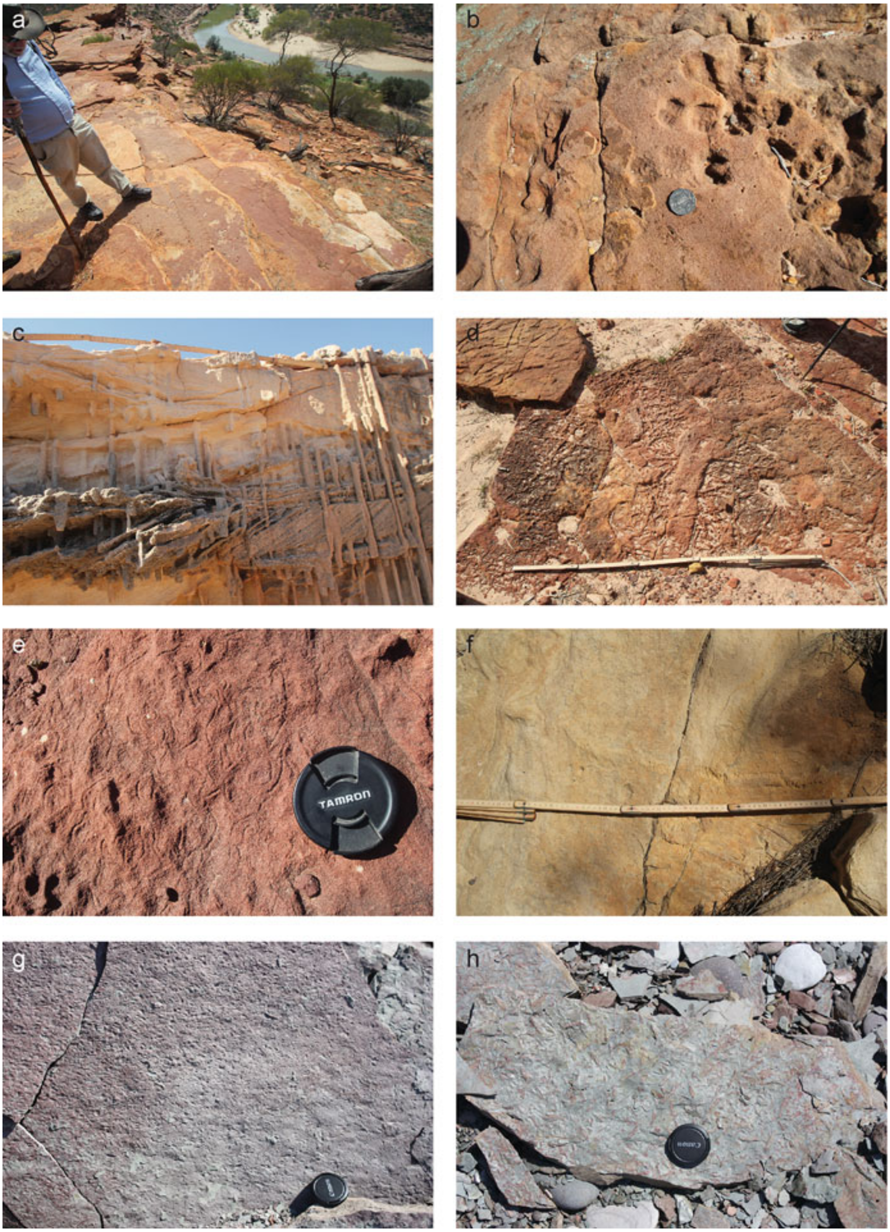

**Fig. 6.1** Silurian trace fossils from the Tumblagooda Sandstone, Australia (**a**–**f**) and Clam Bank Formation of Newfoundland, Canada (**g** and **h**). (**a**) Large *Diplichnites*; (**b**) *Rusophycus*; (**c**) *Skolithos* and *Daedalus*; (**d**) *Heimdallia* overprinted by *Tumblagoodichnus*; (**e**) *Aulichnites* (=*Psammichnites*) cutting across trough-cross bedding planes; (**f**) long *Beaconites*-like trace fossil along the foreset of a trough cross bedded sandy dune form; (**g**) horizontal burrows and halite pseudomorphs in wrinkle-laminated mudstone; (**h**) pervasive burrows in well-bioturbated, occasionally rippled red mudstone

the Cape Storm Formation contains *Palaeophycus*, *Skolithos*, *Arenicolites*, *Diplocraterion*, *Polarichnus*, *Arthraria*, *Bergaueria*, *Gordia*, chevronate trails (*Protovirgularia*; *Uchirites* in the original publication), *Monomorphichnus* and other trackways and scratch marks (*Petalichnus*), simple, actively filled (meniscate) horizontal to oblique burrows (*Beaconites*, *Syncoprulus*), and *Chondrites* (Narbonne et al. 1979; Narbonne 1984).

Intertidal and upper-shoreface deposits of the Port Stephen Formation contain *Skolithos*, *Diplocraterion*, bilobate trails and paired grooves (?*Didymaulichnus*), burrows with horizontal spreiten (*Rhizocorallium*), and three-dimensional spreiten traces (?*Heimdallia*) (Hunter and Lomas 2003). Coastal-braidplain deposits within the Port Stephen Formation contain *Diplocraterion*, passively filled horizontal burrows (?*Didymaulyponomos*), simple horizontal trails (?*Helminthopsis*), bilaterally symmetrical short, scratched burrows (probably *Crescentichnus*; ?*Selenichnites* in the original publication), *Beaconites*, ?*Psammichnites* (?*Taphrhelminthopsis* in the original publication), and ?*Heimdallia* (Hunter and Lomas 2003).

Trough cross-bedded distributary channels on a delta plain in the Major Mitchell Sandstone contain simple, actively filled (meniscate) horizontal to oblique burrows of *Taenidium* (Gouramanis et al. 2003). The burrows are interpreted to have been made whilst the channel-dunes were actively migrating (Gouramanis et al. 2003). Presumed subtidal channel deposits from the Sundvollen Formation contain escape trace fossils (Davies et al. 2006). Small, ephemeral, fluvial channels from backshore settings of the Holmestrand Formation also contain escape trace fossils (Davies et al. 2006), together with *Arenicolites*, *Didymaulichnus*, and *Beaconites* (Dam and Andreasen 1990). Escape trace fossils also occur with *Skolithos* in high-energy shoreface deposits within the Holmestrand Formation (Davies et al. 2006).

### Coastal—Transitional

The Tumblagooda Sandstone of Australia also contains a number of facies associations interpreted as representing alluvial settings (Trewin and McNamara 1995; McNamara 2014), although Buatois et al. (1998a) and Davies et al. (2010) have suggested caution in these environmental interpretations. It also has been observed that the unequivocally fluvial parts of the succession are devoid of trace fossils. In the Tumblagooda Sandstone, deposits considered to represent the tops of shallow, low-sinuosity fluvial channels contain *Diplichnites*, *Crescentichnus* (*Selenichnites* in original publication; see Romano and Whyte 2015) and other, bilaterally symmetrical, short, scratched burrows (*Rusophycus*), bilobate trails and paired grooves (*Tumblagoodichnus*), actively filled (massive) horizontal to oblique burrows (?*Planolites*), *Didymaulyponomos*, *Skolithos*, *Lunatubichnus*, *Diplocraterion*, paired burrows, and *Heimdallia* (Trewin and McNamara 1995; Fig. 6.1a–f). Purported eolian sandsheets and ponds contain a similar trace-fossil assemblage with *Diplichnites* and other trackways and scratch marks (?*Paleohelcura*, ?*Protichnites*, *Siskemia*), *Didymaulichnus*, *Tumblagoodichnus*, meander-loop trails, *Beaconites*, *Skolithos* (including *Tigillites* in the original publication), *Heimdallia*, and paired burrows (Fig. 6.1a–f). A possible tetrapod trackway also has been reported (McNamara 2014); although, whilst undoubtedly a track, it is probably arthropod in origin and requires further study. Intensely bioturbated layers with the complex ichnotaxon *Heimdallia* most likely represent marine incursions (Buatois et al. 1998a), particularly within parts of the succession that otherwise are devoid of trace fossils, and so these assemblages are probably best considered as having formed under at least transitional conditions within a coastal environment.

Also occurring in the Sundvollen Formation is red siltstone that probably represents intertidal conditions. This siltstone contains *Diplocraterion* and *Polarichnus*, combined with a variety of trackways and scratch marks (*Merostomichnites*, *Oniscoidichnus*, *Stiaria* (*Paleohelcura* in the original publication), *Palmichnium*) (Davies et al. 2006). The presence of certain ichnogenera (e.g., *Stiaria*) suggests that some trace-fossil forms may have been emplaced subaerially, which is consistent with the association with mudcracks. However, bryozoans are locally present and indicate periodic marine influence. Coastal-plain, ephemeral-pool deposits in the same unit preserve *Gordia*, *Diplichnites*, *Palmichnium* and other trackways and scratch marks (*Siskemia*), and trails with undulating bars and transverse furrows (*Steinsfjordichnus*) (Whitaker 1979; Davies et al. 2006). By contrast, supratidal deposits contain *Merostomichnites*, *Palmichnium*, *Cruziana*, and *Polarichnus* (Davies et al. 2006).

Within the Holmestrand Formation, lower-energy foreshore deposits contain *Diplichnites*, *Palmichnium*, *Didymaulichnus*, *Cruziana*, *Rusophycus*, possible plug-shaped burrows (*Margaritichnus* in the original publication), *Taenidium*, *Skolithos*, *Diplocraterion*, and *Polarichnus* (Dam and Andreasen 1990; Davies et al. 2006). Dam and Andreasen (1990) noted the presence of sedimentary structures such as mudcracks and adhesion structures that indicate subaerial exposure in these deposits. Backshore deposits from the Holmestrand Formation contain *Diplichnites* and *Palmichnium* (Davies et al. 2006). Hanken and Størmer (1975) also described *Palmichnium* from the Ringerike Group, but the precise location and environmental setting is unclear.

Delta-plain, distal-overbank deposits with local evidence of subaerial exposure in the Major Mitchell Sandstone contain *Diplichnites* and a possible fish trail (Gouramanis et al. 2003). Sheetflood sandstones in the overbank interdistributary areas contain simple, actively filled (meniscate) horizontal to oblique burrows (*Scoyenia*) and *Daedalus* (Gouramanis et al. 2003). Although these two ichnotaxa were regarded as part of the *Scoyenia* Ichnofacies by Gouramanis et al. (2003), *Daedalus* is clearly a marine ichnogenus. The two ichnogenera never occur in association (Gouramanis et al. 2003), and in all probability *Scoyenia* represents overbank deposits of the upper delta plain, whereas *Daedalus* records marine-influenced facies, probably in the lower delta plain.

The Freshwater East Formation contains deposits from low-relief, unconfined, ephemeral fluvial-channels, or a coastal plain with ponds or tidal creeks (Morrissey and Braddy 2004; Marriott et al. 2009). Mudcracks indicate periodic subaerial exposure. The trace-fossil assemblage recorded by these deposits is diverse, consisting of *Diplichnites*, *Palmichnium* and other trackways and scratch marks

(*Striatichnium*), *Didymaulichnus*, *Cruziana* (*Isopodichnus* in the original publication), *Rusophycus*, *Crescentichnus* (*Selenichnites* in the original publication), *Helminthopsis*, *Palaeophycus*, and *Arenicolites* (Morrissey and Braddy 2004; Marriott et al. 2009).

Coastal—Subaerial

A final trace-fossil assemblage from the Tumblagooda Sandstone consists of deposits interpreted as eolian dunes and contains *Diplichnites* (Trewin and McNamara 1995). These may be considered as forming under subaerial conditions within a coastal dune environment.

#### 6.2.1.2 Alluvial Settings

Trace fossils from late Silurian alluvial settings occur from the Stubdal Formation (Ludlow to Prídolí) of the Ringerike Group in Norway (Davies et al. 2006), and the Moor Cliffs Formation (Prídolí) of Wales (Marriott and Wright 2004; Morrissey and Braddy 2004; Marriott et al. 2009). Alluvial trace-fossil assemblages also occur from the uppermost Silurian Dingle Group of Ireland (Horne and Gardiner 1973; Allen and Williams 1981), the likely upper Silurian to Lower Devonian Port Stephens Formation of the Falkland Islands (Hunter and Lomas 2003) as well as the Mount Daubeney Formation of Australia (Neef 2004a).

Alluvial—Subaqueous

In addition to coastal facies, the Port Stephens Formation includes alluvial facies with alluvial-fan and stable fluvial-channel deposits on alluvial plains that contain rare *Skolithos* (Hunter and Lomas 2003).

Alluvial—Transitional

Low-energy, braided fluvial-channel, or crevasse-splay deposits from the Stubdal Formation preserve monotaxic trace-fossil assemblages of *Diplichnites* (Davies et al. 2006). A more diverse trace-fossil assemblage occurs in the Moor Cliffs Formation, where bar tops and crevasse-splay or flood-out deposits contain *Diplichnites*, *Palmichnium*, *Paleohelcura*, *Rusophycus*, *Cochlichnus*, *Beaconites*, and *Palaeophycus* (Marriott and Wright 2004; Marriott et al. 2009).

Floodplain deposits from the Sundvollen Formation with evidence of subaerial exposure contain *Merostomichnites*, *Palmichnium*, *Cruziana*, and *Polarichnus* (Davies et al. 2006). The Mount Daubeney Formation contains trace fossils from terminal alluvial fan settings with ponds and fluvial channels (Neef 2004a). The trace-fossil assemblage is diverse and consists of *Diplichnites*, *Merostomichnites*, *Palmichnium*, *Didymaulichnus*, *Cruziana*, and other bilobate trails and paired grooves (*Diplopodichnus*), *Rusophycus* and *Planolites*. The trace fossils are mostly thought to have formed subaqueously, although there is some evidence of desiccation, and *Diplichnites* and *Palmichnium* are considered to have been produced subaerially (Neef 2004a). The Moor Cliffs Formation contains two tuff beds that contain trace fossils. One of these units, the Rook's Cave Tuff Bed was deposited in floodplain ponds and interpond areas and contains *Palmichnium*, *Diplopodichnus*, *Cruziana*, bilobed trails, grooves, burrow tops, and pellets. The second unit, the Townsend Tuff Bed, was deposited in ephemeral lakes or ponds on mudflats or floodplains within an anastomosing fluvial system. The Townsend Tuff Bed preserves *Diplopodichnus*, *Beaconites*, bilobed trails, trumpet burrows, burrow tops, and pellets (Morrissey and Braddy 2004; Marriott et al. 2009). The Dingle Group also contains ephemeral-pool deposits but houses only *Beaconites* (Horne and Gardiner 1973; Allen and Williams 1981).

#### 6.2.1.3 Lacustrine Settings

Trace fossils from late Silurian lacustrine settings are limited to ephemeral and semipermanent lakes. They occur from the Clam Bank Formation (Přídolí) of Newfoundland (Wright et al. 1995) and Moor Cliffs Formation (Přídolí) of Wales (Marriott and Wright 2004).

##### Lacustrine—Ephemeral

Ephemeral saline-lake deposits from the Clam Bank Formation include *Diplichnites*, *Monomorphichnus*, simple, actively filled (meniscate) horizontal to oblique burrows, and passively filled horizontal to oblique burrows (Wright et al. 1995; Fig. 6.1g–h). Some of the trackways and burrows are observed to cross-cut salt pseudomorphs and so it is likely that the trackways formed subaerially whilst the substrate was drying and was damp but firm (Wright et al. 1995). Additionally, deposits of semipermanent, shallow floodplain lakes from the Moor Cliffs Formation preserve cf. *Planolites* and cf. *Arenicolites* (Marriott and Wright 2004).

### *6.2.2 Silurian Ecospace Occupation and Ecosystem Engineering*

Trace-fossil evidence shows that, in addition to those settings colonized in the Ordovician (subaqueous coastal, transitional coastal, and transitional alluvial), organisms had moved into subaqueous alluvial and ephemeral lacustrine environments by the end of the Silurian (Figs. 6.2 and 6.3). Global ichnodiversity and ichnodisparity for Silurian subaqueous and transitional coastal settings are less than those for the Ordovician examples (see Chap. 5). Silurian subaqueous coastal environments

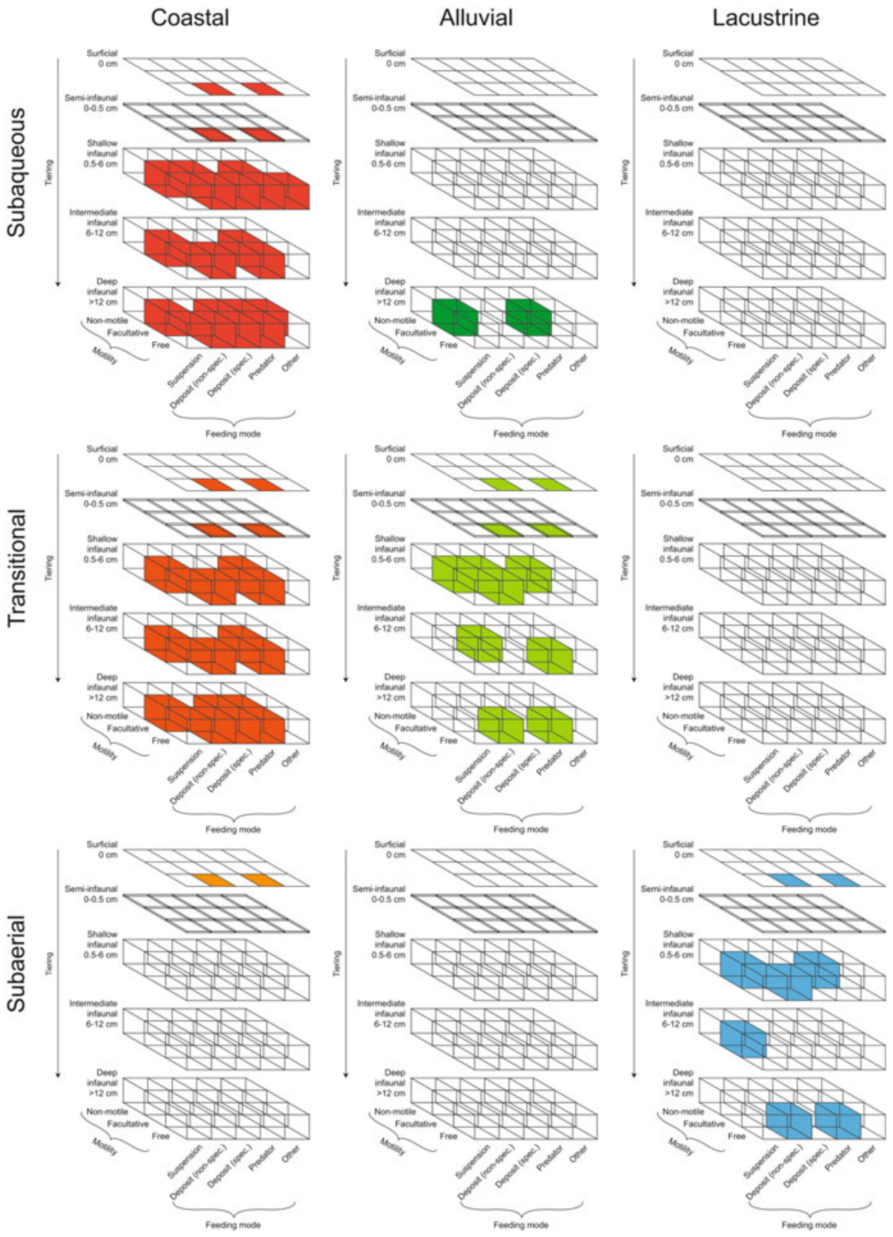

**Fig. 6.2** Silurian ecospace occupation

contain 29 ichnogenera and 17 architectural designs, representing 22 modes of life and 11 methods of sediment modification. These values are similar for transitional coastal environments, which host a global total of 33 ichnogenera and 12 architectural designs that correspond to 18 modes of life and nine methods of sediment modification. Transitional settings in alluvial environments contain 15 ichnogenera and

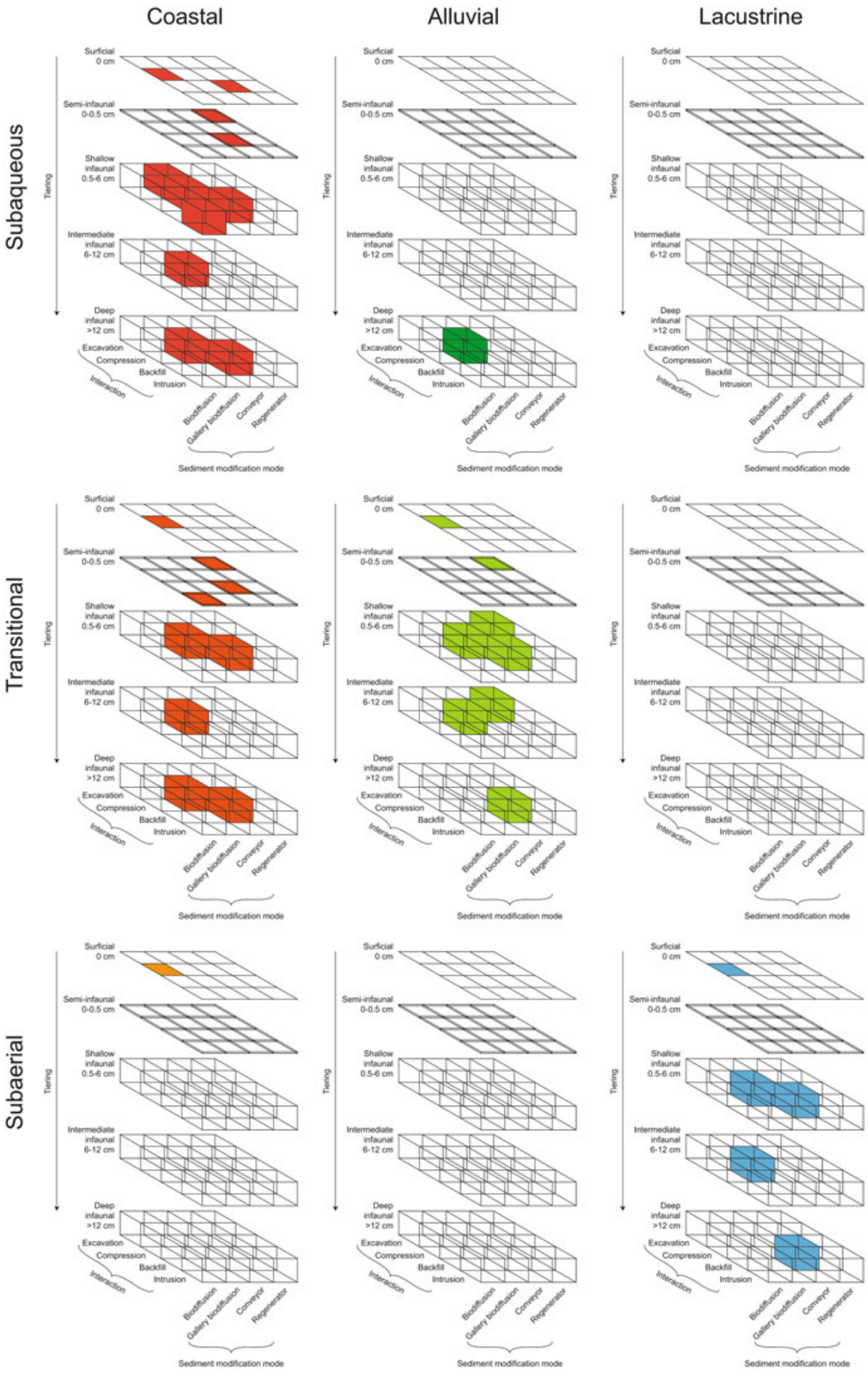

**Fig. 6.3** Silurian ecosystem engineering

nine architectural designs, corresponding to 12 modes of life and eight methods of sediment modification. Ephemeral lacustrine environments show evidence of their initial colonization and globally comprise six ichnogenera and five architectural designs, representing eight potential modes of life and five methods of sediment modification. The presence of organisms also is apparent in subaerial coastal and subaqueous alluvial environments, although only one trace-fossil assemblage has been described from each. The subaerial coastal trace-fossil assemblage comprises just one ichnogenus and architectural design that represents one method of sediment modification but two potential modes of life. In alluvial environments, subaqueous settings also are restricted to just one ichnogenus and architectural design that corresponds to one method of sediment modification and two potential modes of life.

All categories of coastal environments, transitional alluvial environments, and ephemeral lacustrine environments were colonized by freely mobile, nonspecialized deposit feeders or predators that inhabited the surficial tier (Fig. 6.2). This is evidenced by the presence of at least one trackway or scratch-mark ichnogenus, the compressive formation of which would have caused only minimal biodiffusive modification to surficial sediment (Fig. 6.3). *Diplichnites* is ubiquitous across such environments. Transitional coastal environments contain the greatest number of trackway and scratch-mark ichnogenera. *Stiaria*, *Siskemia*, *Striatichnium*, *Oniscoidichnus*, and *Protichnites* are exclusive to transitional coastal environments, whereas *Merostomichnites*, *Paleohelcura*, and *Palmichnium* are shared with transitional alluvial environments. Subaqueous coastal environments harbor different trackway and scratch-mark ichnogenera, namely *Petalichnus* and *Monomorphichnus*, the latter of which is also found in ephemeral lacustrine environments. Organisms with the same mode of life and that modify the sediment in the same way also were responsible for trails with undulating transverse bars and furrows in transitional coastal environments, bilobate trails and paired grooves in transitional alluvial environments, and simple horizontal trails in both. In subaqueous coastal environments, freely mobile, surficial, nonspecialized deposit feeders acted as sediment conveyors, moving through the sediment by backfilling that resulted in the production of simple, actively filled (meniscate) horizontal to oblique burrows (Figs. 6.2 and 6.3).

Freely mobile, nonspecialized deposit feeders and predators occupied the semi-infaunal tier of subaqueous coastal and transitional coastal and alluvial environments (Fig. 6.2). Bilobate trails and paired grooves, and bilaterally symmetrical short, scratched burrows were produced by excavation and the organisms responsible acted as sediment regenerators (Fig. 6.3). Bilobate trails and paired grooves also were produced in the semi-infaunal tier by organisms with the same mode of life that moved through the sediment by intrusion, leading to minimal biodiffusive disruption of the sediment during their creation in transitional coastal environments (Figs. 6.2 and 6.3). In the semi-infaunal tier of subaqueous and transitional coastal environments, simple horizontal trails also were produced by freely mobile, nonspecialized deposit feeders that moved by backfilling and acted as sediment conveyors (Figs. 6.2 and 6.3).

Facultatively mobile suspension feeders and possible predators that inhabited the shallow infaunal tier are present across subaqueous coastal, transitional coastal and alluvial, and ephemeral lacustrine environments (Fig. 6.2). Evidence of their presence is largely in the form of *Palaeophycus*, a passively filled horizontal burrow that acts as a gallery biodiffusion structure and is produced by compression (Fig. 6.3). Organisms with the same mode of life and effect on the sediment also are responsible for plug-shaped burrows in subaqueous and transitional coastal environments as well as dumbbell-shaped burrows in subaqueous coastal environments. Facultatively mobile suspension feeders and possible predators also inhabited the intermediate and deep infaunal tiers of subaqueous and transitional coastal environments, intermediate infaunal tier of ephemeral lacustrine environments, and deep infaunal tier of subaqueous alluvial environments (Fig. 6.2). All of these organisms created gallery biodiffusive structures by compression (Fig. 6.3). The activities of these organisms created vertical simple and single U- and Y-shaped burrows in the intermediate and deep infaunal tiers of subaqueous and transitional coastal environments, plus additional, vertical single U- and Y-shaped burrows in the intermediate infaunal tier of ephemeral lacustrine environments, and vertical simple burrows in the deep infaunal tier of subaqueous alluvial environments.

Freely mobile, nonspecialized deposit feeders inhabited the shallow infaunal tier of transitional alluvial and ephemeral lacustrine environments. Some of these organisms also may have been predatory in subaqueous and transitional coastal environments (Fig. 6.2). In subaqueous coastal environments, these organisms moved through the sediment by backfilling that resulted in minimal biodiffusive disruption to the sedimentary fabric in the production of chevronate trails and vertical displacement burrows (Fig. 6.3). In the remaining environments, organisms with this mode of life moved by backfilling and acted as sediment conveyors, producing simple, actively filled (massive) horizontal to oblique burrows. By contrast, those organisms that produced simple, actively filled (meniscate) horizontal to oblique burrows are restricted to transitional coastal environments (Fig. 6.3).

Nonspecialized deposit-feeding and possible predatory organisms that are freely mobile inhabited the intermediate infaunal tier of subaqueous and transitional coastal environments (Fig. 6.2). They modified the sediment to produce gallery biodiffusive structures by compression that take the form of passively filled horizontal burrows and vertical single U- and Y-shaped burrows (Fig. 6.3). The latter burrows also are present in transitional alluvial environments, where the producers may be exclusively predatory. Nonspecialized deposit feeders and possible predators also occupied the deep infaunal tier of these environments, and also occurred in ephemeral lacustrine environments (Fig. 6.2). They collectively acted as sediment conveyors, creating simple, actively filled (meniscate) horizontal to oblique burrows (Fig. 6.3).

Specialized deposit feeders occupied the deep infaunal tier of subaqueous and transitional coastal environments, where they moved by backfilling and acted as sediment conveyors (Figs. 6.2 and 6.3). Such organisms may be facultatively or freely mobile and produced three-dimensional spreiten trace fossils. Freely mobile, specialized deposit feeders also inhabited the shallow infaunal tier of subaqueous coastal environments (Fig. 6.2). They too, moved through the sediment by backfilling and acted as sediment conveyors in the production of complex, actively filled (meniscate/pelletoidal), horizontal burrows (Fig. 6.3).

Facultatively mobile, nonspecialized deposit feeders acted as sediment regenerators in excavating vertical simple burrows that extend to the shallow and intermediate infaunal tiers of transitional alluvial environments (Figs. 6.2 and 6.3). They also inhabited the shallow infaunal tier of subaqueous coastal environments, but here they produced burrows with horizontal spreiten by compression that acted as gallery biodiffusive structures. Subaqueous coastal environments were also inhabited by organisms with a farming feeding mode that produced gallery biodiffusive structures by compression (Figs. 6.2 and 6.3). Such organisms that were freely mobile inhabited the shallow infaunal tier and produced horizontal helicoidal burrows, whereas others that were facultatively mobile occupied the deep infaunal tier and produced burrows with a shaft or bunch characterized by downward radiating probes.

### 6.2.3 *Silurian Freshwater and Terrestrial Biotas*

Many of the arthropod, fungal, and land-plant lineages initially appear in the fossil record during the latter half of the Silurian. During the Silurian, glacial tillites were deposited in an extensive region of northwestern Africa, the northern Arabian Peninsula and South Africa, a region that underwent multiple glacial episodes, resulting in the formation of freshwater lakes and streams (Hambrey 1985). The lower upper Silurian (Ludlow–Prídolí) Ringerike Group of Norway exposes a variety of associations that preserve trackways, resting trails and burrows in the Sundvollen and Holmestrand formations (Davies et al. 2006). Ichnotaxa from these two units are attributed mostly to arthropod makers and represent a broad coastal assemblage of amphibious taxa occurring in several subenvironments of beach, floodplain, river, and probably small lake environments (Davies et al. 2006).

A different assemblage of organisms is preserved from the probable lower to middle Silurian Tumblagooda Sandstone of Western Australia, characterized by fluvial and eolian deposits punctuated by probable marine incursions and locally displaying bioturbation from indeterminate invertebrates and the sediment-binding effects of bacteria, fungi, and algae (Trewin 1993). Subaerial trackways are present in the Prídolí Clam Bank Formation from Newfoundland, Canada. The ichnofauna consists of trackways likely constructed by an arthropleurid, probably *Eoarthropleura* (Wright et al. 1995), indicating one of the earliest occurrences of this enigmatic myriapod group. Upper Silurian deposits of the Moor Cliffs Formation and superposing tuff unit, also of Prídolí age, occur in southern Wales and preserve arthropod locomotory trackways, foraging traces with associated pelleted coprolites, and burrows (Marriott et al. 2009). These well-preserved trackways record the activities of several arthropod taxa, including a probable myriapod and a possible eurypterid, interpreted as occupants of brackish water and ephemeral channels that occasionally moved subaerially among water bodies (Marriott et al. 2009). Also from the upper Silurian (Prídolí) Old Red Sandstone, but from the more southerly Anglo-Welsh Basin, are continental freshwater trace-fossil assemblages that collectively constitute several ichnogenera representing a diversity of infaunal and epifaunal life habits, featuring arthropod and fish locomotion traces (Morrissey et al. 2012a).

The body-fossil record of continental aquatic and terrestrial organisms begins in the latter half of the Silurian, during the Wenlock through Prídolí stages. Within this interval, at least five groups of arthropods possessing diverse feeding habits have their earliest occurrences in fluvial, lacustrine or adjacent environments in paralic deposits of Euramerica (Jeram et al. 1990; Dunlop and Webster 1999). The represented groups are chelicerate lineages of Scorpionida (scorpions) (Jeram et al. 1990) and Trigonotarbida (trigonotarbid arachnids) (Dunlop 1996), and myriapod lineages of Arthropleurida (arthropleurids) (Shear and Selden 1995), Diplopoda (millipedes) (Almond 1985), and Chilopoda (centipedes) (Shear et al. 1998). The Silurian taxa of two of these lineages—proscorpionid scorpions and kampecarid millipedes—previously were thought to be aquatic (Selden and Jeram 1989; Jeram 2001), but presently are considered as primitively terrestrial and air respiring (Dunlop et al. 2008). These major Silurian arthropod groups, with the exception of hexapods that currently lack Silurian representatives, eventually formed the basis of a Devonian arthropod fauna. Similarly, the later Silurian was a time characterized by considerable innovation in plants, and included the first appearances of several plant lineages (Wellman and Richardson 1993; Kenrick and Crane 1997; Bateman et al. 1998). On land, there was the first major expansion of detritivory by small arthropods (Shear and Kukalová-Peck 1990), although this major trophic expansion was tempered by the beginnings of herbivory (Edwards et al. 1995; Habgood et al. 2004; Labandeira 2007). These continental biotas subsequently diversified and became prominent in the Devonian.

## 6.3 Devonian

Devonian continental trace-fossil assemblages occur from Europe, North America, Asia, Antarctica, and Australia, and span the entire range of the period. A larger number of assemblages occur in fully alluvial settings compared to those of the Silurian. Permanent lake margins were colonized for the first time in the Early Devonian. The first tetrapod trackways occur during the Middle Devonian. Coprolites and a limited variety of plant–arthropod interactions from the Early Devonian provide direct evidence of detritivores, saprobes, herbivores, and carnivores.

### *6.3.1 Early Devonian Trace-Fossil Assemblages*

#### 6.3.1.1 Coastal Settings

Early Devonian trace-fossil assemblages along coastal settings are recorded from the Dniester Formation (Lochkovian) of the Ukraine (Uchman et al. 2004) and Nellenkopfalen Formation (latest Early Emsian) of Germany (Poschmann and Braddy 2010). Additional assemblages, the ages of which are not determined beyond the Early Devonian, occur from the Esopus Formation of Highland Mills in New York state (Marintsch and Finks 1982), the Horlick Formation of Antarctica (Bradshaw 2002, 2010; Bradshaw et al. 2002), and the Muth Formation of India (Draganits et al. 1998, 2001).

The Devonian Taylor Group of Beacon Heights in South Victoria Land in Antarctica comprises a number of formations, the ages of which are not tightly constrained. Their environmental interpretations also have proved contentious (Bradshaw 1981; Gevers and Twomey 1982; Plume 1982; Woolfe 1990). We include the majority of them here within the coastal categories. In ascending stratigraphic order, the Taylor Group comprises: the Windy Gully Sandstone, Terra Cotta Siltstone, New Mountain Sandstone, Altar Mountain, Arena Sandstone, Beacon Heights Orthoquartzite, and Aztec Siltstone formations (Bradshaw 1981). The Aztec Siltstone Formation is late Middle Devonian (Givetian) in age (see Long et al. 2008) and the underlying Beacon Heights Orthoquartzite Formation also is likely late Middle Devonian (McLoughlin and Long 1994), whereas the Terra Cotta Siltstone Formation is Early Devonian in age (Kyle 1977). For the purposes of this review, the succession from the Windy Gully Sandstone Formation through to the Altar Mountain Formation therefore is treated as Early Devonian in age.

### Coastal—Subaqueous

Lagoon deposits from the Dniester Formation contain horizontal burrows with vertical spreiten (*Teichichnus*) and burrows with horizontal spreiten (*Spirophyton*), and simple tubes (Uchman et al. 2004). Mudcracks are also present, which indicate periodic desiccation although this is likely to post-date formation of the trace fossils. The lower part of the Terra Cotta Siltstone Formation contains thin, ripple-marked sandstones with *Diplichnites* and *Didymaulichnus* that are interpreted by Bradshaw (1981) as having formed in a coastal lagoon.

Fluvio-estuarine channel bars and spits from the Dniester Formation contain *Skolithos*, which also is present in storm-surge and swash deposits. Storm-washover or bayhead-delta deposits also contain *Skolithos* and *Planolites*. Channel-mouth bars or washover fills from inshore bays or lagoons preserve *Monomorphichnus*, *Rusophycus*, isolated and serial almond-shaped burrows (*Lockeia*) and simple tubes (Uchman et al. 2004).

The Horlick Formation largely consists of deposits that are interpreted to have formed in subtidal and shoreface settings, although there are trace fossils in longshore or tidal delta channels close to river mouths. The trace fossils consist of *Diplichnites* and other trackways and scratch marks (?*Maculichna*, large tracks); horizontal, branched, concentrically filled burrows (*Asterosoma*); *Diplocraterion* and other vertical, single U- and Y-shaped burrows (aff. *Lanicoidichna*); and *Spirophyton* (Bradshaw 2002, 2010; Bradshaw et al. 2002).

Bradshaw (1981) interpreted the Windy Gully Sandstone through the Altar Mountain Formation as representing shallow-marine to coastal settings, whereas other authors (Plume 1982; Woolfe 1990) interpreted the same deposits as being nonmarine. The Windy Gully Sandstone Formation consists of trough cross-bedded and heavily bioturbated sandstones. Some of these heavily bioturbated units preserve horizontal lamination and mudcracks. The trace-fossil assemblage consists of *Palmichnium*, *Diplichnites*, *Didymaulichnus*, large isolated tracks and epichnial ridges, horizontal branching burrow systems (*Agrichnium*), and *Heimdallia* (Bradshaw 1981). McKelvey et al. (1977) also noted the presence of diverse invertebrate burrows in the Windy Gully Sandstone Formation. The New Mountain Sandstone Formation contains the same types of trace fossils as the Windy Gully Sandstone Formation, and consists of small-scale cross-bedded lithic sandstones and cross-bedded medium- to coarse-grained sandstones alternating with horizontally laminated bioturbated sandstones. Bradshaw (1981) interpreted these sedimentary features and trace fossils to represent a tidally influenced sandflat with distributary channels.

### Coastal—Transitional

The majority of deposits from the Esopus Formation of Highland Mills represent subtidal to offshore settings, although there are some possible intertidal shales containing horizontal burrows with horizontal to vertical branches (*Treptichnus*; *Phycodes* in the original publication) (Marintsch and Finks 1982). Mixed-intertidal flat or point-bar deposits with evidence of subaerial exposure from the Nellenkopfalen Formation contain *Palmichnium*, *Protovirgularia*, *Lockeia*, and burrows with horizontal spreiten (*Lophoctenium*) (Poschmann and Braddy 2010). Very shallow-intertidal through to coastal-dune settings from the Muth Formation contain *Diplichnites*, *Diplopodichnus*, *Palmichnium*, *Crescentichnus* (*Selenichnites* in the original publication), *Didymaulichnus*, meandering grazing trails, *Taenidium*, *Didymaulyponomos*, and vertical burrows (Draganits et al. 1998, 2001).

*Diplichnites*, *Palmichnium*, and large isolated tracks also are found in the Windy Gully Sandstone, but the assemblage is confined to the foresets of low-angle cross-bedded sandstones. Bradshaw (1981) interpreted these deposits as active channels on relatively protected, tidally emergent sandflats within a tide-dominated bay or open estuary. However, Plume (1982) suggested that the Windy Gully Sandstone Formation was deposited by large braided fluvial channels and that some of the cross-bedded units may have been eolian. At the top of the New Mountain Sandstone Formation, *Skolithos* is found in cross-bedded sandstones, which Bradshaw (1981) interpreted as signifying marine conditions. Gevers and Twomey (1982) agreed, interpreting the New Mountain Sandstone Formation as shallow marine due to the presence of *Diplichnites* that they believed to have been produced by trilobites. However, Plume (1982) interpreted this deposit as representing a braided-fluvial system with possible eolian dunes. Herein, we treat these assemblages from the Windy Gully Sandstone and New Mountain Sandstone as belonging to transitional coastal environments.

Two distinct trace-fossil assemblages occur within the Altar Mountain Formation. The first consists exclusively of *Skolithos* in cross-bedded sandstones, and the second comprises *Skolithos* (including *Tigillites* in the original publication), *Diplocraterion*, *Didymaulypnomos*, *Helminthopsis*, *Beaconites*, and horizontal burrows with vertical spreiten (*Halopoa*; ?*Fucusopsis* in the original publication). Webb (1963) noted the presence of interwoven horizontal burrows and trackways in the Odin Arkose Member of the Altar Mountain Formation, and McKelvey et al. (1977) also reported *Beaconites*, tracks, trails, and vertical burrows. Bradshaw (1981) interpreted the Altar Mountain Formation as forming in open, shallow-marine settings, and Gevers and Twomey (1982) interpreted the Odin Arkose Member as estuarine and lagoonal with periodic emergence. However, Woolfe (1990) noted that *Beaconites* occurs in close association with *Skolithos* and *Diplichnites* and probably formed in ephemeral pools, whereas occurrences of *Skolithos* in cross-bedded sandstones indicate high-energy flow rather than necessarily marine conditions. Inferring environmental conditions based upon the trace fossils present introduces circularity, but all other known occurrences of *Beaconites* and *Halopoa* are continental and marine, respectively. In this instance, the trace-fossil assemblage most likely represents a composite suite that developed under transitional conditions in a coastal environment.

The upper part of the Terra Cotta Siltstone Formation contains *Didymaulichnus*, *Cruziana*, *Rusophycus*, trackways and scratch marks (*Petalichnus*), and *Diplocraterion* and *Halopoa* (?*Fucusopsis* in the original publication) in massive muddy or silty deposits. The lower part of the Formation was interpreted by Bradshaw (1981) as a coastal lagoon, but it was noted that the presence of rounded and flattened, sometimes twin-crested, symmetrical ripples indicated some tidal action. Lenticular bedding also suggested tidal influence; and mudcracks indicated periodic emergence. Interstratal shrinkage cracks are also present. However, Plume (1982) stated that $\delta^{13}C$ data from carbonate concretions indicated a freshwater lacustrine setting and the presence of symmetrical ripples and mudcracks indicated a marginal lacustrine environment. Woolfe (1990) also suggested that *Cruziana* and *Rusophycus* in the Terra Cotta Siltstone Formation formed in fluvio-lacustrine settings. We treat this trace-fossil assemblage as belonging to a transitional coastal environment.

#### Coastal—Subaerial

In the Muth Formation, *Diplichnites* and *Palmichnium* specifically are considered to have formed subaerially as the producers migrated up coastal dunes in a direction perpendicular to the shoreline (Draganits et al. 1998, 2001).

### 6.3.1.2 Alluvial Settings

A large number of trace-fossil assemblages from alluvial settings occur from the Early Devonian. In Wales, these are the Freshwater West Formation (Lochkovian) (Morrissey and Braddy 2004; Marriott et al. 2009), St. Maughns Formation (Lochkovian) (Morrissey et al. 2004; Fayers et al. 2010), the Red Marls (Lochkovian) (Allen and Williams 1981), Upper Red Marls Group (Lochkovian) (Smith et al. 2003), Senni Formation (Lochkovian to Pragian), Brownstones Formation

(Lochkovian to Pragian) (Hillier et al. 2008), and Ridgeway Conglomerate Formation (late Lochkovian to early Pragian) (Hillier and Williams 2007; Marriott et al. 2009). Elsewhere in Europe are the Port Dubh Fish Beds (earliest Devonian to no older than Prídolí) (Trewin et al. 2012) and Ochil Volcanic Formation (Pragian) (Batchelor and Garton 2013) of Scotland, the Peel Sandstone Group (Lochkovian to Pragian) of the Isle of Man (Crowley et al. 2009), and Wood Bay Formation (late Lochkovian to middle Emsian or early Eifelian) of Svalbard (Wisshak et al. 2004).

In the Darwin Mountains of Antarctica, the Brown Hills Conglomerate temporally correlates with the Windy Gully Sandstone and Terra Cotta Siltstone formations of the Beacon Heights, and the Junction Sandstone correlates with the New Mountain Sandstone and Altar Mountain formations (Woolfe 1993).

### Alluvial—Subaqueous

Trace-fossil assemblages that may be definitively identified as forming under active fluvial-channel conditions and not during channel abandonment are limited. *Beaconites* has been reported from laterally accreting point-bar deposits of the Red Marls (Allen and Williams 1981), although the deposits are heterolithic sandstone and mudstone that imply variable flow and probable periods of inactivity. The Wood Bay Formation represents a fluvial system, and bilaterally symmetrical, short, scratched burrows (*Svalbardichnus*) occur at the base of intraformational conglomerates and coarse- to very coarse-grained sandstones (Wisshak et al. 2004). The Brown Hills Conglomerate is interpreted as an alluvial-plain deposit with braided fluvial channels that contain *Skolithos* (Haskell et al. 1965; Woolfe 1993).

### Alluvial—Transitional

Abandoned fluvial-channel and associated point-bar deposits contain consistent, generally low diversity trace-fossil assemblages. The Conigar Pit Member of the Freshwater West Formation contains coarse-grained multistory sandstones representing a perennial fluvial system and preserves *Beaconites* (Morrissey and Braddy 2004; Marriott et al. 2009). *Beaconites* occurs together with *Diplichnites* in fluvial-channel deposits of the Ridgeway Conglomerate Formation (Hillier and Williams 2007). *Diplichnites* and *Skolithos* also are reported from channel-margin benches and mid-channel bars of low-sinuosity braided-fluvial systems in the Upper Red Marl Group (Smith et al. 2003). Periodically exposed or abandoned bar tops in low-sinuosity fluvial channels from the Brownstones Formation contain *Diplichnites*, *Beaconites*, and sinuous trails (Hillier et al. 2008). The Ridgeway Conglomerate Formation also contains alluvial-fan debris-flow and fan-lobe deposits with *Beaconites* (Hillier and Williams 2007; Marriott et al. 2009). *Beaconites* also is present, together with *Diplocraterion*, from low-sinuosity, distal, alluvial-fan channels and in the tops of fluvial-channel sandstones of the Peel Sandstone Group (Crowley et al. 2009). The Junction Sandstone Formation of Antarctica is interpreted as the product of unconstrained braided-fluvial channels and ephemeral pools with *Skolithos*, *Diplichnites*, and *Beaconites* (Haskell et al. 1965; Woolfe 1993).

Heterolithic units with dominant mudstone from the Conigar Pit Member of the Freshwater West Formation are interpreted as representing a semiarid, ephemeral, fluvial system, characterized by *Diplichnites*, *Palaeophycus*, and other passively filled horizontal to oblique burrows (*Tumblagoodichnus*) (Morrissey and Braddy 2004; Marriott et al. 2009). Also in the Freshwater West Formation, the Rat Island Mudstone Member contains heterolithic deposits of ephemeral fluvial channels with a diverse trace-fossil assemblage of *Diplichnites*, *Paleohelcura*, *Cruziana*, *Striatichnium*, *Rusophycus*, *Crescentichnus* (*Selenichnites* in the original publication), *Cochlichnus*, *Treptichnus*, *Beaconites*, and *Palaeophycus* (Morrissey and Braddy 2004; Marriott et al. 2009). Probable overbank areas within the overall fluvial system of the Wood Bay Formation contain *Merostomichnites*, *Siskemia*, *Cruziana*, *Beaconites*, and *Planolites* (Wisshak et al. 2004).

The St. Maughns Formation contains *Diplichnites*, *Palmichnium*, and other trackways and scratch marks (*Protichnites*), cf. *Cruziana*, cf. *Cochlichnus*, and other simple horizontal trails (*Undichna*), and *Beaconites* in fluvial-backwater or floodplain-pool deposits associated with rare mudcracks. *Diplichnites* is in places observed to cross-cut *Undichna* (Morrissey et al. 2004; Fayers et al. 2010). The Peel Sandstone Group also contains a diverse trace-fossil assemblage comprising *Diplichnites*, *Protichnites* and other trackways and scratch marks (*Stiallia*), *Diplopodichnus*, ?*Crescentichnus* (*Selenichnites* in the original publication), and *Halopoa* (*Fucusopsis* in the original publication) that formed in shallow ponds and the margins of ephemeral, standing water bodies (Crowley et al. 2009). The Senni Formation also contains desiccated ephemeral-pool deposits that preserve only *Diplichnites* (Hillier et al. 2008).

In Scotland, the Port Dubh Fish Beds are associated with fluvial conglomerates and cross-bedded sandstones that include fine-grained sandstones and red mudstones with mudcracks. These strata are interpreted as low-energy alluvial-plain deposits. The latter deposits contain sparse burrows and indistinct trackways (Trewin et al. 2012). Mudstones and siltstones interbedded with lavas from the Ochil Volcanic Formation of Scotland contain *Paleohelcura* (Batchelor and Garton 2013). The depositional environment of these trackways is not discussed in detail but probably should be assigned to the transitional alluvial category.

### 6.3.1.3 Lacustrine Settings

Trace fossils appear for the first time in lake-margin settings during the Early Devonian. This material occurs from Dunure and Montrose in Scotland but the age is not constrained beyond that of Early Devonian (Smith 1909; Pollard and Walker 1984; Walker 1985). Trace fossils in ephemeral lakes also occur in the Ridgeway Conglomerate Formation (late Lochkovian to early Pragian) (Hillier and Williams 2007; Marriott et al. 2009); Tillywandland Fish Bed (Lochkovian) (Trewin and Davidson 1996); and the Port Dubh Fish Beds of Scotland (Trewin et al. 2012), which probably are earliest Devonian in age and no older than Prídolí.

### Lacustrine—Margin

The material from Dunure and Montrose was first described by Smith (1909). Restudy of this material by Pollard and Walker (1984) and Walker (1985) suggests that the trace fossils formed in very shallow-water conditions, possibly subject to intermittent exposure, at the shoreline of a lake. Trace fossils occur from a number of localities, but overall the trace-fossil assemblage comprises *Merostomichnites*, *Siskemia*, *Stiaria*, *Stiallia*, and other trackways and scratch marks (*Danstairia*, *Keircalia*, *Mitchellichnus*), *Diplopodichnus*, epichnial grooves and trails (*Scolicia* in Pollard and Walker 1984), *Cruziana*, *Rusophycus*, simple horizontal trails (*Mermia*), and *Arenicolites* (Pollard and Walker 1984; Walker 1985; Fig. 6.4).

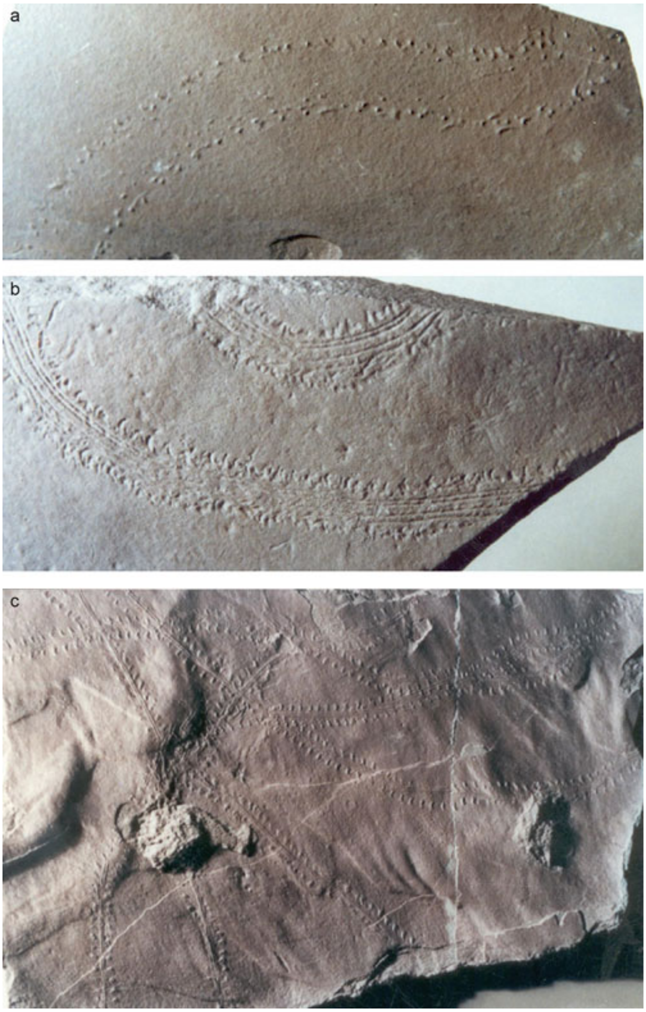

**Fig. 6.4** Devonian trace fossils from the Old Red Sandstone of Dunure and Montrose, Scotland. (**a**) *Danstairia*; (**b**) *Keircalia*; (**c**) *Siskemia*

Lacustrine—Ephemeral

Ephemeral-lake deposits with evidence of desiccation occur in the Ridgeway Conglomerate Formation, and contain *Diplichnites* and *Planolites* (Hillier and Williams 2007; Marriott et al. 2009). The Tillywhandland Fish Beds from the Midland Valley of Scotland represent a short-lived and not especially deep lake. Laminites that accumulated over approximately 2000-years preserve fish body fossils and also contain small burrows. Overlying the laminites, a gradual thickening-upwards of the succession represents shallowing and infilling of the lake and a variety of arthropod trackways and burrows that are preserved within a siltstone horizon (Trewin and Davidson 1996). The Port Dubh Fish Beds consist of grey-green, laminated siltstones that contain body fossils of agnathan fish, myriapods, and a possible eurypterid (Trewin et al. 2012). Also present are the trace fossils *Diplichnites*, *Diplopodichnus* (*Beaconichnus* in the original publication), *Danstairia*, *Siskemia*, *Undichna*, and radial to rosette burrows (*Asterichnus*?). In the case of the latter, Trewin et al. (2012) compared what appear to be radiating grooves at the edges of slabs to *Asterichnus* but acknowledge that the lack of complete material does not permit formal assignment. These deposits are interbedded with red-bed alluvial plain deposits and are interpreted as forming in shallow ephemeral lakes that were created in local topographic hollows (Trewin et al. 2012).

## *6.3.2 Middle Devonian Trace-Fossil Assemblages*

### 6.3.2.1 Coastal Settings

Middle Devonian trace-fossil assemblages reported from coastal settings occur from the Wojciechowice Formation (Eifelian) of Poland (Niedźwiedzki et al. 2010) and Catskill complex of New York (Miller 1979; Knox and Gordon 1999), although the age of the latter is not tightly constrained beyond being Middle Devonian. Other trace-fossil assemblages occur from the Aztec Siltstone Formation (Givetian) of Antarctica (see Long et al. 2008). The underlying Beacon Heights Orthoquartzite Formation is also likely late Middle Devonian in age (McLoughlin and Long 1994). In this review, the Arena Sandstone Formation is treated as Middle Devonian because, together with the Beacon Heights Orthoquartzite Formation, it correlates with the Hatherton Sandstone Formation in the Darwin Mountains of Antarctica (Woolfe 1993).

Coastal—Subaqueous

A number of facies interpreted as having been deposited in alluvial to offshore settings occur from the Catskill complex (Miller 1979; Knox and Gordon 1999). Deposits interpreted as tidal contain arthropod trace fossils, surface trails, *Planolites*, *Spirophyton*, ?*Teichichnus*, *Skolithos*, *Arenicolites*, dumbbell-shaped burrows (*Bifungites*), and large vertical structures (Miller 1979). Knox and Gordon (1999) suggested that they formed in brackish or hypersaline pools or marshes on a tidal flat or floodplain. The Catskill complex also contains what have been interpreted as alluvial deposits and preserves surface trails, *Planolites*, *Spirophyton*, ?*Chondrites*, and *Skolithos* (Miller 1979). Gordon (1988) also identified freshwater-pool deposits that contain *Diplichnites*, *Beaconites*, *Spirophyton*, ?*Planolites*, ?lungfish burrows, small cylindrical burrows, and other trails (Gordon 1988). However, Knox and Gordon (1999) suggested that the occurrence of *Spirophyton* in such settings may reflect colonization by marine organisms during marine incursions over a low-lying coastal plain.

### Coastal—Transitional

The oldest trackways that can be attributed to tetrapods with reasonable confidence come from the Wojciechowice Formation (Niedźwiedzki et al. 2010). The material occurs in deposits that are interpreted as being tidal or possibly lagoonal, with parallel-laminated sediments, mudcracks, and raindrop impressions indicating subaerial exposure (Niedźwiedzki et al. 2010).

The Arena Sandstone Formation of the Beacon Heights area in Antarctica contains planar and trough cross-bedded sandstones that are interpreted as having formed on a low-gradient sandflat adjacent to the sea and contain *Beaconites* (Bradshaw 1981). Bradshaw (1981) also suggested that the *Skolithos*, maze and boxwork burrows (*Ophiomorpha* in the original publication, although pre-Mesozoic reports of this ichnogenus are dubious), *Beaconites*, and sinuous fecal worm trails described by Vialov (1962) from the Beacon Heights Orthoquartzite are in fact likely from the Arena Sandstone. Webby (1968) described "*Scolicia*," which is considered to be *Beaconites* by Bradshaw (1981), from the Arena Sandstone. Webby (1968) also documented vertical simple burrows (*Cylindricum*) as possibly from the Arena Sandstone or Beacon Heights Orthoquartzite. In addition, McKelvey et al. (1977) described the Arena Sandstone as containing diverse trace fossils that include *Beaconites*, although Bradshaw (1981) suggested that these trace fossils may be from the Altar Mountain Formation. Woolfe (1990) suggested that associations of *Beaconites* and *Skolithos*, with the additional occurrence of *Diplichnites*, formed in ephemeral pools. The Beacon Heights Orthoquartzite contains trough cross-bedded sandstone and mudcracks, and is interpreted as having formed in low-sinuosity braided-fluvial channels (Bradshaw 1981). Bradshaw (1981) identified *Beaconites* and possible *Cylindricum*, whereas McKelvey et al. (1977) noted subvertical burrows and tracks. Webby (1968) identified *Skolithos* (including *Tigillites* in the original publication) and *Cylindricum*, and Webb (1963) noted interwoven horizontal burrows, vertical to oblique burrows and walking trails. In the Darwin Mountains of Antarctica, the Hatherton Sandstone correlates with the Arena Sandstone and Beacon Heights Orthoquartzite formations of the Beacon Heights area (Gevers et al. 1971; Woolfe 1993). Haskell et al. (1965) described *Beaconites*, “worm excreta” and parallel grooves, which Gevers et al. (1971) named as *Arthropodichnus darwinum* (= *Diplopodichnus biformis*), in addition to *A. gouldi* (= *Diplichnites gouldi*) and *A. antarcticum* (= *Palmichnium antarcticum*) from the Hatherton Sandstone. Gevers et al. (1971) interpreted these deposits as shallow marine, although Woolfe (1993) favored formation in a braided-fluvial setting. We treat these assemblages as having formed in transitional coastal environments, and those with large *Skolithos* may represent composite assemblages.

The Aztec Siltstone Formation at Beacon Heights in Antarctica is interpreted by Bradshaw (1981) as an alluvial-plain succession deposited by high-sinuosity, meandering-fluvial channels, associated with paleosols, mudcracks, and rootlet horizons. Bradshaw (1981) identified maze and boxwork burrows (*Thalassinoides*) and *Cylindricum*, suggesting that the *Thalassinoides* could have been excavated in the banks of an inlet, and Webb (1963) identified vertical to oblique burrows. The Aztec Siltstone Formation also is present in the Darwin Mountains, where it contains *Beaconites* and *Skolithos*; Woolfe (1993) interpreted the formation as representing an alternation between fluvial and lacustrine deposits on a low-gradient floodplain.

#### 6.3.2.2 Alluvial Settings

A number of Middle Devonian trace-fossil assemblages are reported from alluvial settings. The Battery Point Formation of the Gaspé Sandstone Group of Québec spans the latest Early (early Emsian) to earliest Middle (early Eifelian) Devonian (Braddy and Milner 1998). The Inch Conglomerate and Kilmurry Sandstone formations of Ireland are coeval and assigned a Middle Devonian age (Morrissey et al. 2012b). Other assemblages occur from formations spanning the Middle to Late Devonian, and include additional deposits from the Catskill complex of New York (Gordon 1988), the latest Middle (Givetian) to latest Late (Fammenian) Devonian succession of the Munster Basin in Ireland (O’Sullivan et al. 1986), the ?Middle to Late Devonian McAras Brook Formation of Nova Scotia (Bruck et al. 1985), and latest Middle (late Givetian) to latest Late (Fammenian) Devonian Ravendale Formation of Australia.

##### Alluvial—Transitional

In addition to coastal plain deposits that were originally interpreted as alluvial (Miller 1979; Knox and Gordon 1999), the Catskill complex contains more unequivocal alluvial deposits (Gordon 1988). Abandoned fluvial-channel deposits contain *Diplichnites*, *Rusophycus*, other trails and small cylindrical burrows; channel-bar and levee deposits contain *Diplichnites*, *Beaconites*, bivalve escape trace fossils, ?loop trails and other trails; and crevasse-splay deposits contain *Beaconites*, bivalve escape trace fossils, and ?loop trails (Gordon 1988). Fluvial channel-margin deposits of the Battery Point Formation contain *Palmichnium* (Braddy and Milner 1998). A little known simple, actively filled (meniscate) horizontal to oblique burrow (*Gyrichnites*) has also been reported from this succession (Whiteaves 1882).

The Catskill complex also contains floodplain deposits with *Beaconites*, small cylindrical burrows, ?lungfish burrows, ?bivalve escape trace fossils and ?loop trails (Gordon 1988). Overbank deposits include those of the Munster Basin where non-channelized sheet-flow deposits and ephemeral-pool deposits with evidence of subaerial exposure preserve *Beaconites*-like structures (O'Sullivan et al. 1986). A similar assemblage with *Beaconites*, as well as what are interpreted as probable eurypterid trackways, occurs in overbank deposits with mudcracks and raindrop imprints from the ?Middle to Late Devonian McAras Brook Formation of Nova Scotia (Bruck et al. 1985). Overbank deposits from the Ravendale Formation of Australia contain *Diplichnites* in planar, cross-bedded, fine-grained sandstones that were deposited during waning flow as part of a sheetflood succession (Neef 2004b). *Stiaria* (?*Paleohelcura* in the original publication) also is reported from planar-bedded, fine-grained sandstones (Neef 2004b). However, these trace-fossil identifications are uncertain because the trackway and individual tracks are large and series of three tracks are not observed.

The Inch Conglomerate and Kilmurry Sandstone formations of Ireland contain three facies associations and substrate-restricted trace-fossil assemblages within an arid, intracontinental rift setting (Morrissey et al. 2012b). Sheet and stream flood deposits on an alluvial fan apron in the Inch Conglomerate Formation preserve *Taenidium* and *Scoyenia*. These two trace fossils are also found in ephemeral fluvial deposits that coursed along interdune corridors in the Kilmurry Sandstone Formation. A different assemblage in this unit comprises *Protichnites*, *Rusophycus*, and *Scoyenia* that occurred in a ponded interdune area.

### Alluvial—Eolian

A diverse trace-fossil assemblage is present in eolian barchanoid dune and draa deposits of the Kilmurry Sandstone Formation. This assemblage consists of *Diplichnites*, *Palmichnium*, cf. *Cruziana*, bilobed trails and chambers, ?*Crescentichnus* (cf. *Selenichnites* in the original publication), vertical simple burrows (*Pustulichnus*), simple, actively filled (meniscate) horizontal to oblique burrows (*Entradichnus*), and cf. *Ancorichnus*. However, the latter ichnogenus is known only from marine settings and it is unclear as to which ichnogenus the illustrated specimen belongs: *Palaeophycus* or cf. *Skolithos* (Morrissey et al. 2012b)? These trace fossils represent the first record of the colonization of intracontinental eolian settings (Morrissey et al. 2012b), and can be compared to coastal dunes of the Cambro-Ordovician (MacNaughton et al. 2002; Hagadorn et al. 2011), Silurian (Trewin and McNamara 1995), and Devonian (Draganits et al. 1998, 2001).

#### 6.3.2.3 Lacustrine Settings

Following from the first appearance of trace fossils in lake-margin settings during the Early Devonian, several additional assemblages occur in the Middle Devonian. These are in the Hornelen Basin of Norway (Pollard et al. 1982), and the ?Middle Devonian Stromness Flags (Trewin 1976) and Eday Marls of Orkney, Scotland (Carroll and Trewin 1995).

Lacustrine—Margin

Deposits of the Hornelen Basin represent a lacustrine fan-delta system, where trace fossils occur within ephemeral pools and distributary-channel sand bars (Pollard et al. 1982). Ephemeral-pool deposits contain *Siskemia*, *Merostomichnites*, *Diplopodichnus*, *Cruziana*, *Rusophycus*, ribbon trails, and fine sinuous trails. Small channel sand-bar deposits contain variously oriented burrows (Pollard et al. 1982).

Lacustrine—Ephemeral

The Stromness Flags contain trace fossils in deposits interpreted as those of a shallow lake. Mudcracks above and below the trace-fossil horizon indicate that the lake was subject to frequent desiccation (Trewin 1976). The trace-fossil assemblage comprises *Cruziana*, *Rusophycus*, small horizontal stuffed burrows, and paired burrow endings (U-shaped burrows) (Trewin 1976). The Eday Marls contain *Merostomichnites*, *Beaconites*, and simple vertical burrows (*Cornulatichnus*) in long-lived floodplain-lake deposits (Carroll and Trewin 1995). Carroll and Trewin (1995) also identified some of the non-meniscate burrows associated with *Beaconites* and described by Allen and Williams (1981) as probably *Cornulatichnus*.

### *6.3.3 Late Devonian Trace-Fossil Assemblages*

#### 6.3.3.1 Coastal Settings

The only known trace-fossil assemblage from a coastal setting in the Late Devonian is the Wellsburg Formation of Pennsylvania. It was deposited during the continued accumulation of the Catskill and other delta deposits (Caster 1938).

Coastal—Subaqueous

In the Wellsburg Formation, the trackway *Kouphichnium* is associated with *Nereites*-like complex, actively filled (meniscate/pelletoidal) horizontal burrows, and U-shaped burrows. The environment is interpreted as nearshore marine, possibly lagoonal-mud-flat deposits (Caster 1938). Goldring and Seilacher (1971) suggested that the trace fossil-bearing deposits were unlikely to be of marine origin, although Caster (1938) noted the presence of a sparse marine fauna throughout the relevant unit.

#### 6.3.3.2 Alluvial Settings

Alluvial deposits in the Catskill complex of New York continue up into the Late Devonian with the Oneonta and Walton formations (Frasnian) (Bridge et al. 1986). In Ireland, the Harrylock Formation represents alluvial settings (Bamford et al. 1986), and assemblages also occur from the Upper Devonian to Lower Carboniferous West Cork Sandstone Formation (Horne and Gardiner 1973; Allen and Williams 1981) and Glandahalin, Inshaboy, and Kilmore formations of Kerry Head (Bridge and Diemer 1983).

##### Alluvial—Transitional

In the Oneonta and Walton formations, point-bar deposits preserve *Beaconites*-like structures and arthropod trails (Bridge et al. 1986). Upper point-bar deposits from Kerry Head also contain *Beaconites* (Bridge and Diemer 1983). *Beaconites*-like structures also are present in sandy channel fills in the Harrylock Formation (Bamford et al. 1986).

Proximal crevasse-splay and levee deposits in the Oneonta and Walton formations also preserve *Beaconites*-like structures and trails (Bridge et al. 1986). *Beaconites*-like structures also occur in sheetflood sandstones deposited by waning flows in proximal parts of an ephemeral braided-fluvial system in the Harrylock Formation (Bamford et al. 1986). Additional specimens of *Beaconites* occur in overbank deposits from the Glandahalin, Inshaboy and Kilmore formations of Kerry Head (Bridge and Diemer 1983) as well as in ephemeral-pool deposits of the West Cork Sandstone Formation (Horne and Gardiner 1973; Allen and Williams 1981).

### *6.3.4 Devonian Ecospace Occupation and Ecosystem Engineering*

The principle difference between the Silurian and Devonian is that the margins of persistent lakes (Buatois and Mángano 1993a; Buatois et al. 1998a) and intracontinental eolian (Morrissey et al. 2012b) environments were colonized for the first time during the Devonian (Figs. 6.5 and 6.6). Deposits representing permanently subaqueous deep lacustrine conditions are known from the Emsian to Eifelian Campbellton Formation of New Brunswick but, despite extensive study, these important deposits have yielded no trace fossils (Kennedy and Gibling 2011). The first unequivocal trackways attributable to tetrapods also appear in the Devonian (Niedźwiedzki et al. 2010; Narkiewicz et al. 2015). Fifteen ichnogenera are found globally across Devonian lake-margin environments, representing six architectural designs and modes of life and five methods of sediment modification. Eolian

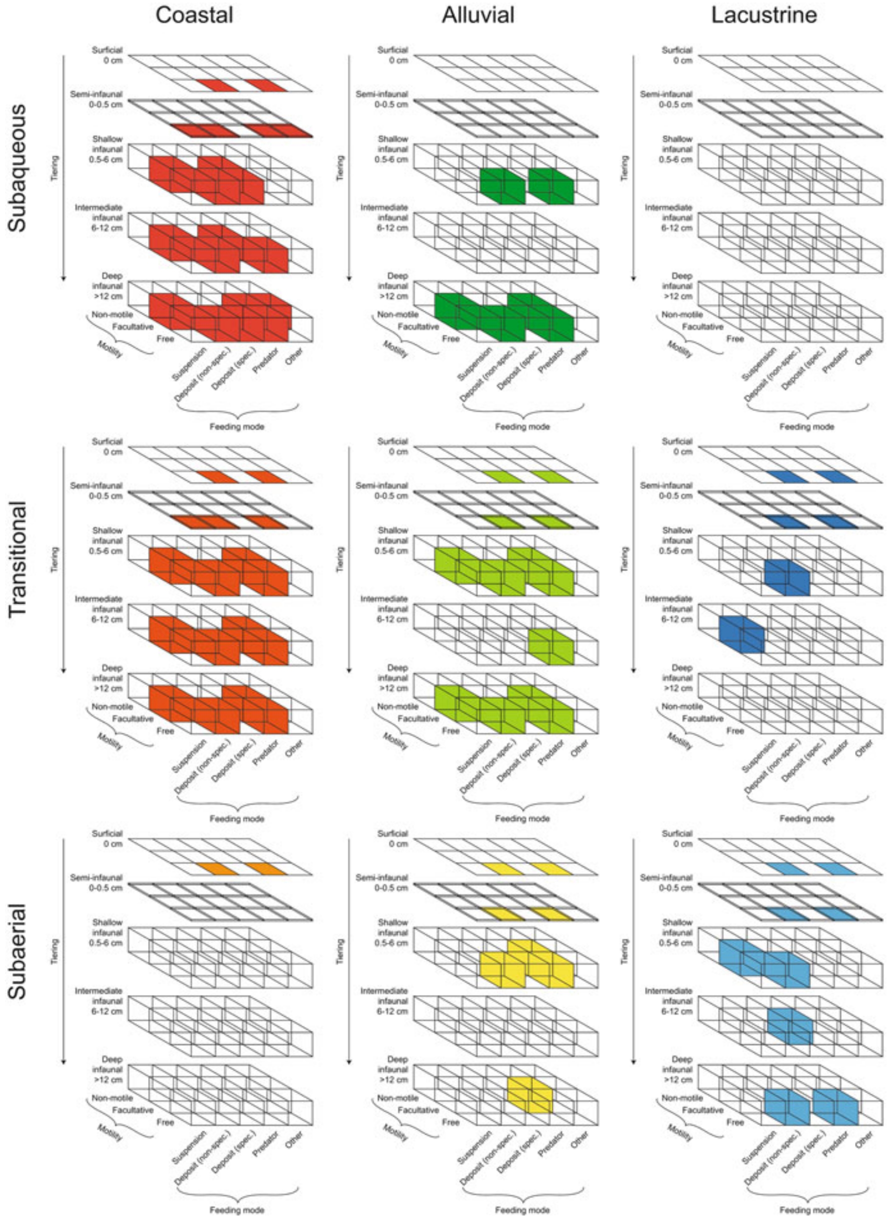

**Fig. 6.5** Devonian ecospace occupation

environments record eight ichnogenera representing a potential eight modes of life, but six architectural designs and methods of sediment modification. Global ichnodiversity is somewhat lower in subaqueous and transitional coastal environments in the Devonian compared to the Silurian, whereas ichnodisparity, the number of modes of life, and methods of sediment modification remain similar. Subaqueous coastal environments comprise 25 ichnogenera, 17 architectural designs, 20 modes

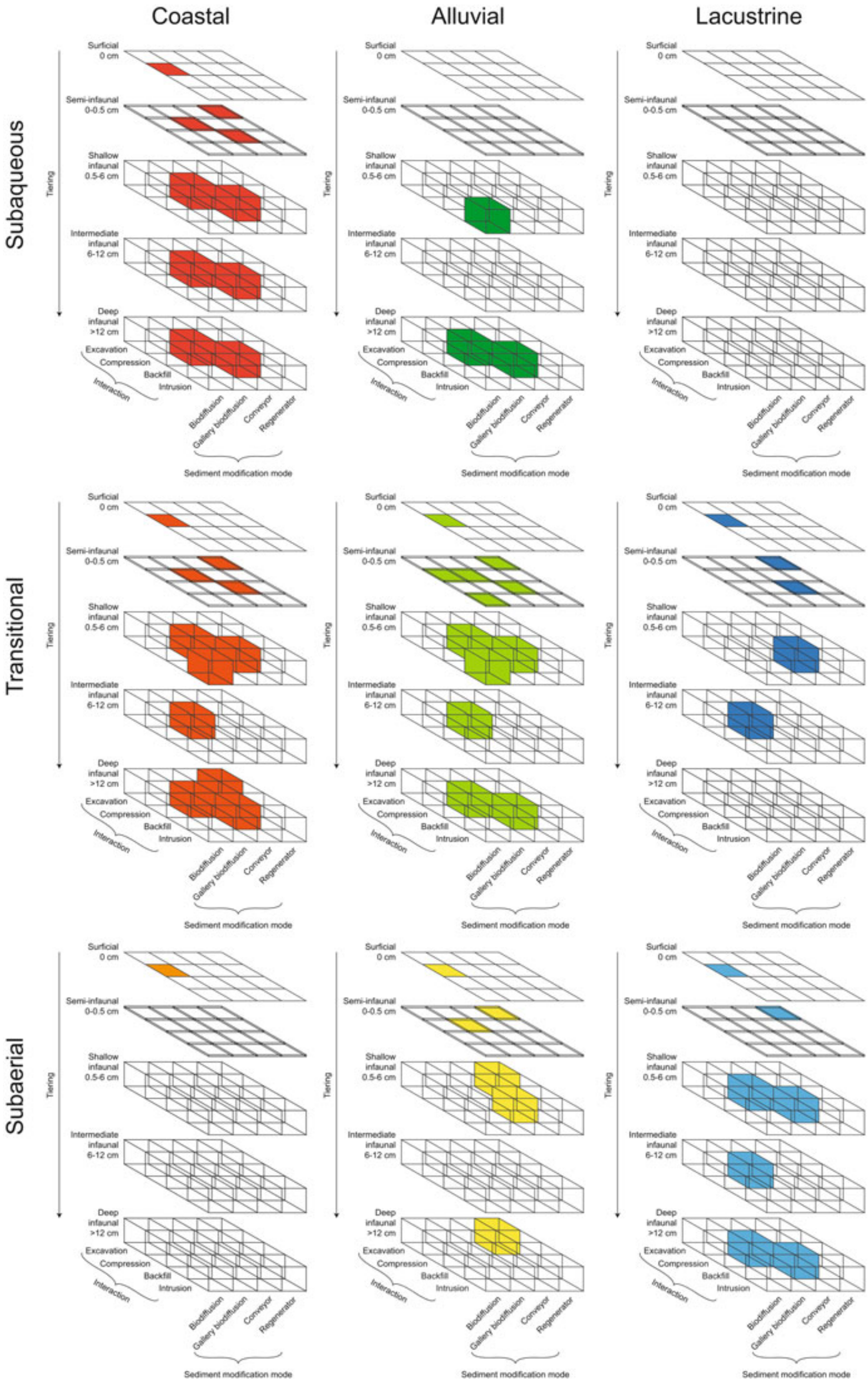

**Fig. 6.6** Devonian ecosystem engineering

of life, and ten methods of sediment modification. Transitional coastal environments consist of 24 ichnogenera, 15 architectural designs, 17 modes of life, and 11 methods of sediment modification. Subaerial coastal, subaqueous alluvial and ephemeral lacustrine environments have very similar numbers of ichnogenera, architectural designs and amounts of ecospace occupation and ecosystem engineering in comparison with their counterparts in the Silurian. Subaerial coastal environments contain two ichnogenera and modes of life, and one architectural design and method of sediment modification. Subaqueous alluvial environments contain three ichnogenera, architectural designs and methods of sediment modification, and six potential modes of life. Ephemeral lacustrine environments contain 13 ichnogenera, nine modes of life and architectural designs, and seven methods of sediment modification. Ichnodiversity approximately doubles in transitional alluvial environments in the Devonian from the Silurian, with 29 ichnogenera. However, the number of architectural designs and modes of life remain similar with 12 and 13 respectively, and there is a slight increase to 12 methods of sediment modification.

Trackways and scratch marks of freely mobile, surficial, nonspecialized deposit feeders and possible predators are found across all environments, apart from subaqueous alluvial settings in the Devonian (Fig. 6.5). This includes the first trackways attributable to tetrapods (Niedźwiedzki et al. 2010), which are found in transitional coastal environments (Narkiewicz et al. 2015). *Diplichnites* is the most common arthropod trackway, occurring across all other environments except for lake margins. Some of these organisms also produced bilobate trails and paired grooves in transitional coastal and alluvial environments, lake margins and ephemeral lakes. Surficial simple horizontal trails also were produced by predatory fish in transitional alluvial and ephemeral lacustrine environments. The compressive formation of such trackways and scratch marks, bilobate trails and paired grooves, and simple horizontal trails would have caused only minimal biodiffusive modification to surficial sediment (Fig. 6.6).

Freely mobile, nonspecialized deposit feeders and possible predators inhabited the semi-infaunal tier of subaqueous and transitional coastal, transitional alluvial, eolian, lake-margin, and ephemeral lacustrine environments (Fig. 6.5). They produced trace fossils with a variety of architectural designs. The majority of these trace-making organisms are likely to be exclusively nonspecialized deposit feeders that constructed simple horizontal trails by backfilling and acted as sediment conveyors in subaqueous coastal, transitional coastal and alluvial, and lake-margin environments (Fig. 6.6). Other organisms acted as sediment regenerators, excavating bilaterally symmetrical short, scratched burrows and bilobate trails and paired grooves in subaqueous and transitional coastal, transitional alluvial, eolian, lake-margin, and ephemeral lacustrine environments (Fig. 6.6). In transitional coastal and alluvial environments, other organisms created horizontal burrows with horizontal to vertical branches by compression that acted as gallery biodiffusive structures (Fig. 6.6). Additional gallery biodiffusive structures produced by compression in the semi-infaunal tier took the form of ovate and circular pits in eolian environments. Morphologically similar isolated and serial almond-shaped burrows that were created by compression and functioned as gallery biodiffusive structures also were constructed by suspension or nonspecialized deposit feeding bivalves in the semi-infaunal tier of subaqueous and transitional coastal environments (Figs. 6.5 and 6.6). In transitional alluvial environments, freely mobile, nonspecialized deposit feeders and likely predators created temporary, passively filled horizontal to oblique burrows in the semi-infaunal tier by moving through the sediment through intrusion and thus only causing minimal biodiffusive disruption to the primary sedimentary fabric (Figs. 6.5 and 6.6). Certain, freely mobile, nonspecialized, deposit-feeding organisms that occupied the shallow infaunal tier also had minimal biodiffusive impact upon the sediment. These organisms moved by backfilling to produce chevronate trails in transitional coastal environments, vertical displacement burrows in transitional alluvial environments, and bilaterally symmetrical short, scratched burrows in subaqueous alluvial environments (Figs. 6.5 and 6.6). Some of the organisms responsible for the latter may also have been predators.

The deep infaunal tier of all alluvial and coastal environments, apart from subaerial coastal environments, was colonized during the Devonian by facultatively mobile suspension feeders and possible predators (Fig. 6.5). These organisms constructed vertical, single U- and Y-shaped burrows in subaqueous and transitional coastal, and transitional alluvial environments. Furthermore, vertical simple burrows were created in subaqueous alluvial and eolian environments. Organisms constructing such burrows in eolian environments probably were predatory chelicerates. Facultatively mobile suspension feeders also occupied the intermediate infaunal tier, creating vertical simple burrows in transitional coastal and vertical single U- and Y-shaped burrows in subaqueous coastal and lake-margin environments (Fig. 6.5). All of these burrows were constructed by compression and functioned as gallery biodiffusive structures (Fig. 6.6). Organisms that had the same mobility, mode of feeding, and effects on the sediment, but inhabited the shallow infaunal tier created a variety of different architectural designs across a number of environments. Vertical simple burrows were produced in transitional coastal environments, whereas dumbbell-shaped burrows and vertical single U- and Y-shaped burrows were created in subaqueous coastal environments. The latter also were produced in ephemeral lacustrine environments. Passively filled horizontal to oblique burrows were produced in transitional alluvial and eolian environments (Fig. 6.5).

A number of organisms with particular modes of life appear limited to subaqueous coastal environments. Facultatively mobile organisms possessing a likely farming mode of feeding and those that were freely mobile specialized deposit feeders colonized the deep infaunal tier of subaqueous coastal environments (Fig. 6.5). Organisms with a farming/chemosymbiotic mode of feeding produced burrows with a shaft or bunch with downwards radiating probes whose compression served as gallery biodiffusive structures. Alternatively, specialized deposit feeders acted as sediment conveyors moving through the sediment by backfilling to produce three-dimensional spreiten traces (Fig. 6.6). Specialized deposit feeders that were facultatively mobile also colonized the intermediate infaunal tier of subaqueous coastal environments and produced burrows with horizontal spreiten by compression that functioned as gallery biodiffusive structures (Figs. 6.5 and 6.6). Organisms harboring this mode of life also colonized ephemeral lacustrine environments where they produced radial to rosette burrows. These burrows also were produced by the same mechanism and had the same effect on the sediment. Additional organisms with a farming mode of feeding but that were freely mobile and occupied the semi-infaunal tier of subaqueous coastal environments produced horizontal branching burrow systems by compression that acted as gallery biodiffusive structures (Figs. 6.5 and 6.6). Burrows with vertical spreiten were produced in the intermediate infaunal tier of subaqueous coastal environments by freely mobile, nonspecialized deposit feeders (Fig. 6.5). Such burrows were produced by backfilling and the culprit organisms acted as sediment conveyors (Fig. 6.6).

Other, freely mobile, nonspecialized deposit feeders and possible predators that moved through the sediment by backfilling and acted as sediment conveyors were more widespread across a variety of environments (Figs. 6.5 and 6.6). Some created simple, actively filled (meniscate), horizontal to oblique burrows that could extend downward to the deep infaunal tier of subaqueous and transitional coastal and alluvial, and ephemeral lacustrine environments. Organisms with the same mode of life but inhabiting the shallow infaunal tier of transitional alluvial and eolian environments produced the same types of burrows and resultant effects on the sediment. Simple, actively backfilled (massive) horizontal to oblique burrows that were limited to the shallow infaunal tier are known from subaqueous and transitional coastal, transitional alluvial, lake-margin, and ephemeral lacustrine environments. Horizontal, branched, concentrically filled burrows also were produced by backfilling with nonspecialized deposit feeders acting as sediment conveyors, but were restricted to the shallow infaunal tier of transitional coastal and alluvial environments (Figs. 6.5 and 6.6). The same architectural design and effects on the sediment also were produced by facultatively mobile suspension feeders in the shallow infaunal tier of subaqueous coastal environments (Figs. 6.5 and 6.6). Also limited to the shallow infaunal tier of subaqueous coastal environments were freely mobile, specialized deposit feeders that moved by backfilling and acted as sediment conveyors to produce complex, actively filled (meniscate/pelletoidal), horizontal burrows (Figs. 6.5 and 6.6).

Organisms with a freely mobile, nonspecialized deposit feeding and possible predatory mode of life also excavated maze and boxwork burrows, and in so doing acted as sediment regenerators that extended down to the deep infaunal tier in transitional coastal environments (Figs. 6.5 and 6.6). In addition, the deep infaunal tier of ephemeral lacustrine environments hosted freely mobile predators that used compression to create gallery biodiffusive structures in the form of vertical simple burrows (Figs. 6.5 and 6.6). Other organisms with the same predatory mode of life and effects on sediment also created vertical, simple burrows that only extended to the intermediate infaunal tier in subaqueous coastal and transitional alluvial environments, whereas those that may also have been nonspecialized deposit feeders produced passively filled horizontal to oblique burrows in transitional coastal environments. Other, freely mobile, nonspecialized deposit feeders created gallery biodiffusive structures by compression in the form of burrows with horizontal spreiten in the shallow infaunal tier of transitional coastal environments (Figs. 6.5 and 6.6).

### *6.3.5 Colonization of Devonian Continental Aquatic Habitats*

Based on the body-fossil record, during the Devonian, there was a parallel exploration by organisms of three fundamental environments: (1) a variety of paralic lacustrine and associated habitats; (2) the spatially confined and physiochemically distinctive setting of sinter lakes; and (3) a broader occupation of land within a typical wetland context. These three, varied environments probably were initially colonized during the late Silurian to Early Devonian by plant, animal, fungal, and microorganismic communities along coastal plains, lakes, deltas, and other brackish-water to paralic environments and inland along fluvial environments (DiMichele and Hook 1992). However, these biotas probably did not extend to regional interfluves or distal hinterlands until later in the Devonian.

#### 6.3.5.1 Paralic Lacustrine Environments

The 60 million-year time interval represented by the Devonian spans several major developments in the establishment of continental aquatic ecosystems (Shear and Kukalová-Peck 1990). For lakes, there was a significant change in the effect of a vegetated landscape on the modes of sediment erosion, transport and deposition that occurred in tandem with increased diversity, abundance, and trophic complexity of an emergent lacustrine biota. Three deposits from Early, Middle, and Late Devonian time illustrate this transformation. The Lower Devonian (Lochkovian) Tillywhandland Fish bed of the Old Red Sandstone crops out in the Midland Valley of Scotland, consisting of repetitively laminated siltstone, carbonate, organic-rich layers and greenish shale in a 2000-year repeated succession under a seasonal climate (Trewin and Davidson 1996). The deposit contains a distinctive freshwater biota of cephalaspid, acanthodian, and shark-like fish, in addition to pterygotid eurypterids, millipedes, a variety of invertebrate burrows, the massive and enigmatic fungal-like *Prototaxites*, and emergent and submerged aquatic plants fringing the lake (Trewin and Davidson 1996; Wilson 2006). This biota represents one of the more trophically stratified food webs of any mid-Paleozoic lake deposit, with evidence for primary producers, decomposers, saprobes, and two or possibly three levels of carnivory (Trewin and Davidson 1996). There is no indication of herbivory. This parallels a pattern also seen in then-contemporaneous terrestrial ecosystems (Labandeira 2007), although in Middle Devonian biotas, microarthropod herbivory is quite evident (Labandeira et al. 2013).

Also from the Old Red Sandstone are lower Middle Devonian (Eifelian) strata of northern Scotland representing thermally stratified lakes with similar microlaminated microstratigraphy (minus the green shale laminae) that vary from deeper stratified to shallower poorly stratified depositional regimes. The strata that are indicative of a deeper stratified lake preferentially contain fish, including acanthodians, placoderms, and lungfish. The considerable organic carbon content of the sediments likely was derived from algae as well as conchostracans (Donovan 1980).

Although no arthropods were reported by Donovan (1980), the inferred abundance of algae and various invertebrates suggests a major link to detritivory and minimal levels of herbivory, supported by two trophic levels of fish carnivore guilds within a reconstructed food web (Donovan 1980).

Toward the western side of the continent, at Chaleurs Bay in Gaspé, Québec, Upper Devonian (Frasnian) strata of the Escuminac Formation have yielded a fish fauna occurring under freshwater to brackish-water conditions and occupying either a lacustrine or estuarine setting (Hesse and Sawh 1992). The fish fauna consists of paleoniscoids, acanthodians, anaspids, arthodires, and crossopterygians such as *Eusthenopteron*; a shelly invertebrate fauna is absent. This suggests a poorly developed local ecosystem consisting of itinerant nektonic taxa engaged in self-contained trophic relationships.

### 6.3.5.2 The Special Environment of Sinter Lakes

The Rhynie Chert deposit is one of several hot-spring deposits that are included in the Windyfield Chert hydrothermal complex of northern Scotland (Anderson and Trewin 2003). Within the Windyfield Chert complex, the Rhynie Cherts unit is a small, isolated deposit within the Dryden Flags Formation, about 50 km west of Aberdeen, Scotland, that consists of cherts, carbonaceous sandstones, shales, and tuffaceous beds. A variety of land plants, fungi, and arthropods inhabited the pool periphery of the deposit and subsequently were incorporated in silicified paleosols that superpose laminated shales and carbonaceous sandstones (Rice et al. 2002; Kerp 2002). The local environment is a continental, silica-rich, hot spring that produced siliceous sinter in small pools and contained a freshwater biota associated with volcanic material washed in from a more elevated basin margin (Rice et al. 2002). Nonvascular plants included cyanobacteria, algal chlorophytes and charophytes, and lichens (Fayers and Trewin 2004). The fungi and fungal-like organisms consisted of nematophytes, the gigantic fungal-like *Prototaxites*, and diverse zygomycetous, ascomycetous, and basidiomycetous fungi representing decomposing, parasitic, and mutualistic forms—the latter consisting of endotrophic mycorrhizal, vesicular-arbuscular mycorrhizal, and lichen associations with plants (Taylor et al. 2004). The Rhynie fauna is represented by seven major groups and 17 species of predominantly terrestrial arthropods, specifically three trigonotarbids, a harvestman, five mites, two myriapods, two crustaceans, two hexapods, and a euthycarcinoid (Anderson and Trewin 2003). The special lacustrine environment represented by the Early Devonian Rhynie biota provides a unique view into the most diverse ecosystem of aquatic and surrounding terrestrial life. However, other deposits representing small sinter lakes are present throughout the fossil record, including occurrences of several deposits in the Late Devonian to late Carboniferous (Pennsylvanian) of northern Queensland, Australia (White et al. 1989), and the noted occurrence in the Miocene Barstow Formation of California (Park and Downing 2001).

#### 6.3.5.3 Colonization of Terrestrial Settings

Other localities, such as the Emsian Battery Point Formation in Gaspé, Québec and the younger Givetian Plattekill Formation in New York State provide evidence for the gradual diversification of plant, arthropod and fungal communities on land (Shear and Kukalová-Peck 1990). During this time there is a distinct trophic shift among microarthropods of these early communities from detritivory to more common modes of feeding on live fungi (Taylor et al. 2004; Labandeira 2007), live plants (Labandeira et al. 2013) and other animals (Shear and Kukalová-Peck 1990). These and particularly other localities toward the end of the period document the gradual root and burrow penetration of terrestrial substrates and the formation of more complex soil profiles, notably the enrichment of carbon at upper horizons (Algeo and Scheckler 1998; Algeo et al. 2001).

## 6.4 Carboniferous

Carboniferous continental trace-fossil assemblages occur from a large number of stratigraphic units across Europe, North America, South America, Australia, and Africa. Deep-lacustrine settings were colonized for the first time during the early Carboniferous (Mississippian). The earliest evidence of insect folivory on seed plants also appears during the Mississippian. By contrast, the late Carboniferous (Pennsylvanian) is characterized by the first appearance of well-integrated component communities of various herbivore and detritivore feeding groups on host plants such as tree ferns and medullosan seed ferns.

### *6.4.1 Mississippian Trace-Fossil Assemblages*

#### 6.4.1.1 Coastal Settings

The oldest Mississippian trace-fossil assemblage from coastal settings is from the Strathclyde Group (Viséan) of Scotland (Pearson 1992). The majority of the trace fossils are of Namurian age (Serpukhovian to early Bashkirian), including the Lower Kinderscout Grit and Grindslow Shales (Eagar et al. 1985; Hampson 1997), the Upper Limestone Group of England (Scarboro and Tucker 1995), and the Limestone Coal Group of Scotland (Briggs et al. 1979). The Guandacol (Limarino et al. 2002; Pazos 2000, 2002a, b; Buatois and Mángano 2003; Buatois et al. 2006, 2010) and El Imperial formations of Argentina (Pazos et al. 2007) are Namurian to early Langsettian–Duckmantian in age (Serpukhovian to Bashkirian). Other assemblages, the ages of which are constrained only to the Mississippian, occur from the Upper Shalwy Beds of Ireland (Buckman 1997) and the Shenango Sandstone Formation equivalent in Pennsylvania (Briggs and Rolfe 1983).

Coastal—Subaqueous

The Lower Kinderscout deltaic succession of England preserves a number of coastal deposits. Within these strata, prodelta shales of the Lower Grindslow Shales are interbedded with turbiditic sandstones and contain *Planolites* (Hampson 1997). The Upper Grindslow Shales represent shallower-water delta-front and abandoned mouth-bar deposits that contain *Cochlichnus*, *Chondrites*, *Lockeia* (*Pelecypodichnus* in the original publication), and cf. *Planolites* (Eagar et al. 1985; Hampson 1997). The horizontal burrow with horizontal to vertical branches, *Intexalvichnus*, is similar to *Treptichnus*, and has been reported from the transition between marine and brackish-water conditions within a deltaic succession in the Upper Shalwy Beds (Buckman 1997). Siltstones interpreted as interfluve deposits from the Lower Kinderscout Grit contain *Planolites* (Hampson 1997).

The Guandacol Formation records a glacial to postglacial transition that developed in a fjord setting under freshwater to brackish-water conditions (Aceñolaza and Buatois 1993; Pazos 2000, 2002a, b; Buatois and Mángano 2003; Buatois et al. 2006, 2010; Schatz et al. 2011). *Cruziana* and *Diplopodichnus* occur in matrix-supported diamictites draped with mud veneers and disrupted by dropstones that were deposited by debris flows and overprinted by ice-rafting and rain-out processes in a fjord setting, most likely under brackish-water conditions (Schatz et al. 2011). Parallel-laminated and ripple cross-laminated sandstones with asymmetrical and near-symmetrical ripples deposited by storm events, and rippled siltstones deposited by low-energy underflows preserve *Cruziana* and *Rusophycus* (Schatz et al. 2011). Finally, prodelta to delta-front deposits developed above a maximum flooding interval contain *Cochlichnus*, *Helminthopsis*, *Mermia*, *Undichna*, and other simple horizontal trails (*Gordia*, *Helminthoidichnites*), circular trails (?*Circulichnis*), *Diplichnites* and other trackways and scratch marks (*Maculichna*, *Orchesteropus*, ?*Umfolozia*), *Rusophycus*, and *Treptichnus* (Aceñolaza and Buatois 1993; Pazos 2000, 2002a, b; Buatois and Mángano 2003; Buatois et al. 2006, 2010). Coeval deposits included in the Malanzán Formation contain a depauperate expression of this ichnofauna, consisting of *Gordia*, *Helminthoidichnites*, and *Planolites* present at the top of thin-bedded turbidites (Buatois and Mángano 1995a). Freshwater conditions were prevalent during most of this deposition because fjords were affected by a strong discharge of freshwater attributable to melting of the ice masses during deglaciation (Buatois et al. 2006, 2010).

The El Imperial Formation contains a number of trace-fossil assemblages that are interpreted to represent a fjord setting with high fluvial input and sporadic marine influence (Pazos et al. 2007). *Treptichnus*, *Helminthoidichnites*, *Mermia*, *Cochlichnus*, *Gordia*, *Diplopodichnus*, *Maculichna*, and *Undichna* occur from delta-front to delta-plain settings that record the postglacial transgression. *Diplopodichnus*, *Diplichnites* and simple horizontal trails (*Archaeonassa*) occur in a unit interpreted to have been deposited by turbidity currents, with evidence of wave activity, suggesting that this trace-fossil assemblage was within shallow water. *Didymaulichnus* and *Diplichnites* are known from black shales that record the maximum flooding interval (Pazos et al. 2007).

#### Coastal—Transitional

In the Upper Limestone Group of England, delta-plain overbank deposits preserve the tetrapod trackway *Baropezia* and small burrows, whereas a transgressive flooding surface records *Teichichnus* (Scarboro and Tucker 1995). An isolated occurrence of *Palmichnium* has been reported from a likely emergent upper delta-plain setting in the Shenango Sandstone Formation (Briggs and Rolfe 1983). Sheetflood or channel-fill deposits within a deltaic succession of the Strathclyde Group contain *Diplichnites* (Pearson 1992). Similar units nearby also preserve large trace fossils similar to *Beaconites* (Pearson 1992). A further report of *Diplichnites* comes from an abandoned-channel deposit within a proximal deltaic setting in the Limestone Coal Group (Briggs et al. 1979).

### 6.4.1.2 Alluvial Settings

The oldest trace-fossil assemblages from alluvial settings of Mississippian age occur in the Tournaisian Maam Formation of Ireland (Graham and Pollard 1982), Snowy Plains Formation of Australia (Garvey and Hasiotis 2008), and late Tournaisian Albert Formation of New Brunswick (Pickerill 1992). Other assemblages occur from the Mauch Chunk Formation (Viséan) of Pennsylvania (Vrazo et al. 2007; Fillmore et al. 2009, 2010; Lucas et al. 2010a, b; Storm et al. 2010; Smith et al. 2012) and Pomquet Formation (likely Viséan to Serpukhovian) of Nova Scotia (Keighley and Pickerill 1997, 1998, 2003).

#### Alluvial—Transitional

Some trace-fossil assemblages are reported from fluvial channel deposits. However, these occurrences likely reflect a hiatus between the deposition of the sediments and their colonization, and hence the nature of the environment reflected by the sediments compared to that of the trace-fossil assemblage. Such assemblages most likely were emplaced following channel abandonment. The Maam Formation preserves *Beaconites* in shallow, possibly ephemeral, fluvial channels and channel margins on a floodplain (Graham and Pollard 1982). High-energy fluvial-channel deposits of the Snowy Plains Formation preserve only *Cruziana* and *Rusophycus* (Garvey and Hasiotis 2008). The Mauch Chunk Formation recently has received a spate of attention in the literature (Vrazo et al. 2007; Fillmore et al. 2009, 2010; Lucas et al. 2010a, b; Storm et al. 2010; Smith et al. 2012). The middle Indian Run Member represents an overall semiarid to arid setting with low-sinuosity, braided fluvial channels. *Planolites* occurs from the tops of beds of low-sinuosity fluvial channels (Fillmore et al. 2010). Fluvial channel infill deposits also are heavily bioturbated by *Planolites*, registering an ichnofabric index of 4 and up to a maximum depth of 1.6 m (Smith et al. 2012).

Moderate-energy channel deposits with evidence of desiccation in the Snowy Plains Formation preserve *Rusophycus*, *Cruziana*, and *Palaeophycus* (Garvey and Hasiotis 2008). *Margaritichnus* also was reported in this facies, but this name should not be used for aligned ball-like structures (Hakes 1976; Pemberton et al. 1988; Mángano et al. 2000). Additionally, the true nature of the illustrated structures is unclear. Low-energy floodplain deposits with evidence of desiccation preserve *Cruziana*, *Rusophycus*, and the passively filled horizontal to oblique burrow *Platicytes* (Garvey and Hasiotis 2008). The actively filled (massive) horizontal burrow *Fuersichnus*, and *Sagittichnus* (junior synonym of *Lockeia*) were reported as well from this facies, but the illustrated forms do not show the diagnostic characteristics of these ichnotaxa. *Undichna* also is known from isolated material. The slabs containing the trails also preserve mudcracks, although the specific facies from which the material is derived is unclear (Garvey and Hasiotis 2008).

In addition to bioturbated channel infills, upper-channel to proximal-floodplain deposits from the middle member of the Mauch Chunk Formation contain evidence of desiccation in the form of mudcracks, rills and raindrop imprints. These strata preserve a diverse trace-fossil assemblage of *Diplichnites*, *Diplopodichnus*, *Kouphichnium*, *Stiallia*, *Stiaria* and tetrapod trackways (*Palaeosauropus*, *Hylopus*), *Planolites*, *Taenidium*, *Undichna* and *Temnocorpichnus*, a bilaterally symmetrical superficial impression interpreted as an amphibian resting trace (Vrazo et al. 2007; Fillmore et al. 2009, 2010; Lucas et al. 2010a, b). Distal-floodplain deposits from the middle member preserve *Cruziana* and *Rusophycus* (Fillmore et al. 2010). The upper Hometown Member, represents overall a higher gradient of an ephemeral braided-fluvial system than the middle member, and the thick, overbank mudstones preserve a very large, obliquely oriented, burrow with a terminal expansion. The burrow is infilled with graded fluvial conglomerate and very coarse- to medium-grained sandstone (Storm et al. 2010).

The Albert Formation contains trace fossils in abandoned fluvial-channel deposits. The trace-fossil assemblage comprises *Rusophycus*, *Cruziana*, *Skolithos*, *Diplichnites*, *Monomorphichnus*, and maze and boxwork burrows (*Spongeliomorpha*). This deposit likely was produced under subaqueous conditions before the channels dried up (Pickerill 1992).

In the Pomquet Formation, fine-grained deposits formed after sheetfloods in areas behind dammed ephemeral fluvial channels or at the end of ephemeral channels. The Pomquet Formation contains *Protichnites* and other trackways and scratch marks (appendage marks), *Diplopodichnus*, bilaterally symmetrical short, scratched impressions (*Gluckstadtella*), *Circulichnis*, and *Gordia* (Keighley and Pickerill 1997, 1998, 2003). Non-channelized sheetflood deposits on a floodplain or in a shallow lake preserve *Diplichnites*, *Protichnites*, *Stiallia*, tetrapod tracks, *Cruziana*, *Rusophycus*, and ?*Crescentichnus* (*Selenichnites* in the original publication). By contrast, other floodplain deposits contain a trace-fossil assemblage comprising *Protichnites*, *Monomorphichnus* and other trackways and scratch marks (*Hexapodichnus*, appendage marks); and bilaterally symmetrical, short, scratched impressions (resting traces) (Keighley and Pickerill 1997, 1998, 2003).

### 6.4.1.3 Lacustrine Settings

The earliest evidence of trace fossils in fully lacustrine settings comes from the Agua Colorada Formation (Buatois and Mángano 1993b, 1995b) and Macharetí Group (Namurian to Langsettian–Asturian, equivalent to Serpukhovian to Moscovian) of Argentina (Buatois and del Papa 2003). However, inferences regarding the salinity of some glacial to interglacial Mississippian, parallel-laminated deposits is problematic: both glacio-lacustrine and glacio-marine settings could have been essentially freshwater environments because of melting and outwash into marine settings during deglaciation. Trace-fossil assemblages from lake-margin settings also occur from the Albert Formation (late Tournaisian) of New Brunswick (Pickerill 1992) and the Pomquet Formation (likely Viséan to Serpukhovian) of Nova Scotia (Keighley and Pickerill 1997, 2003). Additional units with lake-margin settings include the Agua Colorada Formation (Namurian to Langsettian–Asturian, equivalent to Serpukhovian to Moscovian) of Argentina (Buatois and Mángano 1993b, 1995b) and the Seaham Formation (earliest Namurian to Langsettian, equivalent to Serpukhovian to Bashkirian) of Australia (Buatois et al. 2010).

#### Lacustrine—Subaqueous

Shallow-lake settings with turbidite deposits in the Agua Colorada Formation preserve *Gordia*, *Helminthoidichnites*, and *Mermia* on the tops of beds and represent colonization of the substrate surface during breaks in sedimentation (Buatois and Mángano 1993b, 1995b). Deeper-water deposits contain graded fine- and very fine-grained sandstone and mudstone deposits that formed from relatively continuous sedimentation by waning underflow currents. These deposits preserve *Helminthoidichnites*, *Mermia*, *Helminthopsis*, *Treptichnus*, *Gordia* (including *Haplotichnus* in the original publications), *Archaeonassa* (*Aulichnites* in the original publications), *Rusophycus*, *Orchesteropus*, and *Undichna* (Buatois and Mángano 1993b, 1995b). Parallel-laminated mudstones in the Agua Colorada Formation represent deep-lake deposits formed from suspension and muddy turbidity currents and preserve *Gordia*, *Helminthoidichnites*, *Mermia*, *Helminthopsis*, *Cochlichnus*, *Treptichnus*, *Circulichnis*, *Orchesteropus*, rhomboidal traces, and string pits (Buatois and Mángano 1993b, 1995b; Fig. 6.7d). The Agua Colorada Formation contains continentally derived palynomorphs but lacks acritarchs, and likely was deposited in a deep freshwater lake, although it also is possible that it formed in an inner fjord zone affected by strong meltwater discharge (Buatois et al. 2010).

Parallel-laminated mudstones with dropstones that formed from suspension fallout under periglacial conditions in the Itacuamí Formation of the Macharetí Group contain *Diplichnites* and *Diplopodichnus* (Buatois et al. 2010). The Tarija Formation of the Macharetí Group contains *Mermia*, *Gordia*, *Helminthopsis*, *Helminthoidichnites*, *Cochlichnus*, *Diplopodichnus*, and *Diplichnites* in deposits interpreted to have formed from underflow currents associated with oscillatory flows (Buatois and del Papa 2003). Marine macrofossils and acritarchs are absent,

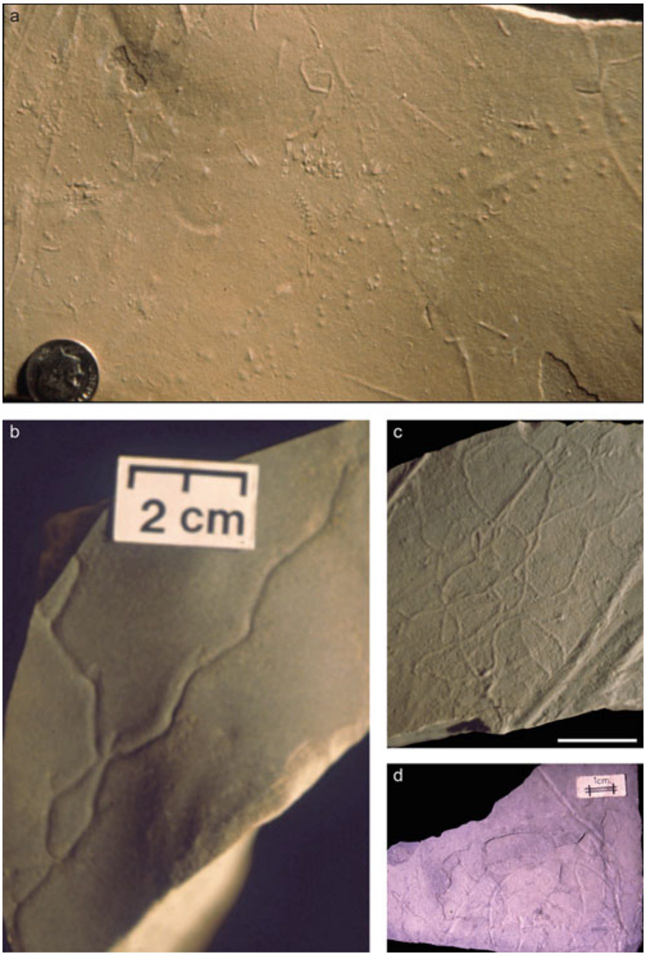

**Fig. 6.7** Carboniferous trace fossils from the Tonganoxie Sandstone Member in Kansas, USA (**a**–**c**) and western Argentina (**d**). (**a**) *Tonganoxichnus*; (**b**) *Treptichnus*; (**c**) *Gordia*; (**d**) *Helminthoidichnites*. Scale bar 10 mm in **c**

suggesting a freshwater lake, although as with the Agua Colorada Formation, a fjord setting with high meltwater discharge cannot be excluded.

### Lacustrine—Margin

The Albert Formation preserves trace fossils in nearshore lake-margin deposits. The trace-fossil assemblage comprises *Palaeophycus*, *Planolites*, *Helminthopsis*, *Gordia*, *Cochlichnus*, and network burrows (*Paleodictyon* in the original publication) in thin sandstones, siltstones, and mudstones (Pickerill 1992). Mudcracks also are present, but not in direct association with the trace fossils, suggesting that the biogenic structures formed under subaqueous conditions. Nearshore lake-margin deposits with possible periodic subaerial exposure from the Pomquet Formation preserve *Rusophycus*, *Cruziana*, *Helminthopsis*, and plug-shaped burrows (Keighley and Pickerill 1997, 2003). In addition to deep-lacustrine deposits, the Agua Colorada Formation also contains lake-margin to shallow-lacustrine deposits (Buatois and Mángano 1993b, 1995b). Fine- to medium-grained sandstones with wave ripples and parallel and current-ripple lamination, interpreted as high-energy and well-oxygenated lake-margin sandflat deposits, contain *Palaeophycus*, *Planolites*, and cf. *Bergaueria* (Buatois and Mángano 1993b, 1995b). The Seaham Formation comprises diamictite, tuffs, and thinly interbedded sandstone and siltstone interpreted as forming in fluvial and lacustrine settings adjacent to a volcanic arc. The trace fossils *Umfolozia* and *Cruziana* have been noted as occurring from siltstones overlying diamictite, although the trace-fossil assemblage has yet to be studied in detail (Buatois et al. 2010).

Escape trace fossils are found in thick sandstones of the Albert Formation that may represent storm deposits (Pickerill 1992). Thick sandstone beds interpreted as lacustrine turbidites in the Pomquet Formation also contain escape trace fossils together with horizontal burrows referred to as cf. *Taenidium* (Keighley and Pickerill 1997, 2003).

## 6.4.2 Pennsylvanian Trace-Fossil Assemblages

### 6.4.2.1 Coastal Settings

A large number of Pennsylvanian (late Carboniferous) trace-fossil assemblages occur from coastal settings. The Joggins Formation (Langsettian, equivalent to late Bashkirian) of Nova Scotia is a world-renown locality (Archer et al. 1995; Falcon-Lang et al. 2006). Deposits of the same age are represented by the Tynemouth Creek Formation (Langsettian) of New Brunswick (Briggs et al. 1984; Falcon-Lang et al. 2010, 2015a), and the Gaisby Rock of the Pennine Lower Coal Measures Formation from the Bolton Wood Quarries in England (Chisholm 1985). Other trace-fossil assemblages are present in the Mansfield Formation (Morrowan to Atokan, equivalent to late Bashkirian to early Moscovian) of Indiana (Archer and Maples 1984; Mángano et al. 2001), the Pottsville Formation (Morrowan, equivalent to late Bashkirian) of Alabama (Minkin 2005; Pashin 2005), the Tupe Formation (Langsettian–Asturian to Stephanian, equivalent to late Bashkirian to Gzhelian) of Argentina (Buatois and Mángano 2002; Desjardins et al. 2010), the San Pedrin Formation (Asturian, equivalent to Moscovian) of Spain (Romano and Meléndez 1985), the Dugger Formation (Desmoinesian, equivalent to late Moscovian) of Indiana (Archer and Maples 1984), and the McAlester Formation (Desmoinesian, equivalent to late Moscovian) of Oklahoma (Lucas et al. 2004). Also from the Pennsylvanian are the Tonganoxie Sandstone Member of the Stranger Formation

(Stephanian, equivalent to Kasimovian to Gzhelian) of Kansas (Buatois et al. 1997a, 1998a, b; Mángano et al. 1997), the Mafra Formation (Stephanian, equivalent to Kasimovian to Gzhelian) (Netto et al. 2009) and overlying Rio do Sul Formation of Brazil (Kasimovian to Gzhelian) (Netto et al. 2009; Buatois et al. 2010; Lima et al. 2015), and the Puertollano fossil site (Stephanian C, equivalent to Gzhelian) of Spain (Soler-Gijon and Moratalla 2001). The age of the Fentress Formation of Tennessee (Miller 1982) is not constrained beyond being Pennsylvanian. The Dwyka Group spans the Pennsylvanian to early Permian (Stephanian, equivalent to Kasimovian to Gzhelian, to Asselian) of South Africa (Savage 1970, 1971; Anderson 1970, 1975a, 1976, 1981; Isbell et al. 2008; Buatois et al. 2010). The Agua Escondida Formation of Argentina also is not tightly constrained in age, and is Pennsylvanian or early Permian (Melchor and Cardonatto 2014).

### Coastal—Subaqueous

Within the Dugger Formation, a number of different trace-fossil assemblages occur across a marine to nonmarine transition (Archer and Maples 1984). Of the more marine facies, lower interdistributary bay deposits preserve *Chondrites*, *Rhizocorallium* and *Planolites*, whereas the same trace fossils plus looping traces are present in the middle interdistributary bay deposits; *Chondrites* alone is found in deposits of the upper interdistributary bay, and tidal flat deposits contain *Diplocraterion* (Archer and Maples 1984). The Fentress Formation preserves bilaterally symmetrical, short, scratched burrows (*Limulicubichnus*), pentameral-shaped impressions and burrows (*Asteriacites*), complex, actively filled (meniscate/pelletoidal) horizontal burrows (*Palaeobullia* in the original publication), vertical, concentrically filled burrows (*Rosselia*), *Gordia*, *Skolithos*, and ?*Thalassinoides* from an interpreted marginal marine setting, or possibly a back-barrier tidal flat (Miller 1982).

In the Joggins Formation, sheet sandstones deposited in prodelta settings by hyperpycnal flows, derived from the distributary channels, contain trace fossils at several intervals (Falcon-Lang et al. 2006). The most diverse trace-fossil assemblage comprises *Kouphichnium*, *Siskemia* (*Protichnites* in Archer et al. 1995), *Arenicolites*, *Cochlichnus*, *Gordia*, *Treptichnus* (including *Haplotichnus*, *Plangtichnus* in the original publication), whereas another assemblage contains *Kouphichnium*, *Cochlichnus*, and cf. *Limulicubichnus* (Archer et al. 1995; Falcon-Lang et al. 2006). Also from the Joggins Formation, an abandoned channel with a transgressive, tidally influenced brackish infill including paired mud drapes and sigmoidal cross-bedding contains *Kouphichnium*, *Protichnites*, *Skolithos*, *Arenicolites*, *Planolites*, *Cochlichnus*, and ?*Rhizocorallium* (Prescott et al. 2014). Prodelta and delta-front facies also occur from the Pottsville Formation at the Union Chapel Mine locality (Pashin 2005). The delta-front deposits contain bilaterally symmetrical short, scratched impressions (*Arborichnus*), whereas deposits of the prodelta preserve *Nereites*, *Protovirgularia* and horizontal burrows. The San Pedrin Formation consists of laminated shales and siltstones, thinly bedded sandstones and muddy, fine-grained sandstones that are suggested to be part of a large delta with channels, levees, and interdistributary areas. However, the presence of crinoids and bivalves indicates marine incursions (Romano and Meléndez 1985). Constituent trace fossils include *Kouphichnium*, *Merostomichnites*, *Arborichnus*, *Petalichnus*, *Psammichnites* (?*Olivellites* in the original publication), and other complex, actively filled (meniscate/pelletoidal) horizontal burrows (?*Psammichnites*; *Scolicia* in the original publication). Distributary-channel mouth-bar or distal crevasse-splay deposits from the Mansfield Formation contain *Palaeophycus*, *Lockeia*, *Rhizocorallium*, and escape trace fossils (Archer and Maples 1984). Also, in the Pottsville Formation, cf. *Skolithos* and other vertical simple burrows (cf. *Monocraterion*) and radial to rosette burrows (cf. *Asterichnus*) occur in sandstones and on mud-draped ripple surfaces of abandoned channels that had been blocked by log jams within a coastal-plain setting (Gastaldo and Degges 2007).

The Agua Escondida Formation of Argentina is composed of cross-bedded sandstones and laminated mudstones, the latter containing a diverse array of trace fossils (Melchor and Cardonatto 2014). Associated sedimentary structures include rhythmic, millimeter-scale laminae, wrinkle marks, flat-topped symmetrical ripples, and lenticular bedding. The trace fossils are found in a number of associations that generally consist of *Diplichnites*, *Dendroidichnites* (including material therein identified as *Protovirgularia*), *Monomorphichnus*, *Umfolozia*, bilaterally symmetrical short, scratched impressions (*Gluckstadtella*, *Huilmuichnus*), *Undichna*, *Archaeonassa*, *Cruziana*, *Rusophycus*, *Helminthoidichnites*, *Helminthopsis*, *Lockeia*, and other isolated and serial, almond-shaped burrows (*Ptychoplasma*), *Palaeophycus*, *Planolites*, *Treptichnus*, brush-like traces, and bilobed traces with crescentic ridges (Melchor and Cardonatto 2014).

Two trace-fossil assemblages are recognized from laminated siltstone and mudstone deposits with dropstones from the Mafra Formation (Netto et al. 2009). The first trace-fossil assemblage comprises *Cochlichnus*, *Gordia*, *Helminthoidichnites*, *Treptichnus*, and other horizontal burrows with horizontal to vertical branches (*Saerichnites*; *Hormosiroidea* in the original publication), *Cruziana*, *Rusophycus*, *Protichnites*, and *Undichna*. The second assemblage comprises just *Diplichnites* and *Diplopodichnus* but is more ubiquitous throughout the succession (Netto et al. 2009). The deposits were originally interpreted as representing a deep glaciolacustrine setting. However, Netto et al. (2009) reinterpreted these deposits as representing shallow-water lakes or ponds on an outwash plain adjacent to a fjord. The lower part of the overlying Rio do Sul Formation contains a trace-fossil assemblage comprising *Diplichnites*, *Diplopodichnus*, *Maculichna*, *Umfolozia*, *Protovirgularia*, *Cochlichnus*, *Saerichnites* (*Hormosiroidea* in the original publication), *Treptichnus*, and *Gluckstadtella*. This assemblage occurs in rhythmites that have been suggested to show evidence of deposition in tidally influenced settings (Netto et al. 2009). The upper part of the Rio do Sul Formation contains *Diplichnites*, *Diplopodichnus*, *Umfolozia*, *Cruziana*, *Rusophycus*, *Gluckstadtella*, and *Helminthoidichnites* (Netto et al. 2009). Elsewhere within the Rio do Sul Formation, Lima et al. (2015) identified two suites of trace fossils: an undermat miner suite comprising *Helminthoidichnites*, *Mermia*, *Treptichnus*, and *Cruziana*; and an overmat suite of grazers consisting of *Diplichnites* and *Umfolozia*, together with other trackways and scratch marks (*Glaciichnium*), plus *Cruziana*, *Diplopodichnus*, *Gluckstadtella*, and *Protovirgularia*.

The Dwyka Group contains glacial diamictites separated by varved shales and siltstones. Trace fossils include *Umfolozia*, *Maculichna*, *Diplichnites*, *Gluckstadtella*, and other bilaterally symmetrical short, scratched impressions (*Kingella*), three-dimensional spreiten traces (*Gyrochorte*), *Protovirgularia*, and *Undichna* (Savage 1970, 1971; Anderson 1970, 1975a, 1976, 1981; Buatois et al. 2010). Although originally interpreted as representing a periglacial lake (Savage 1970, 1971), a fjord setting is the most likely environmental interpretation.

## Coastal—Transitional

Heterolithic units interpreted as microtidal lagoon deposits with some emergent features from the Joggins Formation contain the tetrapod trackway *Limnopus* and cf. *Asterichnus* (Falcon-Lang et al. 2006). Within an overall delta-plain setting of the Joggins Formation, levee deposits contain *Limnopus* and other tetrapod trackways (*Matthewichnus*, *Ornithoides*, *Notalacerta*, and *Pseudeobradypus*), whereas point bars preserve *Diplichnites*, tetrapod trackways (*Dromillopus*), *Taenidium*, and cf. *Beaconites* (Falcon-Lang et al. 2006). Abandoned channel deposits from the Joggins Formation that underlie transgressively infilled fluvial-tidal channels contain *Diplichnites*, *Kouphichnium*, *Cochlichnus*, *Gordia*, *Hylopus*, *Dromillopus*, and *Pseudobradypus* (Prescott et al. 2014). Evidence for a marine incursion in the Tynemouth Creek Formation has been discovered (Falcon-Lang et al. 2015a) and brackish bay deposits contain *Arenicolites*, *Didymaulichnus*, *Helminthoidichnites*, *Cochlichnus*, *Lockeia*, ?*Crescentichnus* (cf. *Selenichnites* in the original publication), cf. *Baropezia*, and crozier-like burrows (Falcon-Lang et al. 2015a, b). Delta-plain deposits from the Bolton Wood Quarries preserve complex, actively filled (meniscate/pelletoidal) horizontal to oblique burrows (*Aulichnites*? in the original publication) and *Arenicolites* (Chisholm 1985). The lower part of the Tupe Formation contains a trace-fossil assemblage consisting of *Helminthopsis* and *Treptichnus* in a coastal-floodplain setting (Desjardins et al. 2010).

Large numbers of Pennsylvanian coastal trace-fossil assemblages, particularly from North America, occur in tidal flats that were formed under essentially freshwater conditions. These deposits consist of thinly laminated siltstones that are grouped into couplets. Such deposits from the Mansfield Formation originally were interpreted as being lacustrine in origin (Archer and Maples 1984), although subsequent analysis identified them as rhythmites that formed in the intertidal zone (Kvale et al. 1989). In the Mansfield Formation, the trace-fossil assemblage comprises *Cochlichnus*, *Treptichnus*, *Gordia*, networks (*Paleodictyon* in the original publication), horizontal spiral burrows (*Spirodesmos* in the original publication), simple, actively filled (meniscate), horizontal to oblique burrows (*Ancorichnus* in the original publication), *Palaeophycus*, *Maculichna*, *Umfolozia*, and other trackways and scratch marks (*Pterichnus*), and tetrapod tracks (Archer and Maples 1984; Maples and Archer 1987; Kvale et al. 1989). Similar, but slightly younger, upper-intertidal mudflat deposits from the Mansfield Formation contain *Treptichnus*, *Gordia*, bilaterally symmetrical, short, scratched impressions (*Tonganoxichnus*), and tetrapod tracks, whereas lower intertidal deposits contain small vertical burrows (Mángano et al. 2001). More diverse, trace-fossil assemblages from Pennsylvanian tidal flats occur from the Pottsville and McAlester formations and the Tonganoxie Sandstone Member. The Union Chapel Mine locality of the Pottsville Formation contains abundant trace fossils from intertidal-mudflat deposits (Minkin 2005; Pashin 2005), similar to the rhythmites from the Mansfield Formation of Indiana. Identified trace fossils include *Cochlichnus*, *Diplichnites*, *Kouphichnium*, *Arenicolites*, *Treptichnus*, *Undichna*, *Matthewichnus*, and *Notalacerta*, in addition to other tetrapod trackways (*Attenosaurus*, *Nanopus*, *Cincosaurus*) (Haubold et al. 2005; Lucas and Lerner 2005; Martin and Pyenson 2005; Rindsberg and Kopaska-Merkel 2005). Additional trace fossils include *Stiaria* and *Tonganoxichnus*. The McAlester Formation preserves *Diplichnites*, *Diplopodichnus*, *Paleohelcura*, *Tonganoxichnus*, *Undichna*, *Notalacerta*, *Pseudobradypus*, *Gordia*, and *Treptichnus* (Lucas et al. 2004). The Tonganoxie Sandstone Member contains *Diplichnites*, *Diplopodichnus*, *Kouphichnium* and other trackways and scratch marks (*Dendroidichnites*, *Mirandaichnium*), *Stiallia*, *Stiaria*, *Tonganoxichnus*, *Undichna*, tetrapod tracks, *Circulichnis*, *Gordia*, *Helminthoidichnites*, *Helminthopsis*, *Treptichnus*, and irregular networks (Buatois et al. 1997a, 1998a, b; Mángano et al. 1997; Fig. 6.7a–c).

Outside of North America, *Undichna*, the tetrapod trackway *Batrachichnus* (*Puertollanopus* in the original publication), and burrows, including *Planolites*, are preserved in siltstones intercalated with tuffs from Puertollano, Spain (Soler-Gijon and Moratalla 2001). The deposits were previously interpreted as lacustrine, although the sediments, geochemistry, and body fossils indicate a marginal-marine setting. More specifically, the deposits are interpreted as representing a humid tidal flat and rapid deposition of volcanic ash permitted the preservation of the traces (Soler-Gijon and Moratalla 2001). In Brazil, another assemblage within the Rio do Sul Formation yields *Diplichnites* and *Diplopodichnus*, as well as interference ripples and microbial structures, but lacks *Umfolozia*. This led to the suggestion that the trace-fossil assemblages containing *Umfolozia* were produced subaqueously, whereas those with *Diplichnites* and *Diplopodichnus* were produced under shallower water to emergent conditions (Netto et al. 2009).

#### 6.4.2.2 Alluvial Settings

Trace fossils from Pennsylvanian alluvial settings include the Upper Haslingden Flags and overlying Rough Rock Group (Bashkirian) of England (Hardy 1970; Chisholm 1983; Eagar et al. 1985; Miller 1986; Kane 2010), the Parrsboro Formation (late Namurian to Langsettian–Duckmantian, equivalent to Bashkirian) of Nova Scotia (Mossman and Grantham 2000), the Grande Anse Formation (latest Namurian to earliest Langsettian–Duckmantian, equivalent to mid Bashkirian) of New Brunswick (Falcon-Lang et al. 2007), the Mansfield Formation (Morrowan, equivalent to late Bashkirian) of Indiana (Archer and Maples 1984), the Joggins Formation (Langsettian, equivalent to late Bashkirian) (Ferguson 1966, 1975; Falcon-Lang et al. 2006), and Smith Point and Pugwash localities (Duckmantian–Bolsovian, equivalent to latest Bashkirian to earliest Moscovian) (Ryan 1986) of the Cumberland Group of Nova Scotia, the Tynemouth Creek Formation (Langsettian, equivalent to late Bashkirian) of New Brunswick (Briggs et al. 1984; Falcon-Lang et al. 2010, 2015b), the Port Hood Formation (Langsettian, equivalent to late Bashkirian) of Nova Scotia (Keighley and Pickerill 1997, 1998, 2003), and the Brahum Formation (Langsettian, equivalent to late Bashkirian) of Germany (Voigt and Ganzelewski 2010). Pennsylvanian trace fossils from alluvial settings also occur from deposits in Mostyn (Langsettian–Duckmantian, equivalent to late Bashkirian) in Wales (Braddy and Anderson 1996), the Wamsutta Formation (Duckmantian–Bolsovian, equivalent to late Bashkirian to early Moscovian) of Massachusetts (Knecht et al. 2011), the Salop Formation (Asturian, equivalent to Moscovian) of England (Tucker and Smith 2004), the Upper Coal Measures of the Writhlington Nature Reserve (Asturian, equivalent to Moscovian) of England (Pollard and Hardy 1991), and the Tupe Formation (Langsettian–Asturian to Stephanian, equivalent to late Bashkirian to Gzhelian) of Argentina (Buatois and Mángano 2002; Desjardins et al. 2010). Younger Pennsylvanian alluvial trace-fossil assemblages occur from the El Cobre Canyon Formation (Missourian, equivalent to Kasimovian) of New Mexico (Lucas et al. 2005a), Montceau-les-Mines (Stephanian, equivalent to Kasimovian to Gzhelian) in France (Rolfe et al. 1982; Briggs et al. 1984), the Monongahela Group (Virgilian, equivalent to Gzhelian) of Ohio (Hembree et al. 2011), the Semily Formation (Stephanian C, equivalent to Gzhelian) of the Czech Republic (Mikulás 1999), and Cape John (Stephanian to early Permian, equivalent to the Kasimovian to early Permian) in Nova Scotia (Ryan 1986).

### Alluvial—Transitional

The Upper Haslingden Flags contain *Kouphichnium*, *Crescentichnus* and other bilaterally symmetrical, short, scratched burrows (*Selenichnites*), and *Lockeia* (Hardy 1970; Chisholm 1983; Eagar et al. 1985). The deposits are interpreted as representing a shallow water, nonmarine environment with fluctuating water levels (Eagar et al. 1985) and may be considered broadly as overbank deposits. Overlying the Upper Haslingden Flags, the Rough Rock Group represents a braided-fluvial system (Miller 1986; Kane 2010). Sheetflood, crevasse-splay or bar deposits within the braided fluvial system preserve *Lockeia*, *Cochlichnus*, *Planolites*, *Palaeophycus*, ?*Didymaulichnus*, and ?*Protovirgularia* (Miller 1986; Kane 2010). Crevasse-splay deposits from the Mansfield Formation display *Lophoctenium* and bilobed trails (Archer and Maples 1984). The Joggins Formation contains deposits from a well-drained alluvial plain in addition to those of coastal plains (Falcon-Lang et al. 2006). Within the alluvial plain facies, *Diplichnites* and tetrapod trackways are found in channel sandstones and levee deposits (Ferguson 1966, 1975; Falcon-Lang et al. 2006). A similar occurrence of *Diplichnites* in levee and crevasse-splay deposits occurs from the Tynemouth Creek Formation (Briggs et al. 1984; Falcon-Lang et al. 2010). In addition, more recently identified from such environments are *Baropezia*, *Batrachichnus*, *Pseudobradypus*, and other tetrapod trackways (cf. *Megapezia*), as well as *Planolites* and a putative arthropod resting trace (Falcon-Lang et al. 2015a). Low-sinuosity fluvial channels at the Smith Point and Pugwash localities within the Cumberland Group also contain *Diplichnites* (Ryan 1986), and *Palmichnium* has been reported from deposits considered to represent the margins of a fluvial channel in Wales (Braddy and Anderson 1996).

*Didymaulichnus*, *Helminthopsis* and *Palaeophycus* are found in channel-dune and bar deposits within a perennial-fluvial system from the Port Hood Formation (Keighley and Pickerill 1997, 2003). Further channel-fill and point-bar deposits from the Mansfield Formation contain *Cochlichnus*, *Palaeophycus* and bilobed trails (Archer and Maples 1984). *Chondrites* also is identified as occurring in this massive sandstone facies in Fig. 8 of Archer and Maples (1984), but such a facies occurrence is not discussed in the text and so we omit this from our analysis. As for many other trace-fossil assemblages in fluvial channel deposits, they most likely formed during or after channel abandonment and so we include these assemblages in the transitional alluvial category. In addition to *Diplichnites* (Briggs et al. 1984; Falcon-Lang et al. 2006) in crevasse-splay deposits and *Beaconites* in channel deposits (Davies pers. obs.), the Tynemouth Creek Formation also preserves *Pseudobradypus*, *Batrachichnus* and *Baropezia* that are interpreted as being preserved on the abandoned floor of a seasonally active, fixed fluvial channel in a dryland environment (Falcon-Lang et al. 2006, 2010). A recent comprehensive summary of the ichnology and sedimentary environments of the Tynemouth Creek Formation (Falcon-Lang et al. 2015b) also has identified *Planolites* and *Diplichnites* in abandoned channel deposits. Gravel-bed channels also contain *Diplocraterion* within beds and *Diplichnites* on top of beds. *Taenidium* additionally is present in sandbed channels. Interfluve channels contain *Diplichnites* and ?*Batrachichnus*, and distal interfluve areas contain *Batrachichnus*, cf. *Baropezia* and *Planolites*. Perennial lakes preserve *Diplichnites*, *Kouphichnium*, *Helminthoidichnites*, *Lockeia*, *Undichna* and resting traces; whereas stagnant ponds contain *Kouphichnium*, *Didymaulichnus*, *Cochlichnus*, and *Lockeia* (Falcon-Lang et al. 2015b). Plant–insect interactions indicating folivory are also found on *Cordaites* leaves that accumulated in abandoned channels (Davies pers. obs.). Deposits of a seasonally active dryland river channel from the Grande Anse Formation also contain *Pseudobradypus* (Falcon-Lang et al. 2007). Abandoned, anastomosing fluvial-channel bars from Cape John also preserve *Diplichnites* (Ryan 1986). In the Port Hood Formation, *Cruziana*, *Rusophycus* and small ovate pits are found in marginal or distal, ephemeral and shallow fluvial channels, whereas sheetflood sandstones that formed in swamp or levee settings preserve *Planolites*, *Taenidium*, *Treptichnus* (*Phycodes* in the original publications), and tetrapod tracks (Keighley and Pickerill 1997, 1998, 2003). Maze and boxwork burrows identified as *Thalassinoides* also are reported from muddy interfluve areas adjacent to low-sinuosity fluvial channels in the Port Hood Formation (Keighley and Pickerill 1997, 2003).

Tetrapod trackways, locally in association with arthropod trackways, have been reported in several Pennsylvanian floodplain deposits. The Salop Formation contains the tetrapod trackways *Dimetropus*, *Ichniotherium*, *Hyloidichnus*, *Limnopus*, and *Batrachichnus* in association with *Diplichnites* within floodplain-sheetflood deposits (Tucker and Smith 2004). The Parrsboro Formation contains *Pseudobradypus*, *Dromillopus*, and other tetrapod trackways (*Hylopus*, *Cursipes*) in well-drained floodplain deposits (Mossman and Grantham 2000). Similarly, the Brahum Formation of Germany preserves *Ichniotherium* and *Dimetropus* in upland alluvial-plain deposits (Voigt and Ganzelewski 2010).

Isolated occurrences of arthropod trackways are reported from a number of floodplain deposits. The El Cobre Canyon Formation contains *Diplichnites* in interfluve or floodplain deposits within a low-sinuosity fluvial system (Lucas et al. 2005a). *Diplichnites* is found in what are considered to be floodplain–overbank deposits from Montceau-les-Mines (Rolfe et al. 1982; Briggs et al. 1984). More diverse floodplain trace-fossil assemblages occur in the Port Hood Formation (Keighley and Pickerill 1997, 1998, 2003). Non-channelized sheetflood deposits that formed on a regularly flooded floodplain or in a shallow lake preserve *Diplichnites*, *Protichnites*, *Stiallia*, *Cruziana*, *Rusophycus*, ?*Crescentichnus* (*Selenichnites* in the original publication), and tetrapod tracks. By contrast, other floodplain-sheetflood deposits preserve an association of *Hexapodichnus*, *Protichnites*, *Monomorphichnus*, appendage marks, and resting traces (Keighley and Pickerill 1997, 1998, 2003).

The Rough Rock Group also contains more distal or lateral sheetflood deposits with *Cochlichnus*, *Planolites*, *Palaeophycus* and ?*Didymaulichnus* (Miller 1986; Kane 2010). Pools and shallow lakes within floodplain settings preserve similar types of trace fossils. *Kouphichnium*, *Cochlichnus*, parallel groove traces (?*Diplopodichnus*), small arthropod trackways (?*Stiaria*), finely constructed irregular trails (?*Mermia*), circular or ovoid traces (?*Lockeia*), tetrapod tracks, and coprolites occur from the Upper Coal Measures at Writhlington (Pollard and Hardy 1991). The ichnofauna is interpreted to have formed on a marginal mudflat of a shallow lake or pool on a floodplain, which may have been temporarily exposed subaerially, although there are no recorded mudcracks (Pollard and Hardy 1991). The Tupe Formation consists of floodplain-pool, overbank, and levee deposits that preserve *Palaeophycus*, *Archaeonassa*, *Helminthoidichnites*, *Didymaulichnus*, and *Planolites* (Buatois and Mángano 2002). The Wamsutta Formation preserves trace fossils on surfaces of fine-grained ripple, cross-laminated sandstones draped with laminated shale that formed within a low relief, wet, and possibly forested alluvial plain (Knecht et al. 2011). The trace fossils include *Cochlichnus*, *Helminthoidichnites*, and an unnamed resting trace that probably represents the oldest ichnofossil of a pterygote insect (Knecht et al. 2011), and likely was formed in an ephemeral pool. *Planolites* and *Palaeophycus* also have been reported from ephemeral pool and channel deposits in the Semily Formation (Mikulás 1999). Very large, complex, branching burrows with diameters over 100 mm also have been recently reported from the Monongahela Group. These burrows have been ascribed to *Thalassinoides* and were excavated within laminated mudstones interpreted as ponds, small lakes or marshes occurring within a distal floodplain setting (Hembree et al. 2011).

#### 6.4.2.3 Lacustrine Settings

Lacustrine trace-fossil assemblages from the Pennsylvanian are reported from the Parrsboro Formation (late Namurian to early Langsettian–Duckmantian, equivalent to Bashkirian) of Nova Scotia (Mossman and Grantham 2000), the East Pennine Coalfield (Langsettian–Asturian, equivalent to late Bashkirian to Moscovian) of England (Elliott 1985), the Emery Brook and Port Hood formations (Langsettian, equivalent to late Bashkirian) of Nova Scotia (Keighley and Pickerill 1997, 1998, 2003) and Bude Formation (Langsettian–Bolsovian, equivalent to late Bashkirian to early Moscovian) of England (Goldring and Seilacher 1971; Higgs 1988). A number of trace-fossil assemblages occur in units that span the late Pennsylvanian to early Permian. These are the Fitzroy Tillite Formation (Stephanian, equivalent to Kasimovian–Gzhelian, to Sakmarian) of the Falkland Islands (Trewin et al. 2002) and the Pennsylvanian to lower Permian Pagoda Formation of Antarctica (Isbell et al. 2001). Two trace-fossil assemblages from lake-margin settings are reported from the Pennsylvanian. These are from the Port Hood Formation (Langsettian, equivalent to late Bashkirian) of Nova Scotia (Keighley and Pickerill 1997, 2003) and the Kladno Formation (Bolsovian, equivalent to Moscovian) of the Czech Republic (Walter 1982; Turek 1989; Mikulás 1999).

##### Lacustrine—Subaqueous

Rhythmites in the Emery Brook Formation contain *Planolites* and *Rusophycus* that were deposited in an offshore lacustrine setting (Keighley and Pickerill 1997, 2003).

In a different setting, lacustrine event beds within the Port Hood Formation preserve *Cochlichnus* and *Undichna* on the top of the beds, and this is considered to represent a return to that particular environment by lake inhabitants following the deposition of the event bed (Keighley and Pickerill 1997, 2003). The Parrsboro Formation discussed by Mossman and Grantham (2000) also contains lacustrine horizons in addition to floodplain facies, and these preserve *Kouphichnium* (Goldring and Seilacher 1971). *Kouphichnium* also occurs in the Bude Formation. The Bude Formation consists of laminated mudstones interbedded with sharp-based beds of very fine-grained sandstones. These beds are considered to have been deposited on the outer shelf or floor of a large lake with the sandstones representing turbidite deposits from river-fed hyperpycnal flows during storm floods (Goldring and Seilacher 1971; Higgs 1988). *Kouphichnium* is found on mudstones in association with *Undichna* (Goldring and Seilacher 1971; Higgs 1988). *Planolites* also occurs elsewhere within the section in interbedded siltstone and mudstone deposits (Goldring and Seilacher 1971). A depauperate trace-fossil assemblage consisting of *Cochlichnus* and *Planolites* is present in laminated mudstone deposits of the East Pennine Coalfield (Elliott 1985). These laminated mudstones are laterally extensive and are interpreted as representing deposits formed by suspension fallout within a large lake (Elliott 1985).

The Fitzroy Tillite Formation of the Falkland Islands consists of diamictite intercalated with sandstones and mudstones. These deposits are considered to represent a glaciolacustrine setting and the trace fossil *Umfolozia* is present (Trewin et al. 2002). The Pennsylvanian to lower Permian Pagoda Formation of Antarctica consists of diamictite and sandstone, preserving *Planolites* and *Cruziana* (*Isopodichnus* in the original publication), and is considered to represent a periglacial and glacial lake (Isbell et al. 2001).

Lacustrine—Margin

The Kladno Formation contains interbedded mudstones, volcanic tuffs and tuffaceous mudstones interpreted as lake-margin deposits (Turek 1989). The trace fossils *Undichna*, *Batrachichnus* (*Gracillichnium* in the original publication), the tetrapod swimming trace *Lunichnium*, *Gordia* (*Haplotichnus* in the original publications), *Diplichnites*, *Cruziana*, ?*Cochlichnus* (*Unisulcus* in the original publication), and *Planolites* have been described (Walter 1982; Turek 1989; Mikulás 1999). The Port Hood Formation contains very fine-grained sandstones interbedded with mudstones. The mudstones are interpreted as representing quiet water, delta-top, lacustrine deposits, whereas the sandstones represent storm or flood event beds (Keighley and Pickerill 1997, 2003). The plug-shaped burrow *Conichnus* is preserved by passive infill by sandstone within the mudstones (Keighley and Pickerill 1997, 2003).

### *6.4.3 Carboniferous Ecospace Occupation and Ecosystem Engineering*

Deep regions of permanent lakes were colonized for the first time during the Carboniferous (Buatois and Mángano 1993a; 1995a, b; Buatois et al. 1998a). However, there is no evidence of trace-fossil assemblages from eolian or playa lake settings during this time (Figs. 6.8 and 6.9). Subaqueous lacustrine settings globally record 19 ichnogenera, seven architectural designs, five modes of life, and six methods of sediment modification. Of the environments that were colonized previously, levels of ichnodisparity, modes of life, and methods of sediment modification remain similar. However, ichnodiversity shows a significant increase, approximately doubling, across all previously colonized environments except for lake margins. Subaqueous coastal environments comprise 50 ichnogenera, 21 architectural designs, 20 modes of life, and 12 methods of sediment modification. Transitional coastal and alluvial environments hosted 48 and 53 ichnogenera, 15 and 14 modes of life, and 10 and 13 methods of sediment modification, respectively. Both contained 17 architectural designs. Lake margins were the only environment to remain similar to the Devonian in terms of ichnodiveristy, ichnodisparity, ecospace occupation, and sediment modification. Globally during the Devonian, 18 ichnogenera are recorded, corresponding to ten architectural designs, nine modes of life, and seven methods of sediment modification.

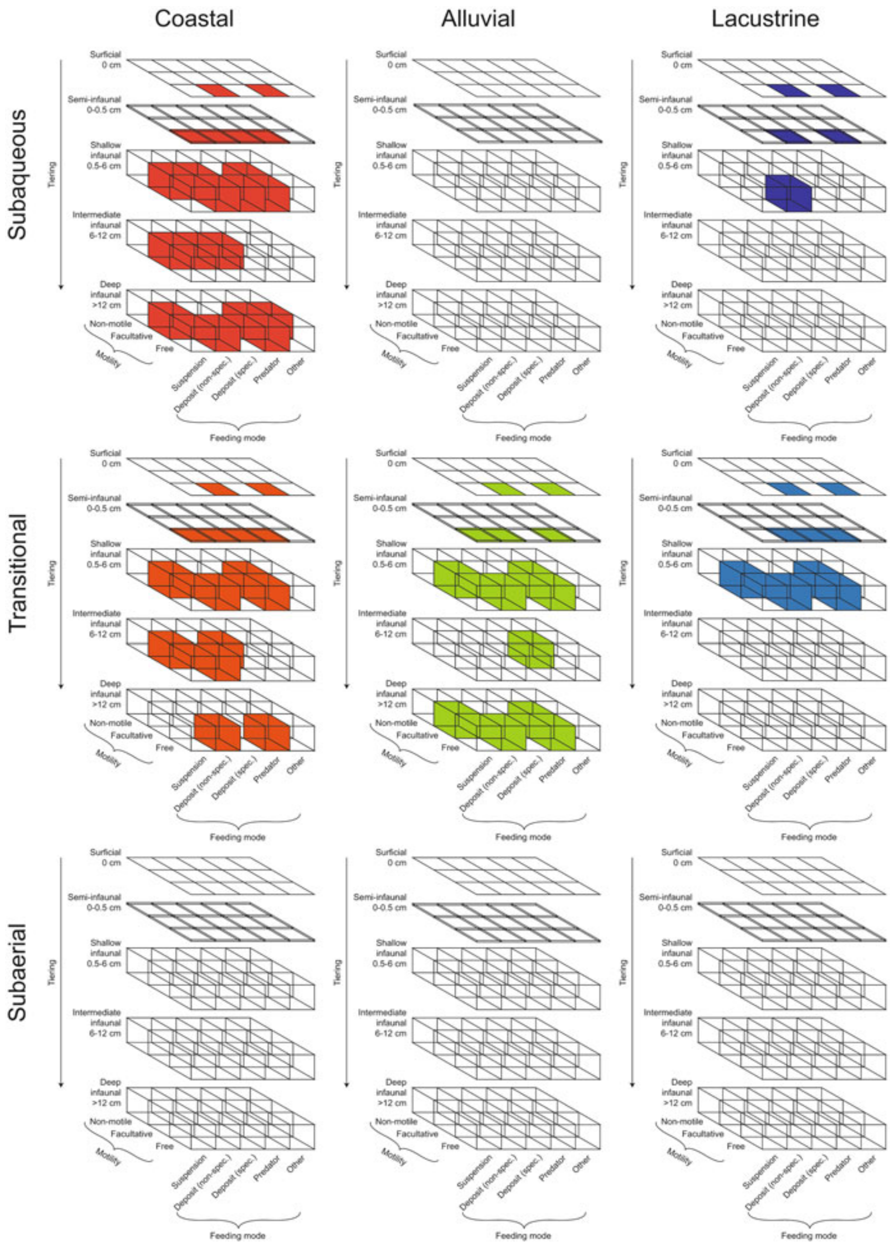

**Fig. 6.8** Carboniferous ecospace occupation

Freely mobile, nonspecialized deposit feeders and predators produced surficial trackways and scratch marks across all of the environments that were occupied during the Carboniferous (Fig. 6.8). These types of trace fossils were produced by both arthropods and tetrapods, but the occurrence of tetrapod trackways is limited to transitional coastal and alluvial environments and lake margins. Arthropods also produced bilaterally symmetrical, short, scratched impressions in subaqueous and transitional coastal environments, whereas both arthropods and tetrapods produced the same architectural designs in transitional alluvial environments. Surficial bilobate trails and paired grooves also were left behind by arthropods occupying subaqueous and transitional coastal, transitional alluvial, and subaqueous lacustrine environments. Evidence for fish is found in the surficial tier of all occupied environments through the occurrence of simple horizontal trails, although vermiform organisms also produced other surficial horizontal trails. Pentamerally shaped impressions and burrows also record the activities of surficial, freely mobile, nonspecialized deposit feeders and possible predators, but are restricted to subaqueous coastal environments. The above trace fossils were produced by compression and the activities of all the producers had minimal biodiffusive impacts upon the sediments (Fig. 6.9). Certain, freely mobile, nonspecialized deposit feeders and possible predators also had a minimal biodiffusive impact upon the sedimentary fabric of the semi-infaunal tier within subaqueous lacustrine environments, using compression to produce bilaterally symmetrical, short, scratched impressions (Figs. 6.8 and 6.9).

Nonspecialized deposit feeders and possible predators inhabiting the semi-infaunal tier produced a range of architectural designs across colonized environments and had a variety of impacts upon the sediment (Figs. 6.8 and 6.9). Organisms that were exclusively nonspecialized deposit feeders produced simple horizontal trails across all occupied environments, whereas circular trails were produced in all environments except for lake margins, and horizontal spiral burrows were produced in transitional alluvial environments. Organisms responsible for these trace fossils moved by backfilling, which resulted from conveying sediment within the semi-infaunal tier (Fig. 6.9). Other semi-infaunal, freely mobile, nonspecialized deposit feeders modified the sediment by creating gallery biodiffusive structures through compression (Fig. 6.9). Freely mobile, nonspecialized deposit feeders produced plug-shaped burrows in transitional alluvial environments; as well as isolated and serial, almond-shaped burrows in the semi-infaunal tier of subaqueous coastal and transitional coastal and alluvial environments. Other organisms possessing this mode of life produced horizontal burrows with horizontal to vertical branches across all other occupied environments except for lake margins. Some isolated and serially deployed, almond-shaped burrows found in the semi-infaunal tier of subaqueous coastal and transitional coastal and alluvial environments were produced by possible suspension feeders. Other, horizontal burrows with horizontal to vertical branches in subaqueous coastal environments were made by specialized deposit feeders (Fig. 6.8). A number of nonspecialized deposit feeders and possible predators inhabiting the semi-infaunal tier acted as sediment regenerators, excavating bilaterally symmetrical short, scratched burrows in subaqueous coastal, transitional alluvial, subaqueous lacustrine, and lake-margin environments (Figs. 6.8 and 6.9). They also excavated bilobate trails and paired grooves across all occupied environments.

In the shallow infaunal tier, nonspecialized deposit feeders acted as sediment conveyors and created simple, actively backfilled (massive) horizontal to oblique burrows across all occupied environments (Figs. 6.8 and 6.9). Others produced three-dimensional spreiten burrows in subaqueous coastal environments. Those organisms that may also have had a predatory mode of life were responsible for

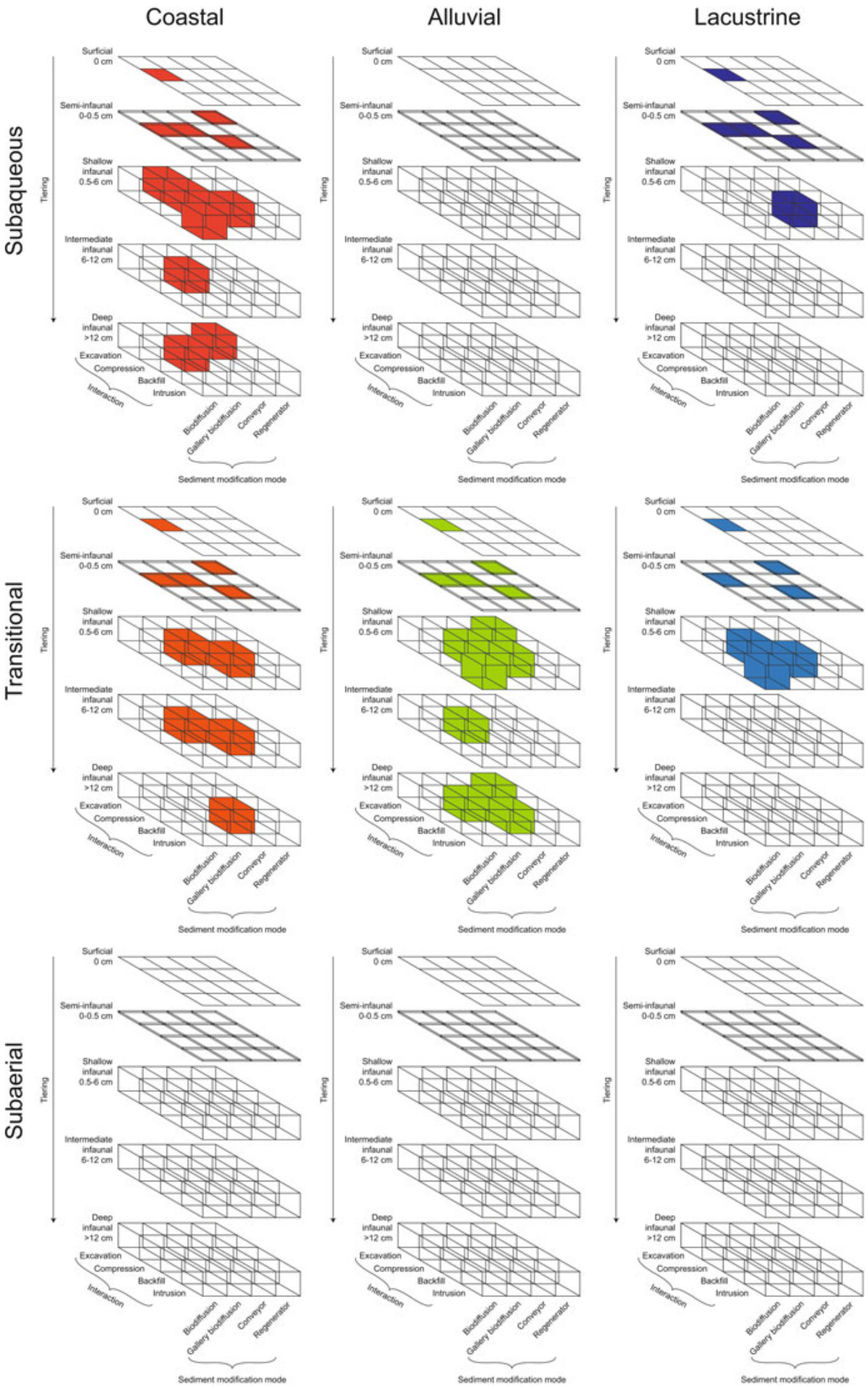

Fig. 6.9 Carboniferous ecosystem engineering

complex, actively filled (meniscate/pelletoidal), horizontal burrows in transitional coastal environments, and simple, actively filled (meniscate), horizontal to oblique burrows in transitional coastal and alluvial environments and lake margins (Fig. 6.8). Organisms with the same mode of life that moved through the sediment by intrusion had minimal biodiffusive impact upon the fabric as they created chevronate trails in subaqueous coastal and transitional alluvial environments. These organisms also made vertical displacement burrows in subaqueous coastal and lake-margin environments (Fig. 6.9). Additional organisms produced branching spreiten burrows by compression that acted as gallery biodiffusive structures in transitional alluvial environments (Fig. 6.9).

Further nonspecialized deposit feeders that acted as sediment conveyors produced simple, actively backfilled (massive) horizontal to oblique burrows that extended to the deep infaunal tier of transitional alluvial environments, and vertical spreiten burrows that extended to the intermediate, superjacent infaunal tier of transitional coastal environments (Figs. 6.8 and 6.9). Organisms that may have employed a predatory mode of life and also acted as sediment conveyors created simple, actively filled (meniscate), horizontal to oblique burrows that could extend downward to the deep infaunal tier of transitional coastal and alluvial environments (Figs. 6.8 and 6.9). Shallow and deep-tier, nonspecialized deposit feeders and possible predators also were capable of acting as sediment regenerators, excavating mazes and boxworks in subaqueous coastal and transitional alluvial environments (Figs. 6.8 and 6.9). Other organisms with the same mode of life and impact on sediment in transitional alluvial environments excavated passively filled, horizontal burrows.

Facultatively mobile, shallow infaunal tier suspension feeders produced plug-shaped burrows in lake-margin environments (Fig. 6.8). Passively filled, horizontal burrows were also produced by organisms with the same mode of life, although some of these may have been predators in subaqueous and transitional coastal, transitional alluvial, and lake-margin environments (Fig. 6.8). Organisms with the same mode of life created vertical simple burrows that extended to the shallow infaunal tier of subaqueous and transitional coastal environments, and the deep infaunal tier of subaqueous coastal and transitional alluvial environments (Fig. 6.8). Vertical U- and Y-shaped burrows were produced by facultatively mobile suspension feeders in the intermediate infaunal tier of subaqueous and transitional coastal environments and deep infaunal tier of subaqueous coastal and transitional alluvial environments (Fig. 6.8). Restricted to subaqueous coastal environments are intermediate, infaunally tiered, facultatively mobile suspension feeders and nonspecialized deposit feeders that produced vertical, concentrically filled burrows (Fig. 6.8). These types of trace fossils were produced by compression and functioned as gallery biodiffusive structures (Fig. 6.9).

Freely mobile, specialized deposit feeders that moved by backfilling and acted as sediment conveyors produced horizontally branching burrow systems in the semi-infaunal tier of transitional coastal and lake-margin environments. These types of deposit feeders also created complex, actively filled (meniscate/pelletoidal), horizontal burrows in the shallow infaunal tier of subaqueous coastal environments (Figs. 6.8 and 6.9). Other specialized deposit feeders were facultatively mobile, occupied the intermediate infaunal tier, and were responsible for radial branching structures in subaqueous and transitional coastal environments (Fig. 6.8). These burrows typified gallery biodiffusive structures and were produced by compression (Fig. 6.9). Deep, infaunally tiered, facultatively mobile organisms with a farming mode of feeding produced gallery biodiffusive burrows by compression that consisted of a shaft or bunch that downwardly projected radiating probes in subaqueous coastal environments (Figs. 6.8 and 6.9). Also occurring in subaqueous coastal environments were gallery biodiffusive structures in the form of burrows with horizontal spreiten, excavated by shallow-infaunal tier, facultatively mobile, nonspecialized deposit feeders (Figs. 6.8 and 6.9). Other gallery biodiffusive structures were produced by compression in the form of passively filled, horizontal burrows made by facultatively mobile, intermediate infaunal tier predators in transitional alluvial environments (Figs. 6.8 and 6.9).

#### 6.4.3.1 Varied Types of Carboniferous Lake Deposits

With few exceptions (Greiner 1974), the Mississippian lacks a significant record of well-documented lake deposits and their biotas. However, one deposit, East Kirkton in the West Lothian area of southern Scotland, stands out as an important site for understanding the paleoecology of a biota inhabiting a well-developed lake during the late Viséan. The East Kirkton paleolake was shallow, ephemeral (few tens of millennia in duration), contains numerous tuff horizons, and formed when volcanic activity blocked a drainage system (Clarkson et al. 1993). The lacustrine and surrounding terrestrial biota includes stromatolites, ostracods, bivalves, eurypterids, a scorpion, a harvestman arachnid, millipedes, and diverse amphibians, including temnospondyls and “reptiliomorph” tetrapods (Rolfe et al. 1993; Jeram and Selden 1993; Shear 1993). The surrounding woodland was dominated by arborescent pteridosperms and conifers, and toward the end of lacustrine deposition, by lycopsids (Brown et al. 1993), in an environment with periodic fire. Curiously, this biota lacks fish and hexapods (Rolfe et al. 1993), indicating abbreviated aquatic food-chain links. Although much of the East Kirkton biota is clearly terrestrial, the presence of ostracods, bivalves, eurypterids, and amphibious and probably aquatic tetrapods suggests a low diversity ecosystem that was at ecological variance with the much more diverse surrounding land biota. Unfortunately, we are unaware of reports of trace fossils from the East Kirkton paleolake. By contrast, ichnologic information reveals extensive colonization of Gondwanan glacial lakes during the Carboniferous (Netto et al. 2012), but the body-fossil record of these environments is meager, to say the least. Therefore, trace fossils represent so far the only source of information to reconstruct benthic communities in Carboniferous glacial lakes.

#### 6.4.3.2 The Pennsylvanian Wet Biome: Mazon Creek

During the Pennsylvanian, two major types of ecosystem appeared that were spatially segregated by differing environmental conditions. The Wet Biome emerged during the earlier Pennsylvanian and included a wide variety of wetland environments, notably the coal-swamps that consisted of lycopsids, sphenopsids, medullosan seed ferns, and arborescent marattialean ferns, tolerant of high soil moisture and occupying much of humid equatorial Euramerica during parts of glacial-interglacial cycles (DiMichele 2014). By contrast, macrofossil evidence for a Dry Biome in lowland, basinal settings appeared toward the later part of the Early Pennsylvanian (Langsettian; Bashforth et al. 2014), was clearly present in the later Middle Pennsylvanian (Asturian; Falcon-Lang et al. 2009; Plotnick et al. 2009), and was the predominant form of lowland, equatorial vegetation during the early Permian in Euramerican portions of Pangea, when xeric habitats predominated at most times (Kerp 1996; Tabor et al. 2013). The Dry Biome included communities dominated by a desiccation-tolerant biota, such as cordaites, noeggeranthialeans, conifers, gigantopterids, peltasperms, and probably cycads that occupied more continental, seasonally wet environments (Opluštil et al. 2013). Both Wet and Dry Biomes housed a variety of continental environments, each with a distinctive biota, including a variety of lakes with distinctive biotas.

One of the best examples of the Wet Biome is the Mazon Creek biota of Middle Pennsylvanian age in north-central Illinois (Johnson and Richardson 1966; Labandeira 2001). Mazon Creek deposits are part of the Francis Creek Shale Member of the Carbondale Formation, of which the Braidwood Facies contains a nonmarine assemblage preserved in taphonomically complex, siderite concretions (Baird et al. 1985, 1986). The local environment included river systems, distributary channels and tidally controlled estuaries (Park and Gierlowski-Kordesch 2007). The dominant aquatic taxa of the Braidwood Biota are a heterogeneous assemblage of taxa living either in fresh or brackish water, inhabiting lakes or other bodies of water, and occurring on land near water bodies whose submerged flotsam often formed habitats for aquatic organisms. The fossil plants were lycopsids, calamitalean and equisetalean sphenopsids, marattialean tree ferns, filicalean ferns, medullosan pteridosperms, and cordaitaleans (Wittry 2006).

Invertebrates of the Wet Biome ranged from fully nonmarine aquatic to seemingly fully terrestrial taxa. The invertebrates included bivalves, gastropods, crustaceans, chelicerates, myriapods, and hexapods. The crustaceans (taxonomy after Schram 1986) were branchiopods, conchostracans, malacostracans (syncarids, belotelsonids, phytocephalomorphs, lophogastrids, hemicarids and edrioiphthalmids), phyllopods (phyllocarids), and maxillopods (cirripedians) (Nitecki 1979; Schram et al. 1997; Shabica and Hay 1997). Chelicerates included eurypterids, horseshoe crabs, some of which also existed subaerially (Fisher 1979), terrestrial scorpions, arachnids (ricinuleids, phalangotarbids, trigonotarbids, uropygids, amblypygids, and araneids) (Beall and Selden 1997), and abundant, mostly wood-associated mites (Labandeira et al. 1997; Falcon-Lang et al. 2015c). Myriapods included arthropleurids, millipedes, centipedes and the remotely affiliated euthycarcinoids (Hannibal 1997; Schram and Rolfe 1997). Insects occurring in marginally aquatic and wetland terrestrial habitats were diverse, and included dasyleptid monurans, meganeurid dragonflies (Kukalová-Peck 1997, 2009) (Fig. 6.10), diverse paleodictyopteroids (Labandeira and Phillips 1996), mayflies, ancestral cockroaches (Kukalová-Peck 1991), a large variety of stem-group and related orthopteroids (Béthoux and Briggs 2008), perhaps early stonefly lineages (Carpenter 1997),

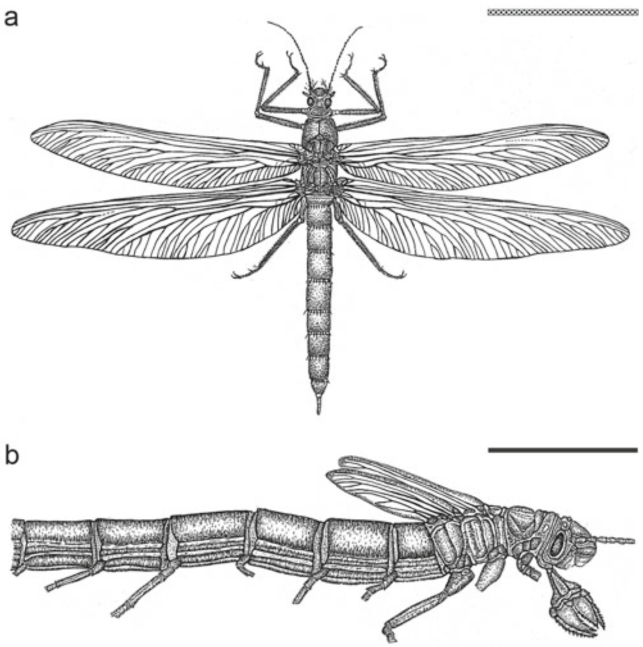

**Fig. 6.10** Predaceous, Euramerican odonatopteran members of the earliest continental aquatic biotas with macroscopic invertebrates. (**a**) An adult of the gigantic meganeurid Meganisopteran dragonfly, *Meganeurula selysii*, with a wingspan of 74 cm, from the early Late Pennsylvanian lacustrine deposits at Commentry, France (specimen 1422 of the Muséum National d'Histoire Naturelle in Paris, France); (**b**) a naiad of *Draconympha srokai*, with an estimated length of 5.0 cm, from the late-Middle Pennsylvanian fluvio-lacustrine deposits of Mazon Creek, Illinois, USA (specimen ISM-004ab of the Illinois State Museum in Springfield, IL, USA). Note extended raptorial labial mask at lower-right. Both specimens are redrawn from Kukalová-Peck (2009)

and the earliest lineages of holometabolous insects (Labandeira 2011), such as probable beetle-like forms (Béthoux 2008) and the earliest holometabolous larvae as foliage-feeding caterpillars (Haug et al. 2015). Some of these taxa also are known from other mid-Pennsylvanian deposits similar to Mazon Creek in eastern and midcontinental North America and Western Europe. Vertebrate taxa include hagfish, xenacanth and hybodontiform sharks, acanthodians, lungfish, coelacanths, ray-finned fishes, and temnospondyl and aistopod amphibians (Shabica and Hay 1997).

Perhaps the most notable aspect of the Mazon Creek biota for understanding the development of lacustrine ecosystems is the recent discovery of the immature aquatic naiads of meganeurid dragonflies, which supports assertions of a massive, labial mask used for raptorial predation (Kukalová-Peck 2009; Fig. 6.10). Previously, it was thought that the naiads of meganeurid dragonflies had terrestrial life habits, and that truly aquatic insects were absent from Carboniferous ecosystems (Sinitshenkova 2002). With few exceptions, insects were largely absent from Mazon Creek aquatic ecosystems and there is no evidence for either primary producers or their arthropod herbivores. Whereas the aquatic naiads of one lineage of mayflies are known for the early Permian (Kukalová 1968), no mayfly, nor for that matter any other, naiad-bearing taxa are known from the Pennsylvanian. Based on current knowledge, this would indicate that aquatic ecosystems were trophically based on detritivory, principally driven by crustacean taxa, and that the upper carnivore trophic levels were occupied by protodonatan naiads and vertebrates. The trophic development of late Middle Pennsylvanian aquatic ecosystems contrasts significantly with diverse, dominantly herbivore functional feeding groups in early Late Pennsylvanian land-based ecosystems (Labandeira 2006).

## 6.5 Permian

Permian continental trace-fossil assemblages have been reported from Europe, North America, South America, Africa and Antarctica. An important ecological event was the expansion of arthropod herbivory beyond the swampy and wet soil communities of the Wet Biome during the Pennsylvanian, and into the seasonally dry habitats of the early Permian, which were dominated by dry-adapted plants that hosted new lineages of plant-interacting insects.

### *6.5.1 Early Permian Trace-Fossil Assemblages*

#### 6.5.1.1 Coastal Settings

Early Permian trace-fossil assemblages from coastal settings are known from deposits in North and South America. These are the lower Abo Formation (early Wolfcampian, equivalent to Asselian) (Lucas and Lerner 2004), Earp Formation (Wolfcampian, equivalent to Asselian–Artinskian) (Lucas and Hunt 1995) and Robledo Mountains Formation (late Wolfcampian, equivalent to Artinskian), all of New Mexico (Hunt et al. 1993; Lucas et al. 1995a, 1998a, b), the Clear Fork Formation (Leonardian, equivalent to Kungurian) of Texas (Lucas et al. 2011), and the Ecca Group (Asselian–Capitanian) in South Africa (Anderson 1975b, 1976, 1981; Stanistreet et al. 1980; Turner et al. 1981; López-Gamundí 2010; Buatois et al. 2010).

Coastal—Subaqueous

The Ecca Group has a complex depositional history with likely variable salinity levels (Buatois et al. 2010). The trace fossils *Umfolozia* and *Undichna* have been reported from numerous turbidite and basin-center facies (Anderson 1976, 1981). *Kouphichnium* has been reported from shales, sandstones, and siltstones that are interpreted as representing shallow-marine to paralic settings (Anderson 1975b).

*Skolithos*, *Diplocraterion* and obliquely oriented burrows also have been reported from mouth-bar deposits within a lower delta plain, whereas *Helminthopsis* and vertical simple burrows (*Siphonichnus*) occur in interdistributary-bay deposits (Turner et al. 1981). In addition, within the Vryheid Formation of the Ecca Group prograding delta deposits contain *Diplocraterion* in the delta front, *Skolithos* and *Thalassinoides* in the interdistributary bay, and *Arenicolites*, *Monocraterion*, *Rhizocorallium*, and *Nereites* (= *Scalarituba* in Turner et al. 1981) in sand-barrier deposits. Transgressive sandsheets within an abandoned delta system also contain *Planolites*, *Siphonichnus* and *Skolithos* (Stanistreet et al. 1980).

A trace-fossil assemblage of *Palaeophycus* and *Protovirgularia* with a relatively high degree of bioturbation is present at two horizons within multistory ripple-laminated sandstones of the Abo Formation (Lucas and Lerner 2004). This assemblage has been interpreted as having formed in an estuarine sandflat under brackish conditions rather than a nonmarine overbank sandflat (Lucas and Lerner 2004).

### Coastal—Transitional

A number of trace-fossil assemblages occur in the Robledo Mountains Formation. One comprises *Batrachichnus*, *Dimetropus*, *Limnopus*, *Hyloidichnus*, and other tetrapod trackways (*Dromopus*, *Gilmoreichnus*), horizontal helicoidal burrows (*Augerinoichnus*), *Dendroidichnites*, *Stiaria*, and other trackways and scratch marks (*Lithographus*), *Tonganoxichnus*, and circular pits (Lucas et al. 1995b; Minter et al. 2008; Minter and Braddy 2009). These trace fossils are preserved in reduced sediments in association with an abundance of ripple cross-lamination, large conglomeratic channel deposits, and carbonized plant debris, suggesting a fluvio-deltaic shoreline setting (Lucas et al. 1995b). An additional trace-fossil assemblage from the Robledo Mountains Formation is incredibly diverse and abundant. These trace fossils generally have been interpreted as having formed on an intertidal flat but under essentially freshwater conditions with substantial periods of subaerial exposure (Hunt et al. 1993; Lucas et al. 1995a, 1998a, b). However, a systematic study of strata within the Robledo Mountains Formation has determined that the principal trace-fossil bearing lithologies represent distal crevasse-splay deposits on a low-relief coastal floodplain with common periods of subaerial exposure (Voigt et al. 2013). The study found no evidence of rhythmic bedding in these deposits that may be indicative of intertidal conditions, and therefore suggested that they are likely upper supratidal in nature in an essentially fluvially controlled freshwater ecosystem (Voigt et al. 2013). The trace-fossil assemblage comprises *Augerinoichnus*, *Cochlichnus*, *Dendroidichnites*, *Diplichnites*, *Diplopodichnus*, *Kouphichnium*, *Lithographus*, *Palmichnium*, *Stiallia*, *Stiaria*, *Striatichnium*, and other trackways and scratch marks (*Octopodichnus* and several enigmatic trackways and other traces). Also present are bilaterally symmetrical short, scratched burrows *Faciemichnus* (*Selenichnites* in original publication; see Romano and Whyte 2015), *Selenichnites*, *Tonganoxichnus*, and other bilaterally symmetrical short, scratched impressions (*Rotterodichnium*), *Treptichnus*, *Batrachichnus*, *Dimetropus*, *Dromopus*, *Gilmoreichnus*, *Hyloidichnus*, *Limnopus*, and other tetrapod trackways (*Serpentichnus*, cf. *Erpetopus*), *Lunichnium*, *Undichna*, cf. *Lockeia*, spiral graphoglyptids (cf. *Spirorhaphe*), simple horizontal trails (looping trails), and actively filled (massive) horizontal burrows (Hunt et al. 1993; Braddy 1995a; Haubold et al. 1995a; Hunt et al. 1995a; Kozur and LeMone 1995; Braddy 1998; Braddy and Briggs 2002; Braddy et al. 2003; Minter and Braddy 2006a, b, 2009; Minter et al. 2006, 2008; Lerner and Lucas 2015).

Laminated- to flaser-bedded dolomitic siltstones with mudcracks, raindrop impressions and microbial structures of the Clear Fork Formation are interpreted as representing the deposits of an unconfined sheetflood on a muddy coastal plain (Lucas et al. 2011; Nelson et al. 2013). These record *Diplichnites*, *Batrachichnus*, *Dromopus* and other tetrapod trackways (cf. *Amphisauropus*), and simple, actively filled (pelletoidal) horizontal burrows (*Walpia*). Deposits representing small, infilled fluvial-channels with a basal conglomerate, very fine-grained sandstone, siltstone, and mudstone also record *Treptichnus* and a tetrapod trackway (Lucas et al. 2011).

The Earp Formation contains trace fossils within mudstone and ripple-laminated siltstone deposits. Root casts and other nodules also are present, indicating pedogenesis. The deposits are considered to represent tidal and supratidal flats (Lucas and Hunt 1995). Reported trace fossils include *Batrachichnus*, *Dromopus*, *Limnopus*, *Planolites*, *Skolithos*, *Taenidium*, and invertebrate trails (Lucas and Hunt 1995; Minter and Braddy 2009).

Large burrows from the Speiser Shale (Hembree et al. 2004) occur in lenses of massive, calcareous, silty mudstone with rhizoliths and desiccation cracks that interfinger with pedogenically altered mudstone. These burrows are interpreted as having formed within the deposits of shallow, ephemeral ponds on a coastal plain.

#### 6.5.1.2 Alluvial Settings

Early Permian trace-fossil assemblages from alluvial settings occur from the Hillsborough River (Stephanian to Artinskian) and Kildare Capes formations (Wolfcampian, equivalent to Asselian–Artinskian) of the Pictou Group of Prince Edward Island (Calder et al. 2004; Brink et al. 2012), the Speiser Shale (Wolfcampian, equivalent to Asselian to Artinskian) of Kansas (Hembree et al. 2004), the Sangre de Cristo Formation (Wolcampian, equivalent to Asselian to Artinskian) of New Mexico (Hunt et al. 1990), the Robledo Mountains Formation (late Wolfcampian, equivalent to Artinskian) of New Mexico (Voigt et al. 2013), the Tambach Formation (likely Sakmarian) of Germany (Eberth et al. 2000), the Tor Bay Breccias (Sakmarian to Artinskian) of England (Ridgway 1974), the Abo Formation (mid-Wolfcampian to possibly early Leonardian, equivalent to Sakmarian–Kungurian) of New Mexico (Hunt et al. 1995b), the Michelbach Formation (Artinskian) of Germany (Kozur et al. 1994), the Saint-Xist Formation (Artinskian to early Kungurian) of France (Debriette and Gand 1990), the Laguna Polino Member (Artinskian to Kungurian) of the La Golondrina Formation of Argentina (Buatois et al. 1997b), the Standenbühl Formation (Artinskian to

Wordian) of Germany (Roscher and Schneider 2006), the Sagra and La Cuesta formations (early Leonardian, equivalent to Kungurian) of Spain (Gand et al. 1997), and the Tiddas Basin (Kungurian) of Morocco (Voigt et al. 2011). A number of relevant formations are present in the Provence Basin of France (Demathieu et al. 1992) that are Roadian to Wordian in age (Cassinis and Santi 2005). These include the Pradineaux, Mitan, Muy, and Motte formations.

Other assemblages whose ages are not tightly constrained beyond being early Permian occur from the Calencó Member of the Carapacha Formation of Argentina (Melchor and Sarjeant 2004) and La Dorada Formation of Argentina (Aceñolaza et al. 1983; Aceñolaza and Buatois 1993). Trace fossils also have been reported from the Mount Glossopteris and Polarstar formations of Antarctica (Tasch 1968a, b), although the ages of these formations are not constrained beyond being Permian, and the depositional environment of the latter unit is unclear.

A number of trace-fossil assemblages occur from eolian settings during the early Permian. The most famous of these is undoubtedly the Coconino Sandstone (Leonardian, equivalent to the Kungurian, in part) of Arizona (Gilmore 1926, 1927; Brady 1947, 1949, 1961; Baird 1952; Alf 1968; Keighley and Pickerill 1994; Kozur et al. 1994; Braddy 1995b; Kramer et al. 1995; McKeever and Haubold 1996). Additional early Permian trace-fossil assemblages from eolian settings occur from the DeChelly Sandstone (Leonardian, equivalent to the Kungurian) of Arizona (Sadler 1993; Braddy 1995b; Haubold et al. 1995b; Lockley et al. 1995; Morales and Haubold 1995; McKeever and Haubold 1996) and the coeval Lyons Sandstone Formation of Colorado (Henderson 1924; Toepelmann and Rodeck 1936; Dorr 1955; Braddy 1995b; Lockley and Hunt 1995; Lockley et al. 1995). Other assemblages from formations the ages of which are only constrained to the early Permian occur from the Cedar Mesa Sandstone of Utah (Loope 1984; Lockley and Madsen 1993; Lockley and Hunt 1995; Lockley et al. 1998), Casper Sandstone Formation of Wyoming and Colorado (Hanley et al. 1971), the Corncockle and Locharbriggs Sandstone formations of Scotland (Duncan 1831; Delair 1966, 1967, 1991; Brookfield 1978; McKeever 1991, 1994a, b; McKeever and Haubold 1996), and the Patquía Formation of Argentina (Krapovickas et al. 2010).

A large number of ichnogenera, especially those attributed to arthropod trackways, have been described from Permian assemblages of Germany (e.g., Holub and Kozur 1981; Walter 1983, 1984). However, these assignments are in need of extensive revision and minimal, detailed sedimentological data have been presented to facilitate inclusion within this analysis.

#### Alluvial—Subaqueous

In a recapitulation of many alluvial trace-fossil assemblages from the Devonian, the Tor Bay Breccias represent braided-stream deposits within a wadi environment. These deposits contain large, simple, actively filled (meniscate) horizontal to oblique burrows similar to *Beaconites* preserved within channel-bar deposits (Ridgway 1974, 1976; Pollard 1976).

### Alluvial—Transitional

The Laguna Polino Member of the La Golondrina Formation contains ripple cross-laminated and trough cross-bedded sandstones, mudstones, and conglomerates that represent a braided-fluvial system with moderate channel sinuosity. The trace fossils *Cochlichnus*, *Helminthoidichnites*, *Helminthopsis*, and horizontal to oblique branching burrows (*Ctenopholeus*) occur in current-rippled, muddy sandstones that are interpreted as forming in ponds adjacent to channel levees (Buatois et al. 1997b; Fig. 6.11a). Tabular shales and siltstones interbedded with sheet sandstones in the Tambach Formation preserve mudcracks and raindrop imprints and are interpreted as interfluve deposits that contain cylindrical invertebrate feeding traces (?*Planolites*) (Eberth et al. 2000).

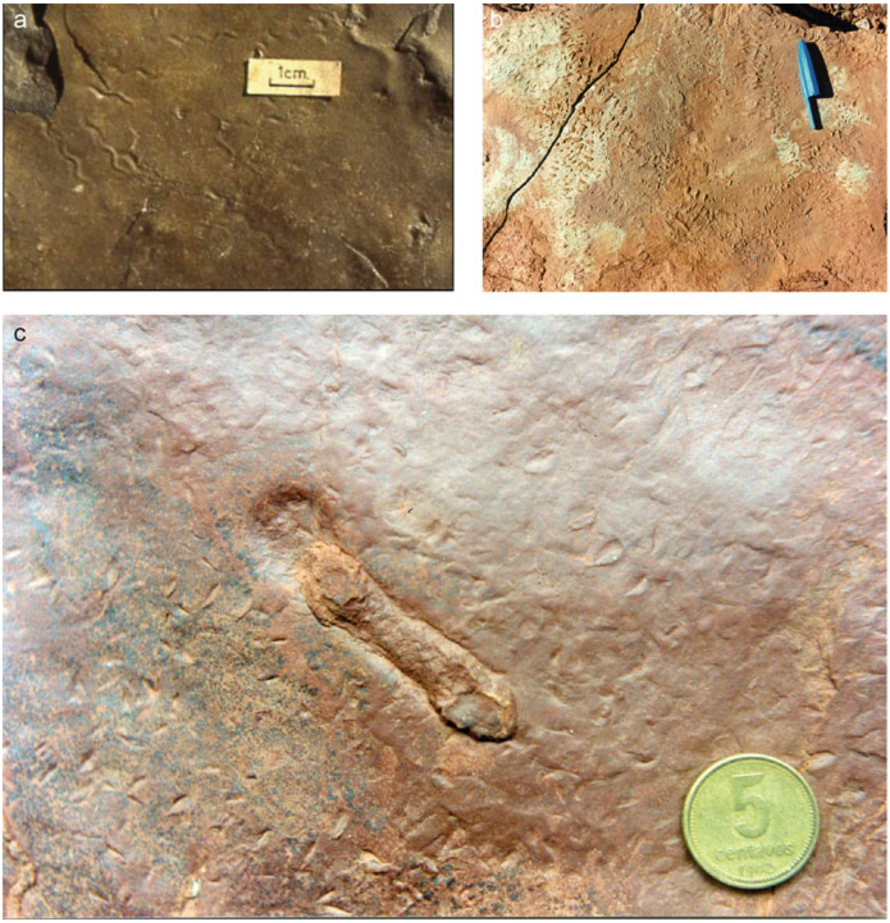

**Fig. 6.11** Permian trace fossils from the La Golondrina Formation (**a**) and Patquia Formation (**b** and **c**), Argentina. (**a**) *Cochlichnus*; (**b**) *Umfolozia*; (**c**) arthropod trackway omission surface and *Diplocraterion*

Tabular mudstones and fine-grained sandstones with parallel lamination and ripple cross-lamination from the Patquía Formation are interpreted as floodplain deposits within a fluvial setting. These floodplain deposits contain *Cruziana*, *Rusophycus*, *Taenidium* (*Ancorichnus* in the original publication), *Didymaulichnus*, and *Palaeophycus* (Aceñolaza and Buatois 1993; Krapovickas et al. 2010). The La Dorada Formation of Argentina contains *Didymaulichnus*, *Cruziana* (*Isopodichnus* in part in the original publication), *Rusophycus* (*Isopodichnus* in part in the original publication), and *Diplopodichnus* (*Beaconichnus* in the original publication). This ichnofauna occurs in massive and parallel-laminated fine- to medium-grained sandstones that record deposition in shallow, ephemeral pools formed on floodplains (Aceñolaza and Buatois 1993).

The Abo Formation comprises conglomerates, sandstones, and mudstones interpreted as representing an alluvial-plain setting with sinuous channels. A number of trace-fossil localities at different stratigraphic levels and paleogeographic positions are present, although the majority of trace fossils essentially occur in laterally extensive and tabular sandstones with ripple cross-lamination and claystone drapes that are interpreted as sheetflood sandstones deposited on a broad floodplain (Hunt et al. 1995b; Lucas et al. 1995c, 2005b, c). Identified trace fossils include *Arborichnus*, *Augerinoichnus*, *Cochlichnus*, *Lithographus*, *Monomorphichnus*, *Stiaria*, *Tonganoxichnus*, *Amphisauropus*, *Batrachichnus*, *Dimetropus*, *Dromopus*, *Gilmoreichnus*, *Hyloidichnus*, *Ichniotherium*, *Limnopus*, and other tetrapod trackways (*Varanopus*), *Lunichnium*, and an unnamed arthropod trackway (Hunt et al. 1995b, 2005; Lucas et al. 1995c, 2001, 2005b, c, 2009; Minter et al. 2008; Minter and Braddy 2009). A lungfish aestivation burrow also has been identified from an interbedded mudstone facies considered to represent overbank fines within the Robledo Mountains Formation (Voigt et al. 2013).

The La Cuesta Formation probably represents a floodplain, with mudcracks indicating desiccation. This deposit contains *Scoyenia* and *Skolithos* (Gand et al. 1997). *Cochlichnus* has been reported from floodplain deposits of the Mount Glossopteris Formation of Antarctica (Tasch 1968a) together with *Gordia*-like traces and indeterminate pits from the Polarstar Formation of Antarctica (Tasch 1986b). However, the environmental context of the *Gordia*-like traces is unclear.

A number of formations are also present in the Provence Basin of France (Demathieu et al. 1992; Cassinis and Santi 2005). The Pradineaux Formation represents a fluviolacustrine setting with *Batrachichnus* (*Antichnium* in the original publication), *Dromopus*, *Hyloidichnus*, *Varanopus*, and *Scoyenia*. The Mitan Formation represents floodplain and alluvial-fan settings, whereas the Muy Formation represents lacustrine and alluvial-fan settings. Both of these formations contain *Batrachichnus* (*Antichnium* in the original publication), *Dromopus*, *Hyloidichnus*, and *Limnopus*. Additionally, the Motte Formation contains a diverse trace-fossil assemblage (Demathieu et al. 1992) from a floodplain setting, comprising *Batrachichnus* (*Antichnium* in the original publication), *Dimetropus*, *Dromopus*, *Hyloidichnus*, *Limnopus*, *Varanopus*, and other tetrapod trackways (*Chelichnus*; *Laoporus* in the original publication), *Lithographus* (including *Acanthichnus* and *Bifurculapes* in the original publication), *Diplichnites* (including *Beaconichnus*, *Tasmanadia*, and *Trachomatichnus* in the original publication), *Danstairia*, *Dendroidichnites*, *Octopodichnus*, and other trackways and scratch marks (*Ichthyoidichnites*), *Gordia* and *Undichna* (*Cochlea* in the original publication; see Benner and de Gibert 2009), *Planolites*, *Scoyenia*, ?*Archaeonassa* (*Palaeobullia* in the original publication), and *Skolithos*.

Deposits of the Tiddas Basin comprise conglomerates, parallel-stratified or cross-bedded sandstones, parallel-laminated to massive mudstones and minor coal, limestone, and tuffs (Voigt et al. 2011). Overall, these deposits are interpreted as representing alluvial fans and braided-fluvial systems that were transitional to a flood basin with swamps or shallow lakes. Root traces, soils, mudcracks and raindrop impressions indicate a tropical monsoonal regime with wet and dry seasons. *Scoyenia*, *Amphisauropus*, *Batrachichnus*, *Dimetropus*, *Dromopus*, *Hyloidichnus*, *Limnopus*, *Varanopus*, and tetrapod swimming traces are found in interbedded to laminated fine-grained sandstones, siltstones, and mudstones with raindrop imprints that are interpreted as mudflats (Voigt et al. 2011).

A noted locality for trace and body fossils occurs in the Tambach Formation at the Bromacker Quarry in Germany. This deposit is interpreted as representing an overall alluvial-plain setting with minor fluvial channels, far removed from estuarine or coastal swamps or plains (Eberth et al. 2000). Trace fossils occur in fine- to medium-grained parallel-stratified to parallel-laminated sandstones with mudstone drapes. Mudcracks and raindrop imprints also are present. The sandstones have sheet geometries, and are interpreted as being deposited in low-sinuosity, shallow fluvial-channels during flood events, with the mudstone drapes forming during mud-laden, slackwater conditions that drowned the channels following the flood events (Eberth et al. 2000; Voigt et al. 2007). These deposits preserve *Scoyenia*, *Striatichnium* and other trackways and scratch marks (*Tambia*), *Amphisauropus*, *Dimetropus*, *Ichniotherium*, *Varanopus*, and other tetrapod trackways (*Tambachichnium*) (Martens 1975, 1982; Voigt et al. 2007). Deposits from the Sangre de Cristo Formation are correlatable with the Abo Formation and preserve trace fossils in sheet sandstones with raindrop imprints that represent unconfined sheetflood deposits as part of an alluvial-fan complex that formed under a seasonally dry climate (Hunt et al. 1990; Rinehart et al. 2015). Trace fossils include *Diplichnites*, *Diplopodichnus*, cf. *Lithographus*, cf. *Tonganoxichnus*, cf. *Treptichnus*, *Batrachichnus*, *Dromopus*, *Gilmoreichnus*, *Hyloidichnus*, *Ichniotherium*, *Limnopus*, *Undichna*, and tetrapod swimming traces (Hunt et al. 1990; Minter and Braddy 2009). Additional deposits considered to represent crevasse-splay sediments in a floodplain or overbank environment occur in the Kildare Capes Formation of the Pictou Group. The Kildare Capes strata also contain *Ichniotherium* and *Striatichnium*, as well as *Amphisauropus* and *Dimetropus*/*Varanopus* (Brink et al. 2012). The older Hillsborough River Formation of the Pictou Group preserves *Notalacerta* and *Gilmoreichnus* in overbank deposits (Calder et al. 2004). In addition to sheetflood deposits, the Abo Formation contains sediments interpreted as ephemeral-pool deposits. These deposits record *Cruziana*, *Diplichnites*, *Monomorphichnus*, *Palaeophycus*, *Rusophycus*, and *Striatichnium* (Minter and Lucas 2009).

The Standenbühl Formation represents an overall semiarid to arid alluvial-plain to playa setting (Roscher and Schneider 2006). The trace fossils of this deposit were most likely preserved in ephemeral water bodies (Schmidtgen 1927). Identified trace fossils include *Diplopodichnus*, cf. *Diplichnites*, *Lithographus*, *Paleohelcura*, *Stiaria*, *Striatichnium* and other trackways and scratch marks (*Heterotripodichnus*), *Treptichnus*, ?*Tambia*, insect landing traces, *Amphisauropus*, *Batrachichnus*, *Dimetropus*, *Dromopus*, and *Ichniotherium* (Schmidtgen 1927; Boy 1976; Minter et al. 2007a; Voigt 2007).

The Sagra Formation consists of fining-upward successions of conglomerate to cross-bedded coarse-grained sandstones, medium- to fine-grained cross-laminated sandstones and siltstones. Mudcracks, raindrop imprints, adhesion ripples, and oscillation ripples also are present, indicating deposition in shallow water subject to frequent desiccation and most likely on a floodplain (Gand et al. 1997). The occurrence of oscillation ripples also indicates that ephemeral water bodies were present. Described trace fossils include *Cruziana*, *Scoyenia*, ?*Skolithos* (*Ancorichnus* in the original publication), *Spongeliomorpha* (cf. *Steinichnus* in the original publication), cf. *Limnopus*, and *Hyloidichnus*. Some of the tetrapod tracks are overprinted by raindrop imprints or are cross-cut by *Scoyenia* burrows, suggesting transitional conditions (Gand et al. 1997).

The Michelbach Formation contains ephemeral-pool deposits with a low diversity trace-fossil assemblage consisting of *Stiaria* (*Paleohelcura* in the original publication) and *Chelichnus* (*Laoporus* in the original publication) (Kozur et al. 1994). However, the latter ichnotaxon is not figured and so this identification cannot be evaluated. The Calencó Member of the Carapacha Formation contains solely cf. *Amphisauropus* in floodplain deposits (Melchor and Sarjeant 2004).

The Saint-Xist Formation contains pool or shallow-lake deposits within a floodplain. These deposits preserve *Cruziana* and *Rusophycus* (*Isopodichnus* in the original publication), *Diplichnites* (*Trachomatichnus* in the original publication), *Scoyenia*, *Batrachichnus* (*Antichnium* and *Salichnium* in the original publication), *Dromopus* and *Limnopus* (Debriette and Gand 1990).

### Alluvial—Eolian

Described trace fossils from the eolian Coconino Sandstone include *Chelichnus*, *Diplopodichnus*, *Lithographus*, *Octopodichnus*, *Paleohelcura*, *Oniscoidichnus*, *Taenidium*, and complex, actively filled (meniscate/pelletoidal) horizontal burrows (*Scolecocoprus*) (Gilmore 1926, 1927; Brady 1947, 1949, 1961; Baird 1952; Alf 1968; Keighley and Pickerill 1994; Kozur et al. 1994; Braddy 1995b; Kramer et al. 1995; McKeever and Haubold 1996; Fig. 6.12). A similar trace-fossil assemblage comprising *Chelichnus*, *Dromopus*, *Lithographus*, *Octopodichnus*, and *Paleohelcura* occurs in the DeChelly Sandstone (Sadler 1993; Braddy 1995b; Haubold et al. 1995b; Lockley et al. 1995; Morales and Haubold 1995; McKeever and Haubold 1996).

Less diverse assemblages than those of the Coconino and DeChelly Sandstones, comprising only *Chelichnus*, occur in eolian deposits of the Corncockle and Locharbriggs Sandstone formations (Duncan 1831; Delair 1966, 1967, 1991; Brookfield 1978; McKeever 1991, 1994a, b; McKeever and Haubold 1996).

**Fig. 6.12** Permian trace fossils from the Coconino Sandstone in Arizona, USA. *Chelichnus*, *Diplopodichnus*, *Entradichnus*, and partial *Paleohelcura* and *Octopodichnus*. Scale bar 50 mm

Additionally, the Lyons Sandstone Formation contains *Chelichnus* and *Paleohelcura* (Henderson 1924; Toepelmann and Rodeck 1936; Dorr 1955; Braddy 1995b; Lockley and Hunt 1995; Lockley et al. 1995). *Chelichnus* and other tetrapod trackways (cf. *Stenichnus*), and cf. *Planolites* also have been reported from eolian deposits of the Cedar Mesa Sandstone of Utah (Loope 1984; Lockley and Madsen 1993; Lockley and Hunt 1995; Lockley et al. 1998). Other horizontal *Palaeophycus*-like burrows occur in the Casper Sandstone Formation of Wyoming and Colorado (Hanley et al. 1971). In addition to floodplain deposits, the Patquía Formation also contains an interval with parallel-laminated, ripple cross-laminated and planar cross-stratified sandstones that are interpreted as low-angle eolian sand sheets and merge upward into thick, high-angle, cross-stratified sandstones interpreted as eolian dune deposits (Krapovickas et al. 2010). These deposits contain *Palaeophycus*, *Skolithos*, an arthropod trackway similar to *Octopodichnus*, *Chelichnus*, and various other tetrapod trackways (Krapovickas et al. 2010).

#### 6.5.1.3 Lacustrine Settings

Reports of early Permian trace-fossil assemblages from fully lacustrine deposits are limited. Fully lacustrine assemblages have been documented from the Vrchlabí Formation (Asselian) of the Czech Republic (Mikulás 1999) and the Mackellar Formation of Antarctica (Miller and Isbell 2010). Early Permian trace-fossil assemblages from lake-margin settings also are somewhat limited, occurring from the Vrchlabí and Prosecná formations (Asselian) of the Czech Republic (Mikulás

1999), Collio and Monte Luco formations (Artinskian) of Italy (Avanzini et al. 2011), Wellington Formation of Oklahoma (Swanson and Carlson 2002) and the Mackellar Formation of Antarctica (Briggs et al. 2010). The ages of the latter two are not constrained beyond being early Permian. Diverse trace-fossil assemblages from lower Permian, playa-lake deposits are from the Clear Fork Formation (Artinskian) of Texas (Minter et al. 2007b; Nelson et al. 2013), Rabejac Formation (Artinskian to early Kungurian) of France (Gand 1994), Salagou Formation (Kungurian to Wordian) of France (Gand 1994), and Patquía Formation of Argentina (Aceñolaza and Buatois 1993; Krapovickas et al. 2010). Trace fossil assemblages have also been reported from a shallow floodplain lake and ephemeral lake from the Tregiovo Formation (Kungurian) of Italy (Marchetti et al. 2015).

#### Lacustrine—Subaqueous

The Mackellar Formation typically represents a deep-lacustrine setting consisting of shale, siltstone and thin-bedded sandstone attributed to underflow and turbidity currents in a large and deep freshwater lake (Miller and Isbell 2010). Trace fossils include *Cochlichnus*, *Mermia*, *Treptichnus*, *Planolites*, *Palaeophycus*, and *Cruziana*-like bilobate trails. Quiet lake-center deposits from the Vrchlabí Formation contain *Planolites* and ?*Cochlichnus* (*Unisulcus* in the original publication) (Mikulás 1999).

#### Lacustrine—Margin

Shales, dolomites, and sandstones of the Wellington Formation show evidence of shallow-water deposition in the form of mudcracks and algal structures (Swanson and Carlson 2002). These deposits are interpreted as representing a lake margin, where the salinity may have fluctuated, and channel sandstones also are present. A number of trackways are described in open nomenclature but are compared with *Limnopus*, *Baropezia*, *Gilmoreichnus*, *Dimetropus*, and *Dromopus* (Swanson and Carlson 2002). In addition to deep-lacustrine deposits, the Mackellar Formation also contains deposits with symmetrical ripples that indicate a shallow-lake margin and possibly a partially emergent setting. These deposits record the trace fossils *Diplichnites*, *Diplopodichnus*, and bilaterally symmetrical short, scratched impressions (*Orbiculichnus*) (Briggs et al. 2010). Deltaic deposits from the Vrchlabí Formation contain *Planolites* and lake-margin deposits of the Prosecná Formation contain *Diplichnites*, *Lithographus* (*Permichnium* in the original publication), and tetrapod trackways (*Saurichnites*) (Mikulás 1999).

#### Lacustrine—Ephemeral

Diverse trace-fossil assemblages occur from a number of lower Permian playa-lake deposits. The Clear Fork Formation contains trace fossils in a unit representing playa-lake deposits within an alluvial plain (Minter et al. 2007b). The trace-fossil assemblage comprises *Diplichnites*, *Lithographus*, *Cruziana*, *Rusophycus*, *Gordia*, *Helminthoidichnites*, *Treptichnus*, *Planolites*, *Taenidium*, cf. *Kouphichnium*, cf. *Walpia* (nodular trails in the original publication), unilobate trails, branching networks, *Dromopus*, *Erpetopus*, *Varanopus*, and cf. *Amphisauropus* (Haubold and Lucas 2001, 2003; Minter et al. 2007b; Lucas et al. 2011; Fig. 6.13). Playa-lake deposits from the Patquía Formation contain *Cruziana*, *Diplocraterion*, *Kouphichnium*, *Merostomichnites*, *Mirandaichnium*, *Monomorphichnus*, *Palaeophycus*, *Umfolozia*, and cf. *Diplopodichnus* (Aceñolaza 1978; Aceñolaza and Buatois 1993; Zhang et al. 1998; Fig. 6.11b and c). The trace fossils are cast on the soles of climbing and wave rippled, cross-laminated, fine-grained sandstones that were deposited by flood events, periodically entering an ephemeral lake, and then reworked by wave action. The trace fossils were produced in the lake sediments under conditions that varied from soft, slightly subaqueous sediments to firm, desiccated substrates, and overprinted suites of traces were produced under the two conditions (Zhang et al. 1998). The Rabejac and Salagou formations contain *Rusophycus* (*Isopodichnus* in the original publication) in playa-lake deposits (Gand 1994).

The Collio Formation represents cyclic floodplain sheetflood sandstones and shales interbedded with parallel-laminated lacustrine deposits, floodplain and playa-lake deposits, and alluvial-fan to lacustrine deposits (Ronchi and Santi 2003; Santi 2005; Avanzini et al. 2011). The trace fossils in this unit tend to occur in lake-margin mudstones and consist of *Amphisauropus*, *Batrachichnus*, *Dromopus*, *Erpetopus* (*Camunipes* in the original publication), *Ichniotherium*, *Varanopus*, *Diplichnites*, *Diplopodichnus*, *Lithographus* (*Dendroidichnites* in the original publication), *Stiaria* (*Paleohelcura* in the original publication), cf. *Tonganoxichnus* (*Heterotripodichnus* in the original publication), *Circulichnis*, *Cochlichnus*, *Cruziana*, ?*Gordia* (cf. *Cochlea* in original publication), *Planolites*, *Palaeophycus*, *Taenidium* (?*Scoyenia* in the original publication), and a number of poorly preserved and indeterminate arthropod trackways (*Acripes* and *Bifurculapes* in Ronchi and Santi 2003) (Ronchi and Santi 2003; Santi 2005; Avanzini et al. 2011). The ichnogenera *Palaeobullia*, *Permichnium*, *Secundumichnus*, and *Tambia* also are identified, but cannot be confirmed from the figured material or otherwise are not figured. The Monte Luco Formation records *Amphisauropus*, *Batrachichnus*, *Dromopus*, *Erpetopus* (*Camunipes* in the original publication), *Varanopus*, *Diplichnites* (*Permichnium* in the original publication), *Cochlichnus*, *Gordia*, *Helminthoidichnites* (*Helminthopsis* in the original publication), and *Palaeophycus* occurring in a similar environment.

The Tregiovo Formation of Italy contains a facies association comprising interbedded dark grey siltstones and claystones, root traces, desiccation cracks, load casts, rare marls and chert, together with pyrite associated with plant fossils that has been interpreted as a shallow ephemeral floodplain lake with periods of anoxia in the sediment (Marchetti et al. 2015). Trace fossils are represented by *Gordia*, *Helminthoidichnites*, *Octopodichnus*, appendage marks, *Batrachichnus*, and *Dromopus*. This facies association is transitional to what has been interpreted as

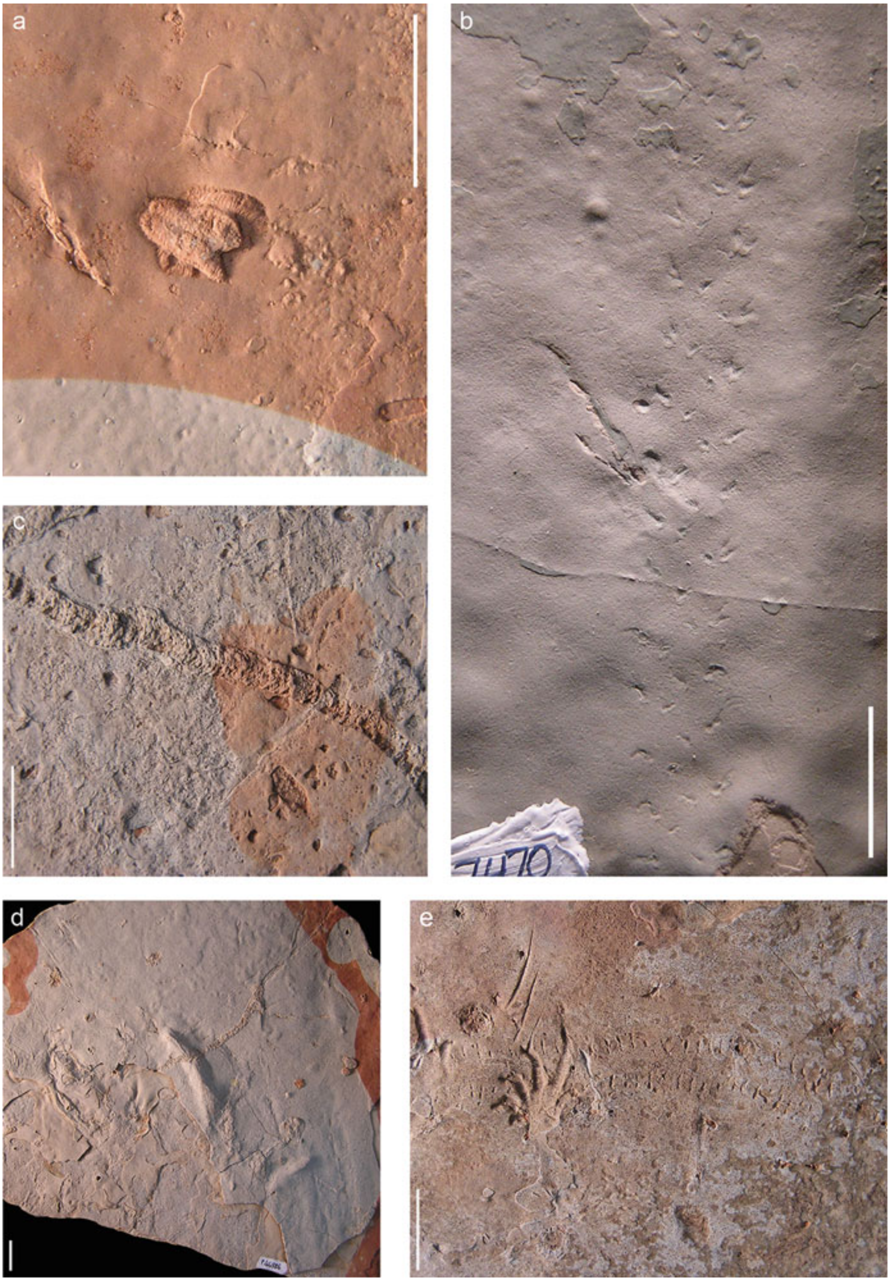

**Fig. 6.13** Permian trace fossils from the Choza Formation in Texas, USA. (**a**) *Rusophycus*; (**b**) *Lithographus*; (**c**) *Taenidium*; (**d**) *Dromopus* cross-cut by *Taenidium*; (**e**) *Diplichnites* overprinted by *Erpetopus*. Scale bars 10 mm

another ephemeral lacustrine association but one that formed under drier climatic conditions (Marchetti et al. 2015). Here, light grey limestones alternate with dark grey laminated mudstones. Marly and microbial or micritic limestones, wrinkle structures, desiccation cracks, syneresis cracks and symmetrical ripples are also present. A wider variety of tetrapod trackways are preserved than in the earlier facies association; *Batrachichnus*, *Dromopus*, *Erpetopus*, and *Hyloidichnus* co-occur with rare arthropod trackways assigned to *Octopodichnus* (Marchetti et al. 2015). Overlying distal alluvial fan deposits do not contain any trace fossils.

## *6.5.2 Late Permian Trace-Fossil Assemblages*

### 6.5.2.1 Alluvial Settings

Trace-fossil assemblages from alluvial settings occur in the Ikakern Formation (Wordian to Changhsingian) of Morocco (Voigt et al. 2010; Hminna et al. 2012) and Lower Beaufort Group (Wuchiapingian to Changhsingian) of South Africa (Smith 1987; 1993). An assemblage also occurs from the upper Permian Vyatkian Gorzont locality (Changhsingian) of Russia which is 50 m below the Permo-Triassic boundary (Surkov et al. 2007). Additional assemblages are reported from the lower Feather Conglomerate (middle to late Permian) of Antarctica (Fitzgerald and Barrett 1986), the Urre-Lauquen Member (early late Permian) of the Carapacha Formation of Argentina (Melchor and Sarjeant 2004), the Arenaria di Val Gardena Formation (late Permian) of Italy (Valentini et al. 2007), and the Takrouna (Zawaskie et al. 1983) and Buckley (late Permian) formations of Antarctica (Miller and Collinson 1994; Briggs et al. 2010).

#### Alluvial—Subaqueous

The lower Feather Conglomerate Formation represents an overall braided-fluvial system that was a considerable distance from the paleoshoreline (Fitzgerald and Barrett 1986). *Skolithos* occurs in fine- to very coarse-grained sandstones to conglomerates with trough cross-bedding, planar cross-bedding and horizontal bedding that are interpreted as sandy-braided, fluvial-channel deposits (Fitzgerald and Barrett 1986). *Monocraterion*, *Skolithos*, ?*Archaeonassa* (*Aulichnites* in the original publication) and horizontal backfilled epichnial traces (?*Planolites*) occur in similar facies in the Takrouna Formation (Zawaskie et al. 1983). The composition of the trace-fossil assemblage led to the suggestion that there was some marine influence (Zawaskie et al. 1983), but Fitzgerald and Barrett (1986) noted that the Takrouna and Feather Conglomerate formations probably were part of the same drainage system and therefore would have been several thousand kilometers from the paleoshoreline.

### Alluvial—Transitional

Fining-upward cycles of sandstone to shale from the Buckley Formation represent a braided-fluvial system on an alluvial plain (Miller and Collinson 1994; Briggs et al. 2010). Miller and Collinson (1994) described four types of trace fossils in open nomenclature: vertical to oblique burrows similar to *Skolithos*, bilobed endostratal traces with scratch marks similar to *Cruziana*, unlined horizontal burrows, and chevron trace fossils. The trace fossils occur in deposits with rippled surfaces and within trough cross-bedded sandstones and sandstones with claystone drapes. They are interpreted to represent colonization of fluvial-channel bar sands during times of waning or low flow (Miller and Collinson 1994; Miller 2000; Miller et al. 2002). Depressions in upper point-bar deposits filled with ripple-laminated muddy sandstones in the Lower Beaufort Group are bioturbated (Smith 1987) evidently with *Skolithos*. These depressions are interpreted to have formed when the point bars were exhumed and waning flow allowed muddy sediments to accumulate. Additionally, mudstone veneered, thin, ripple cross-laminated fine-grained sandstones deposited during abandoned channel fill contain *Planolites* and *Undichna* (Smith 1987). Similar deposits representing upper point-bar ridges and swales in the Lower Beaufort Group contain *Planolites*, *Undichna*, septate burrows (?*Beaconites*), bilobate septate trails (?*Protovirgularia*), and arthropod trackways (Smith 1993). The Ikakern Formation contains *Hyloidichnus* and other tetrapod trackways (*Pachypes*) in firm sandy fluvial streambeds (Voigt et al. 2010). Parallel-laminated, muddy siltstones and fine-grained sandstones interpreted as slackwater deposits in fluvial channels also contain *Spongeliomorpha*, *Striatichnium*, *Amphisauropus*, *Hyloidichnus*, *Erpetopus*, and *Dromopus* (Hminna et al. 2012).

Also from the Buckley Formation is *Diplichnites*, which has been reported from parallel-laminated sandstones that thin laterally and interfinger with mudstones adjacent to cross-laminated sandstones. These trackway-bearing deposits are interpreted as crevasse splays (Briggs et al. 2010). Proximal crevasse-splay and distributary-channel deposits of the Lower Beaufort Group preserve sedimentary structures such as adhesion ripples and runnels that indicate falling water levels and contain *Umfolozia*, *Undichna*, *Planolites*-like burrows, beaded scribble trails (?*Gordia*), meandering septate grooves (?*Protovirgularia*), and five different types of tetrapod trackways (Smith 1993). *Undichna*, beaded scribble trails (?*Gordia*), arthropod trackways and tetrapod trackways also occur in more distal crevasse-splay and marginal-lacustrine deposits (Smith 1993). Proximal sandy sheetflood deposits of the Urre-Lauquen Member of the Carapacha Formation contain unidentified burrows; distal sheetflood deposits house unidentified burrows and arthropod trackways (Melchor and Sarjeant 2004).

There are a number of reports of tetrapod tracks from the late Permian. The Vyatkian Gorzont locality contains tetrapod tracks identified as *Brontopus* in ephemeral-pool deposits adjacent to fluvial channels (Surkov et al. 2007). Additionally, *Sukhonopus* has been reported from the late Permian of Russia (Gubin et al. 2003). However, these trackways currently have been placed in *Pachypes* (Valentini et al. 2009). The Arenaria di Val Gardena Formation appears to contain a diverse assemblage of tetrapod tracks comprising *Rhynchosauroides*, *Ganasauripus*, *Ichniotherium*, *Pachypes*, *Janusichnus*, *Hyloidichnus*, *Dicynodontipus*, ?*Paradoxichnium*, ?*Chelichnus*, and indeterminate gorgonopsian and chirotherian tracks (Valentini et al. 2007), although there are few details on facies relationships.

#### Alluvial—Eolian

The Hopeman Sandstone Formation (late Permian) of Scotland is eolian in origin and contains the trackway *Chelichnus* (Benton and Walker 1985). *Chelichnus* also occurs from eolian deposits of the Cornberger Sandstone Formation (Capitanian to Wuchiapingian) of Germany (Schmidt 1959; Haubold et al. 1995b; McKeever and Haubold 1996; Hunt and Lucas 2006).

### 6.5.2.2 Lacustrine Settings

Late Permian trace-fossil assemblages from lacustrine settings occur from the Brenton Loch Formation (Capitanian) of the Falkland Islands (Trewin 2000; Trewin et al. 2002), Urre-Lauquen Member (early late Permian) of the Carapacha Formation of Argentina (Melchor and Sarjeant 2004), and the Severodovinskian Gorizont locality (Capitanian to Changhsingian) of Russia (Tverdokhlebov et al. 1997).

#### Lacustrine—Subaqueous

In the Falkland Islands, the Brenton Loch Formation (Capitanian) consists of massive turbidites and rhythmically laminated sandstone and mudstone couplets attributed to underflow currents. Overall, the succession represents a prograding delta slope and there is no evidence for marine conditions (Trewin et al. 2002). The Cantera Member contains the trace fossils *Umfolozia*, *Kouphichnium*, *Cochlichnus*, *Helminthoidichnites*, *Undichna*, and arthropod resting traces (Trewin 2000; Trewin et al. 2002). The overlying Saladero Member contains a similar trace-fossil assemblage of *Umfolozia*, *Undichna*, *Planolites*, *Diplocraterion*, and *Spirodesmos* (Trewin et al. 2002).

#### Lacustrine—Ephemeral

The Urre-Lauquen Member of the Carapacha Formation also contains trace fossils in playa-lake mudflat and shallow freshwater pond and lake deposits (Melchor and Sarjeant 2004). The most diverse trace-fossil assemblage occurs from freshwater ephemeral-lake deposits, and comprises *Helminthoidichnites*, *Palaeophycus*, *Rusophycus*, *Scoyenia*, arthropod trackways, unidentified and segmented burrows, *Batrachichnus*, *Hyloidichnus*, cf. *Amphisauropus*, ?*Undichna*, *Characichnos*, and other unidentified tetrapod swimming traces. Playa-lake mudflats preserve arthropod trackways, unidentified burrows, *Batrachichnus*, and *Hyloidichnus* (Melchor and Sarjeant 2004). Deposits interpreted as representing a shallow, ephemeral lake margin from the Severodovinskian Gorizont locality contain *Batrachichnus* (*Antichnium* in the original publication) (Tverdokhlebov et al. 1997).

### *6.5.3 Permian Ecospace Occupation and Ecosystem Engineering*

All possible marginal-marine and terrestrial environments, apart from subaerial coastal settings, show trace-fossil evidence of being occupied during the Permian (Figs. 6.14 and 6.15). Of those environments that were occupied during the Carboniferous ichnodiversity generally decreases, whereas the number of architectural designs, ecospace occupation, and methods of ecosystem engineering remain similar or decrease slightly. The exception is in transitional alluvial environments where there is a large increase in ichnodiversity compared to the Carboniferous. Transitional alluvial environments globally record 62 ichnogenera, corresponding to 13 architectural designs, 16 modes of life, and 14 methods of sediment modification. Values of the three latter parameters are very similar to those of the Carboniferous. In comparison to the Carboniferous, ichnodiversity decreases significantly to 16 ichnogenera in subaqueous coastal environments. Ichnodiversity and the number of modes of life decrease to 10 and 13 respectively, whereas the number of methods of sediment modification decreases slightly, to nine, compared to the Carboniferous. Transitional coastal environments show similar levels in the Permian compared to the Carboniferous. Globally they record 37 ichnogenera, 13 architectural designs, 12 modes of life, and ten methods of sediment modification. The same is true for subaqueous lacustrine environments. These environments record 13 ichnogenera, nine architectural designs, eight modes of life, and eight methods of sediment modification. Lake-margin environments show a relatively large decrease from the Carboniferous to 11 ichnogenera but ecospace occupation and ecosystem engineering are especially limited. They contain just four architectural designs, three modes of life, and two methods of sediment modification. There are no records of trace-fossil assemblages from eolian environments and ephemeral lakes in the Carboniferous. Eolian environments are known from the Mississippian but most are Pennsylvanian or span the Pennsylvanian–Permian boundary (Rodríguez-López et al. 2014). There is no reason not to expect the presence of bioturbation in Carboniferous eolian environments (Ahlbrandt et al. 1978). Possible records that we currently are aware of relate to uncertain identifications as burrows or rhizoliths, come from marine and channel fill facies or deflation surfaces associated with eolian facies, and are from deposits that span the Pennsylvanian–Permian boundary (Doe and Dott 1980; Driese 1985; Loope 1985; Jordan and Mountney 2010). Permian eolian environments demonstrate similar levels of occupation to those found in the Devonian. Eolian environments comprised 13 ichnogenera, seven

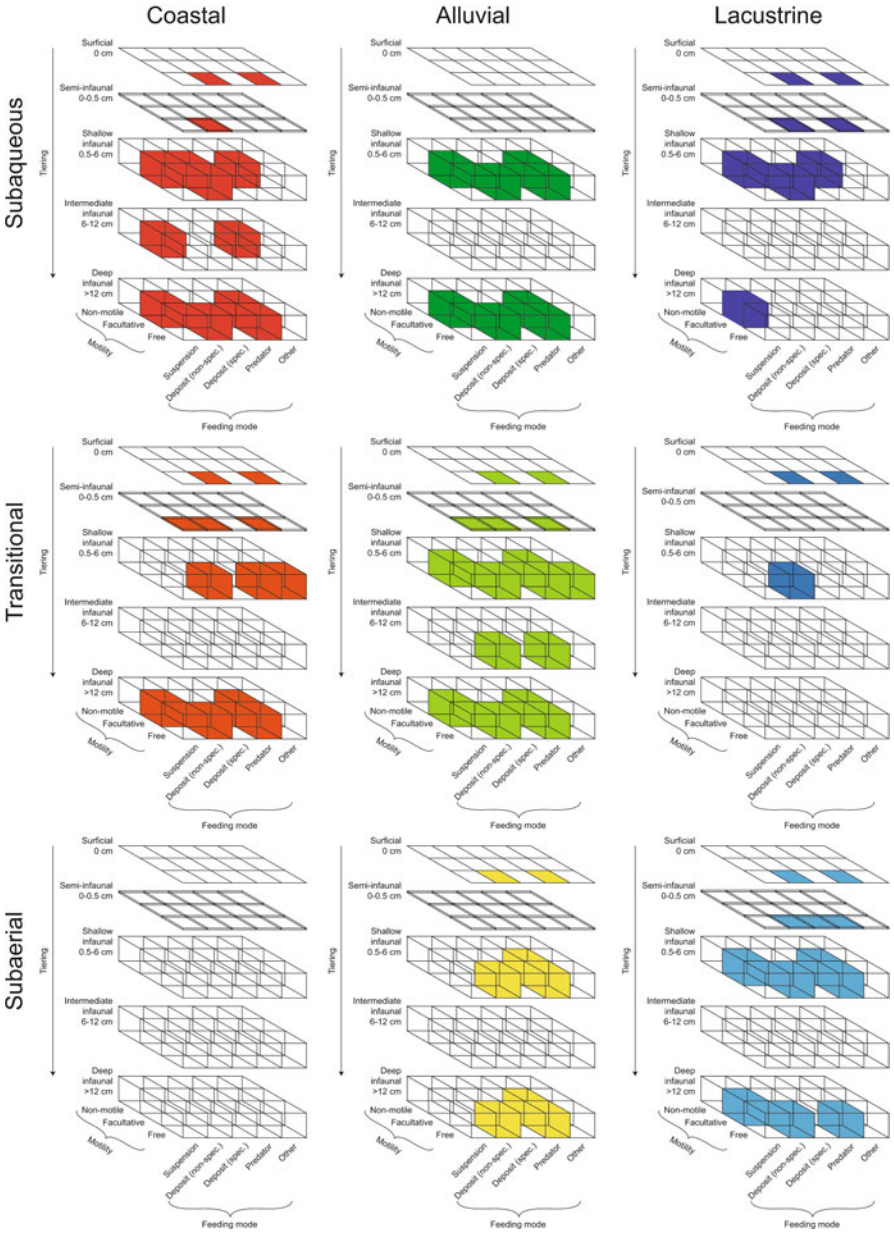

**Fig. 6.14** Permian ecospace occupation

architectural designs, eight modes of life, and five methods of sediment modification. Ephemeral lacustrine environments show a fourfold increase in ichnodiversity to 35 ichnogenera, compared to the Devonian. However, ichnodisparity, ecospace occupation, and ecosystem engineering show only modest increases, with 12 architectural designs and modes of life, and nine methods of sediment modification.

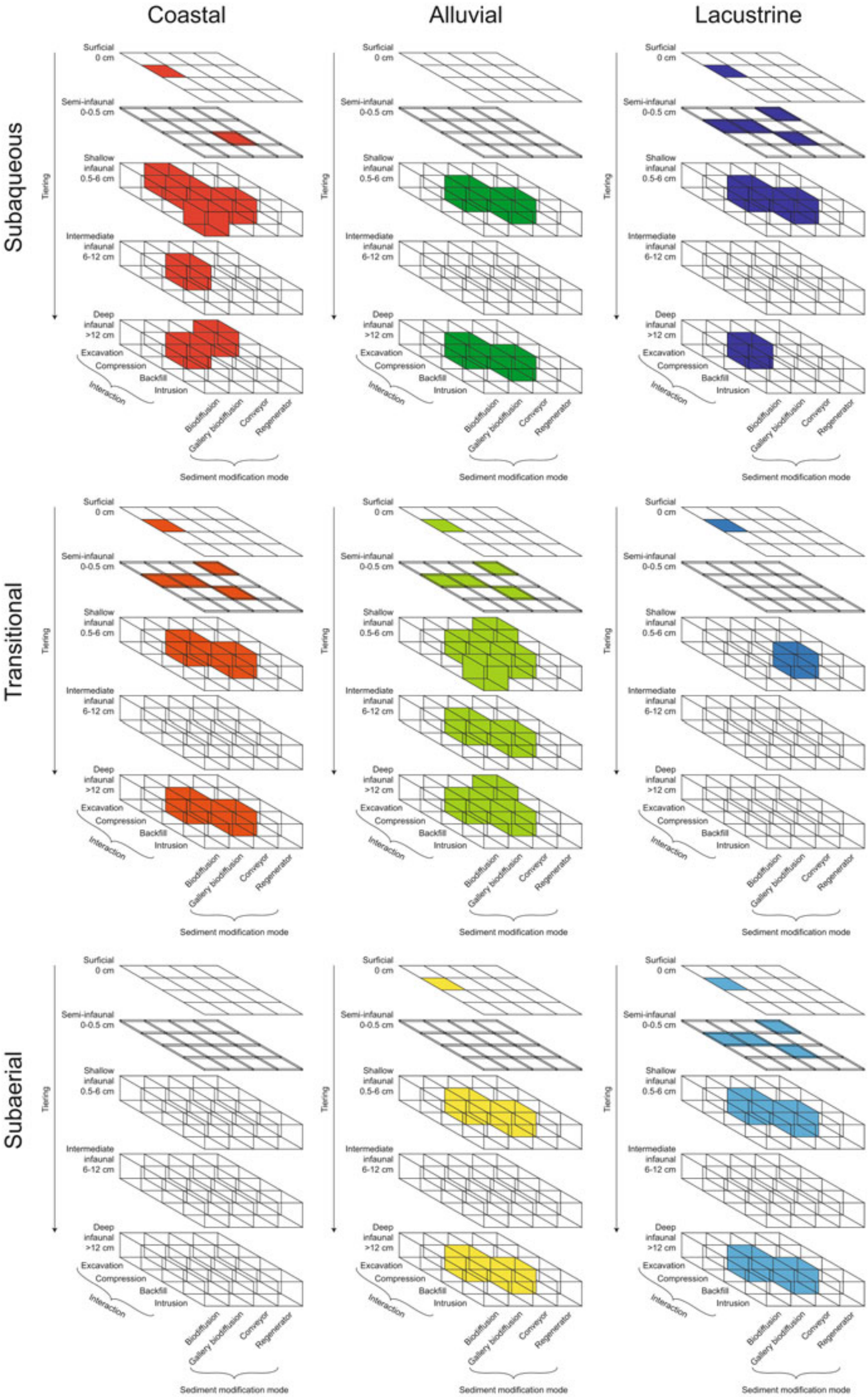

Fig. 6.15 Permian ecosystem engineering

In the surficial tier of all environments except for subaqueous alluvial environments, the presence of freely mobile, nonspecialized deposit feeders and possible predators is evidenced by a diverse array of trackways and trails (Fig. 6.14). There is no evidence of any organisms inhabiting the surficial tier of subaqueous alluvial environments. Bilobate trails and paired grooves of surficial, freely mobile, nonspecialized deposit feeders and possible predators also are found across all occupied environments except for the subaqueous settings of coastal, alluvial, and lacustrine environments. Bilaterally symmetrical, short, scratched, impressions were largely produced by freely mobile, nonspecialized deposit feeders. They occur from transitional coastal environments, transitional alluvial environments, and all related lacustrine environments. Examples that may have been formed by predators also occur in transitional alluvial environments. Surficial, freely mobile, nonspecialized deposit feeders are documented by simple horizontal trails in transitional coastal and ephemeral lacustrine environments. Those that also may have had a predatory mode of feeding additionally are evidenced from transitional alluvial environments. Simple horizontal trails produced by organisms that were likely to have been exclusively predatory were more widespread across environments, occurring from subaqueous and transitional coastal environments, transitional alluvial and subaqueous lacustrine environments, and ephemeral lakes. Some simple horizontal trails of freely mobile, nonspecialized deposit feeders extended from the surficial to the semi-infaunal tier. Such trace fossils are found in Permian transitional coastal, transitional alluvial, subaqueous lacustrine, and ephemeral lacustrine environments. The activities of these myriad organisms on the surficial tier of all occupied environments, except for subaqueous alluvial environments, remarkably, would have had little impact upon the sediment. All types of these trace fossils were produced by compression, which would have caused only minimal biodiffusive disruption to the sediment, and the effects were limited to the surficial tier (Fig. 6.15).

Simple horizontal trails also were produced in the semi-infaunal tier of subaqueous and transitional coastal environments, transitional alluvial environments, and subaqueous and ephemeral lacustrine environments. The organisms responsible were freely mobile, nonspecialized, deposit feeders that moved by backfilling and acted as sediment conveyors within the semi-infaunal tier (Figs. 6.14 and 6.15). Other organisms that inhabited the semi-infaunal tier and had the same mode of life and impact upon the sediment produced circular trails in ephemeral lacustrine environments, horizontal spiral burrows in subaqueous lacustrine environments, and simple, actively filled (meniscate) horizontal to oblique burrows in transitional coastal environments and ephemeral lakes (Fig. 6.14). Simple, actively filled (meniscate) horizontal to oblique burrows also were produced by freely mobile, nonspecialized, deposit feeders and possible predators that occupied the shallow infaunal tier of transitional alluvial and ephemeral lacustrine environments (Fig. 6.14). These organisms also functioned as sediment conveyors, and in some instances their activities extended to the deep infaunal tier (Fig. 6.15). Simple, actively filled (meniscate) horizontal to oblique burrows that extended to the deep infaunal tier occurred in transitional coastal, subaqueous, and transitional alluvial environments, eolian environments, and ephemeral lakes. Other burrows were limited in depth to the intermediate tier and are known from transitional alluvial environments. Simple, actively backfilled (massive) burrows in the shallow infaunal tier were ubiquitous across all environments that were occupied in the Permian, and were also produced by freely mobile nonspecialized deposit feeders that moved by backfilling and impacted the substrate by acting as sediment conveyors (Figs. 6.14 and 6.15). Similar organisms that may also have been predators but had the same impacts upon the sediment, were responsible for complex, actively filled (meniscate/pelletoidal) horizontal burrows in the shallow infaunal tier of subaqueous coastal and alluvial environments, transitional alluvial environments, and eolian environments (Figs. 6.14 and 6.15).

Organisms with a freely mobile, nonspecialized mode of deposit feeding and possible predatory life habits had a variety of other impacts on sediments (Fig. 6.14). These include excavating and acting as sediment regenerators, as well as creating gallery biodiffusive structures by compression, and causing biodiffusion of sediment through compression and intrusion (Fig. 6.15). Excavation and regeneration of sediment occurred in the semi-infaunal, shallow and deep infaunal tiers. In the semi-infaunal tier, this is recorded by the presence of bilobate trails and paired grooves in subaqueous lacustrine, transitional alluvial, and ephemeral lacustrine environments. Bilaterally symmetrical short, scratched burrows also were produced in transitional coastal, transitional alluvial, and ephemeral lacustrine environments. In the shallow infaunal tier of transitional alluvial environments, organisms with a deposit-feeding mode of life that excavated and regenerated the sediment were responsible for scratched, spirally coiled structures. Maze and boxwork burrows were produced by excavation, with freely mobile, nonspecialized deposit feeders and possible predators regenerating sediment from the deep infaunal tier of subaqueous coastal and transitional alluvial environments. Freely mobile, specialized deposit feeders also acted as sediment conveyors within the semi-infaunal tier of ephemeral lacustrine environments, moving by backfilling and producing branching networks (Figs. 6.14 and 6.15).

Freely mobile, nonspecialized deposit feeders were responsible for producing a variety of gallery biodiffusive structures by compression (Figs. 6.14 and 6.15). These structures included horizontal burrows with horizontal to vertical branches in the semi-infaunal tier of transitional coastal, transitional alluvial, subaqueous lacustrine, and ephemeral lacustrine environments (Fig. 6.14). The same structures also were produced in the shallow infaunal tier of transitional alluvial environments (Fig. 6.14). The same effects on the sediment were produced in the semi-infaunal tier of transitional coastal environments through the construction of isolated and serial almond-shaped burrows by freely mobile organisms that were deposit feeders but also may have been suspension feeders (Figs. 6.14 and 6.15). Gallery biodiffusive structures in the form of large vertical burrows also were produced by compression by freely mobile predators in the deep infaunal tier of transitional coastal environments, and vertical simple burrows in the intermediate infaunal tier of transitional alluvial environments (Figs. 6.14 and 6.15). In the shallow infaunal tier, horizontal helicoidal burrows in transitional coastal and alluvial environments, and spiral graphoglyptids in transitional coastal environments, represented gallery biodiffusive structures produced by compression from freely mobile organisms with a likely farming method of feeding (Figs. 6.14 and 6.15).

Within the infaunal realm, some organisms only had minimal biodiffusive impacts on the sediment (Fig. 6.15). These effects may have resulted from both compression and organisms moving by intrusion. In the semi-infaunal tier of transitional coastal environments, freely mobile, nonspecialized deposit feeders compressed the sediment to produce isolated and serially deployed, almond-shaped burrows (Figs. 6.14 and 6.15). Chevronate trails were produced by intrusion in the shallow infaunal tier of subaqueous coastal and transitional alluvial environments (Fig. 6.15). Nonspecialized deposit feeders that were facultatively rather than freely mobile occupied the shallow infaunal tier of subaqueous coastal environments (Fig. 6.14). The deposit feeders excavated the sediment to produce gallery biodiffusive structures in the form of burrows with horizontal spreiten (Fig. 6.15).

Facultatively mobile organisms largely adopted a suspension feeding or predatory mode of feeding and produced gallery biodiffusive structures by compression (Figs. 6.14 and 6.15). Vertical simple burrows were produced in the shallow infaunal tier of subaqueous coastal and alluvial environments, the intermediate infaunal tier of subaqueous coastal and transitional alluvial environments, and the deep infaunal tier of subaqueous and transitional coastal and alluvial environments (Fig. 6.14). Vertical simple burrows also are found in the deep infaunal tier of eolian environments where they were produced by facultatively mobile predators (Fig. 6.14). Passively filled horizontal burrows functioned as gallery biodiffusive structures in the shallow infaunal tier of subaqueous and transitional coastal, transitional alluvial, eolian, subaqueous lacustrine, and ephemeral lacustrine environments (Fig. 6.15). These burrows were produced by facultatively mobile suspension feeders and predators (Fig. 6.14). Vertical, single U- and Y-shaped burrows also were produced by compression by facultatively mobile suspension feeders and functioned as gallery biodiffusive structures in the intermediate and deep infaunal tier of subaqueous coastal environments, and in the deep infaunal tier of subaqueous and ephemeral lacustrine environments (Figs. 6.14 and 6.15).

### *6.5.4 Expansion of Continental Biotas During the Permian*

There was an extension of the arthropod and vertebrate fauna into new aquatic habitats during the Permian, although most of these lineages were decimated or extinguished by the Permian–Triassic ecologic crisis (see Chap. 7). Body-fossil evidence for the colonization of new habitat space principally is known from lake deposits, and to a much lesser extent river systems. Two of the most diverse Permian insect faunas—Elmo from Kansas in the USA and Chekarda from Uralian Russia—have diverse assemblages of arthropods and vertebrates that suggest a modestly developed aquatic and amphibiotic fauna. In contrast to body-fossil evidence, much of the trace-fossil evidence for Permian faunas comes from insect herbivore relationships with plants from fluvial environments.

#### 6.5.4.1 Expansion of Aquatic Continental Biodiversity

A varied ichnological literature has supported a gradual but significant increase in lentic and lotic faunal diversity throughout the Permian (Buatois and Mángano 1993a; Buatois et al. 1998a; Miller and Labandeira 2002). This diversification of aquatic biotas occurred throughout Permian Pangaea in North America (Beckemeyer 2000; Lucas et al. 2011), and Europe (Gand et al. 1997; Gaupp et al. 2000; Legler et al. 2004), in North and South China (Wartes et al. 2000; Zhao and Tang 2000), and in "Gondwanan" Pangaea (Smith 1993; Buatois et al. 1997b; Beatty 2007; Aceñolaza and Buatois 1993), including the earliest freshwater decapod crustaceans in Antarctica (Babcock et al. 1998). This legacy was disrupted by the collapse of continental aquatic ecosystems at the Permian–Triassic boundary (Wignall 2007) (see Chap. 7). During the Permian the tropical to paratropical Wet Biome diminished significantly, at least in North America and Europe, although it survived largely intact in China (Wang 1989; D'Rozario et al. 2011). By contrast, the Dry Biome, present during the Pennsylvanian (Opluštil et al. 2013), temporally overlapped with the Wet Biome, and became prominent in drier basins of the Permian as it assumed a distinctive biotal character in many habitats. The Permian Dry Biome (Tabor et al. 2013) in North America and Europe occurred in sites surrounding rivers, floodplains, ponds, and lakes; consisting of new plant and arthropod lineages that entered the continental aquatic realm and a variety of aquatic and amphibious vertebrate taxa (Beckemeyer 2000; Hotton et al. 2002; Schachat et al. 2014). Major lacustrine deposits occur at Elmo, in central Kansas, in North America (Beckemeyer 2000); at Chekarda, in Uralian Russia (Novokshonov 1998); and various Gondwanan occurrences (Schlüter 2003), such as intervals within the Newcastle Coal Measures of southeastern Queensland and northern New South Wales of Australia (Beatty 2007). The dry-biome insect and associated organisms of Lake Elmo are one of the best documented of any Permian locality.

#### 6.5.4.2 The Early Permian Dry Biome: The Elmo Biota

Aquatic continental ecosystems were transformed during the Permian, in which insect lineages became a major feature of lotic and lentic environments. The Elmo deposit demonstrates the early ecologic impact of aquatic insect lineages on lacustrine ecosystems during the mid early Permian (Artinskian) (Dunbar and Tillyard 1924; Beckemeyer 2000). This deposit consists of a playa environment proximal to a coastline in which 22 orders, 52 families and 195 species of aquatic and terrestrial insects are preserved (Beckemeyer and Hall 2007). Of these taxa, aquatic insects representing one or more developmental stage tied directly or indirectly to water consist of six orders (one-fourth), ten families (one-fifth), and 34 species (one-sixth) of the total. Trace fossil assemblages provide additional examples of insects inhabiting playa lakes of the Permian Dry Biome from a number of regions (Zhang et al. 1998; Melchor and Sarjeant 2004; Minter et al. 2007a; Avanzini et al. 2011).

Of the six taxonomic orders of aquatic insects at Elmo, the Dasyleptidae of the Archaeognatha (bristletails) represents a lineage associated with water-body margins (Mángano et al. 1997, 2001). Of the three major aquatic lineages of

Paleoptera, the Protodonata remains a holdover from the Pennsylvanian, and includes *Meganeuropsis permiana*, an insect with a 74 cm wingspan and probable endothermic metabolism (May 1982). Its naiad stage, currently unknown, would similarly have been large, based on the size of closely related meganeurid taxa from Mazon Creek (Kukalová-Peck 2009; Fig. 6.10). Elmo Odonata (dragonflies) are another order of aquatic insects, distant in ancestry to the modern dragonfly and damselfly fauna (Graham et al. 1995). The remaining paleopteran lineage, the Ephemeroptera, consisted of the Protereismatidae, known from naiad specimens in coeval beds at Midco, Oklahoma, that bore external abdominal gills that were "clearly adapted for an aquatic life" (Kukalová 1968: 326). Of the neopteran insect lineages, aquatic forms include the lemmatophorids of the Plecoptera (stoneflies), and other related species that had aquatic, detritivorous naiads, similar to their extant stonefly descendants (Beckemeyer 2000). The only Elmo holometabolan insects that had immature species tied to an aquatic ecosystem probably were the Mecoptera (scorpionflies).

The Elmo insect fauna is the earliest, well-documented fossil assemblage that possesses a reasonably diverse aquatic biota. Like other assemblages throughout the late Paleozoic, Elmo lacks aquatic herbivores. Although nearby lakeshore plants were relatively rare but typical of the Dry Biome found in coeval deposits further south (Beck and Labandeira 1998; Labandeira and Allen 2007; Schachat et al. 2014, 2015), they probably provided input that fed aquatic insect detritivory. Although there was an extensive terrestrial and amphibious biota that likely frequented lakeshore habitats (Beckemeyer 2000), the aquatic insect biota was not extensive at Elmo (Raasch 1946). Notably, there is a general absence of an aquatic vertebrate fauna as well. These absences likely resulted in foodweb shortening at Lake Elmo, which was bereft of upper-level carnivore predation. It appears that Elmo, in contrast to other Permian deposits possessing many more aquatic arthropods and vertebrates, possessed a depauperate aquatic fauna likely attributable to stressful salinity conditions.

#### 6.5.4.3 Aquatic Insects from Other Permian Localities

Other Permian localities of mostly the middle and late Permian possessed a greater variety of aquatic insects than those at Lake Elmo (Sinitshenkova 2002). Ephemeropteran naiads of the Jarmilidae are known from Obora, Czech Republic (Hubbard and Kukalová-Peck 1980), as are the Misthidotidae of Chekarda, Russia (Tschernova 1965), also occurring at Elmo. Plecopteran lineages, such as the Tschekardoperliidae, Palaeonemouridae, and Perlopseidae, inhabited lacustrine ecosystems occurring in upper Wuchiapingian deposits from Uralian Russia and elsewhere (Carpenter 1969; Riek 1973; Tillyard 1935; Sinitshenkova 1987). In several, upper Permian deposits, aquatic beetles of Schizophoridae (Coleoptera) occur, consisting of larvae and adults (Sinitshenkova 2002). The immatures of other holometabolous insects such as the alderflies and dobsonflies (Megaloptera) and caddisflies (Trichoptera) were present in aquatic communities by the end Permian (Sinitshenkova 2002). However, aquatic herbivory was still absent, in contrast to a pulse of significant herbivory on land since the Late Pennsylvanian (Labandeira 2006).

## 6.6 Discussion

Several issues emerge from this review and interpretation of the continental ichnological record during the Silurian to Permian (Figs. 6.16, 6.17, 6.18, 6.19, 6.20, 6.21, 6.22, 6.23, and 6.24). An obvious consideration is how the infaunal colonization of lacustrine environments occurred and whether there are distinctive, spatiotemporal patterns of tiering, ichnodisparity, and diversity of ichnotaxa. Related to these basic ichnologic patterns are developments among the global terrestrial and freshwater biotas during the Silurian to Mississippian that would have an effect on the ichnologic record, such as soil stabilization and nutrient supply.

### *6.6.1 Quality of the Continental Trace Fossil Record*

No discussion of trends in ichnodiversity and ichnodisparity, together with colonization of ecospace and ecosystem engineering, should be without appropriate consideration of the quality of the trace-fossil and geological records that are being scrutinized. The completeness of the geological record may bias literal reading of the fossil record and results of meta-analytical studies (Benton and Simms 1995; Smith and McGowan 2007; Kalmar and Currie 2010; Mannion et al. 2011). The general pattern for ichnodiversity across different environments demonstrates decreases from the previous period in the Silurian, Devonian, and Permian. However, the Silurian and Carboniferous (Mississippian + Pennsylvanian) are represented by similar volumes of terrestrial clastic deposits when normalized for the duration of the period, whereas the volumes are greater for the Devonian and Permian (Ronov et al. 1980). Therefore, decreases in observed ichnodiversity are unlikely to be a function of available volume of rock for study. The records for some environments are admittedly incomplete. Subaerial coastal, subaqueous alluvial, eolian and ephemeral lacustrine environments all have data on trace fossils absent from at least one geologic period and trends observed here should be treated with caution. Other environments, subaqueous and marginal lacustrine, are only represented by a short period of occupation within the range of this study, limited as it is to the Silurian to Permian. Subaqueous coastal, transitional coastal, and transitional alluvial environments all have a good trace fossil record and it is possible to be confident in the observed trends, at least at the geologic period level of analysis. Incorporating data from the prelude to continental invasion (Chap. 5) and calculating the residuals by comparing observed trends in ichnodiveristy within each of these environments to null models demonstrates that the trends are not simply an artifact of sampling. This analysis follows the approach developed by Smith and McGowan (2007) and Lloyd (2012) and uses the data of Ronov et al. (1980) as the proxy of available terrestrial clastic rock volume. The null models assume that ichnodiversity is constant through time and therefore that observed values are purely a function of the proxy, be it rock volume, number of formations, or number of

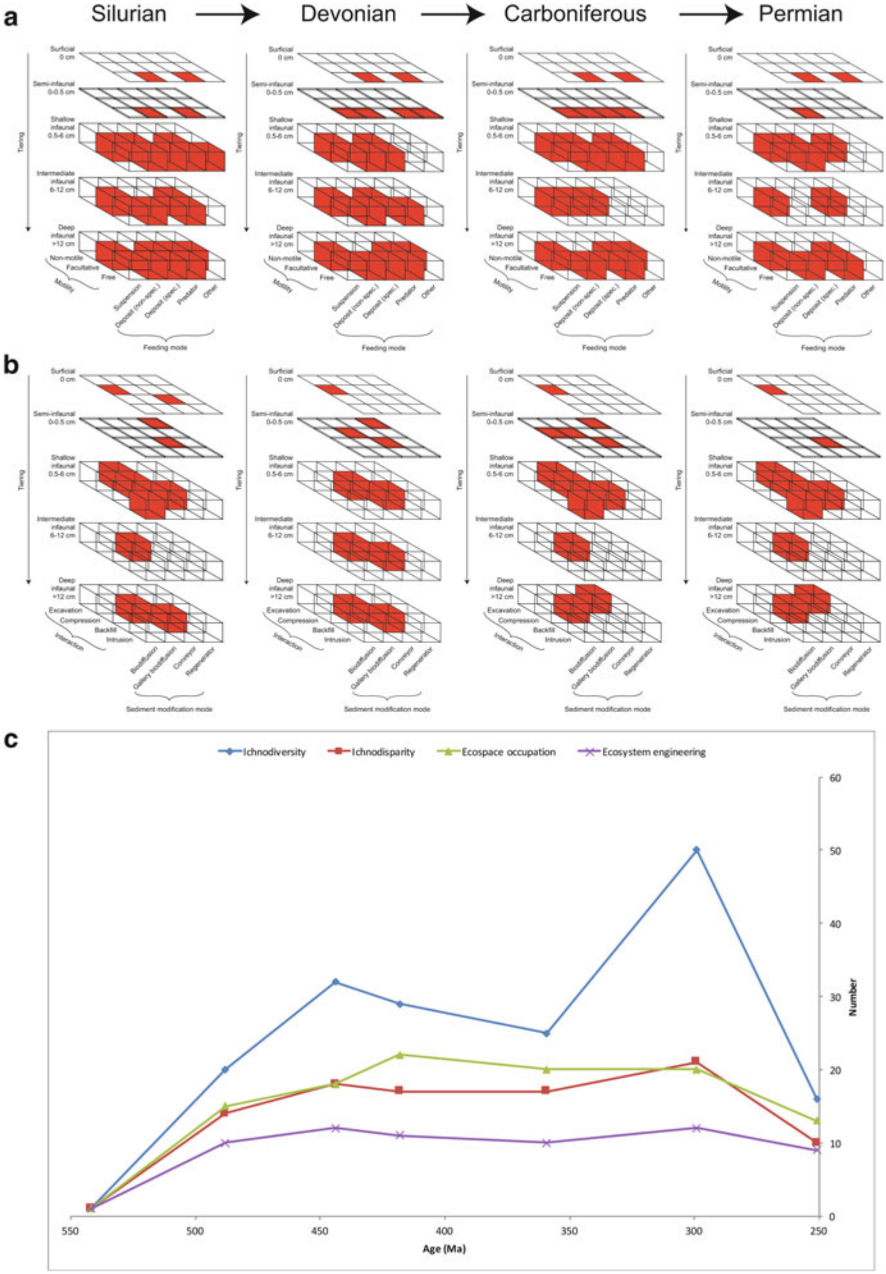

**Fig. 6.16** Colonization of subaqueous coastal environments. (**a**) Ecospace occupation; (**b**) ecosystem engineering; (**c**) plot of ichnodiversity, ichnodisparity, ecospace occupation in terms of number of modes of life, and ecosystem engineering in terms of number of modes of sediment modification for the Ediacaran to Permian

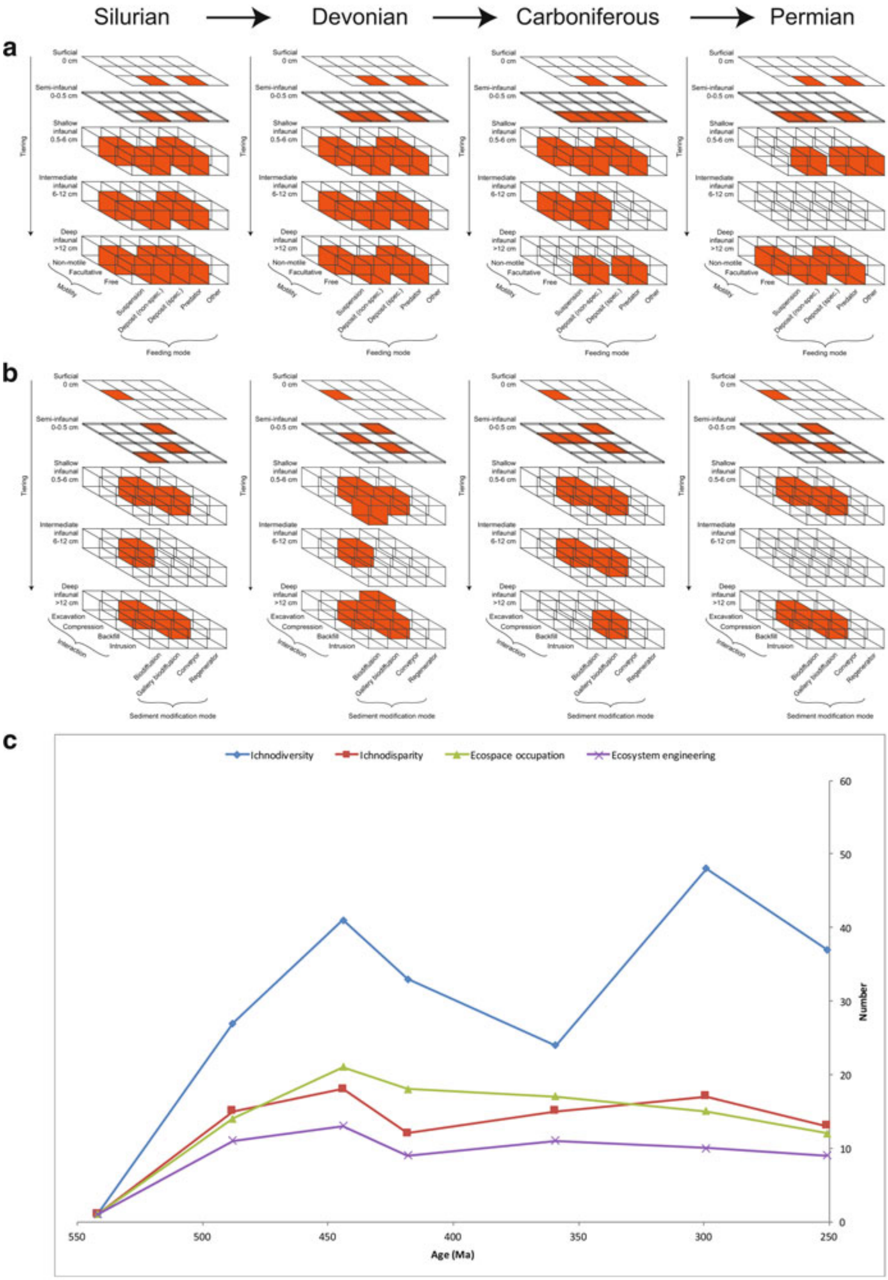

**Fig. 6.17** Colonization of transitional coastal environments. (**a**) Ecospace occupation; (**b**) ecosystem engineering; (**c**) plot of ichnodiversity, ichnodisparity, ecospace occupation in terms of number of modes of life, and ecosystem engineering in terms of number of modes of sediment modification for the Ediacaran to Permian

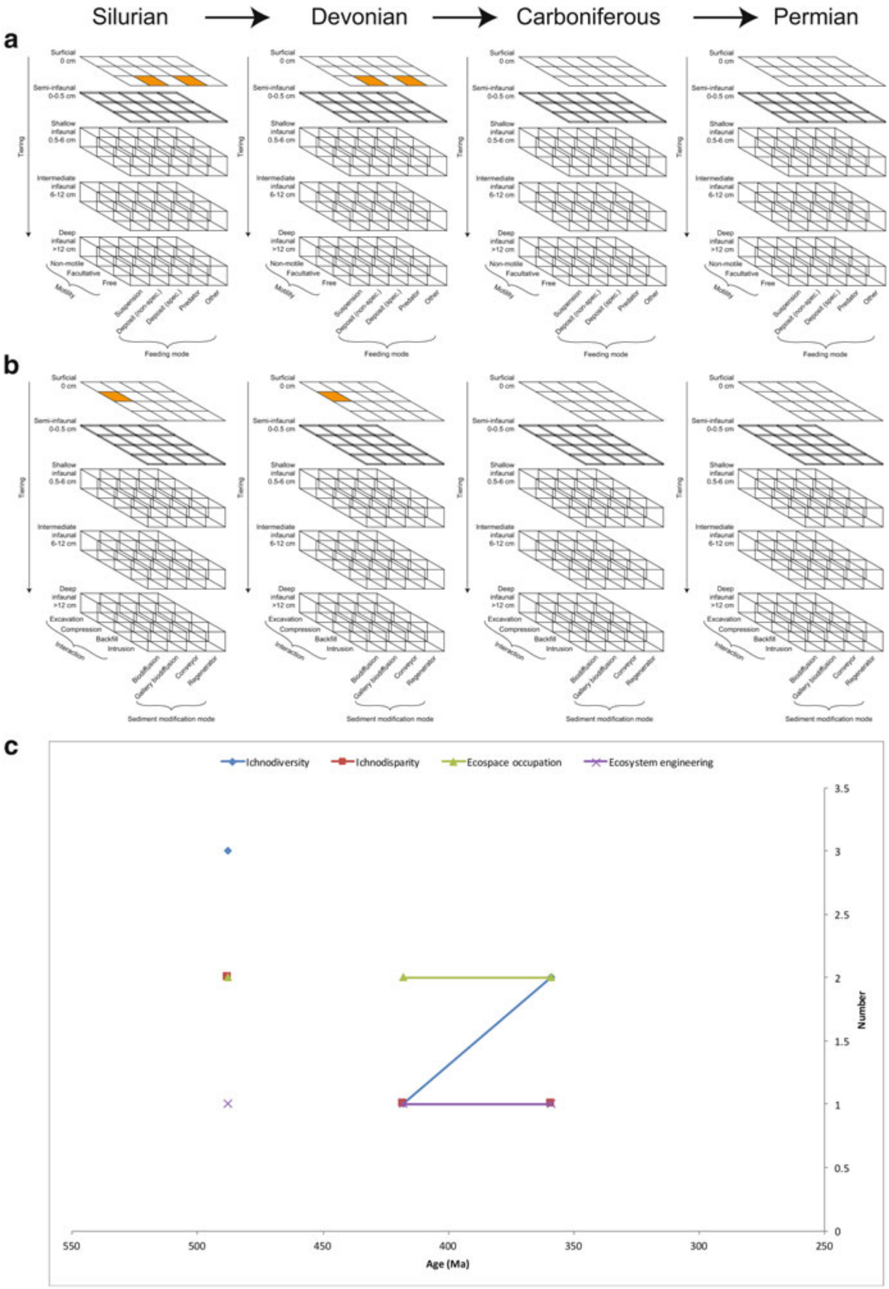

**Fig. 6.18** Colonization of subaerial coastal environments. (**a**) Ecospace occupation; (**b**) ecosystem engineering; (**c**) plot of ichnodiversity, ichnodisparity, ecospace occupation in terms of number of modes of life, and ecosystem engineering in terms of number of modes of sediment modification for the Ediacaran to Permian

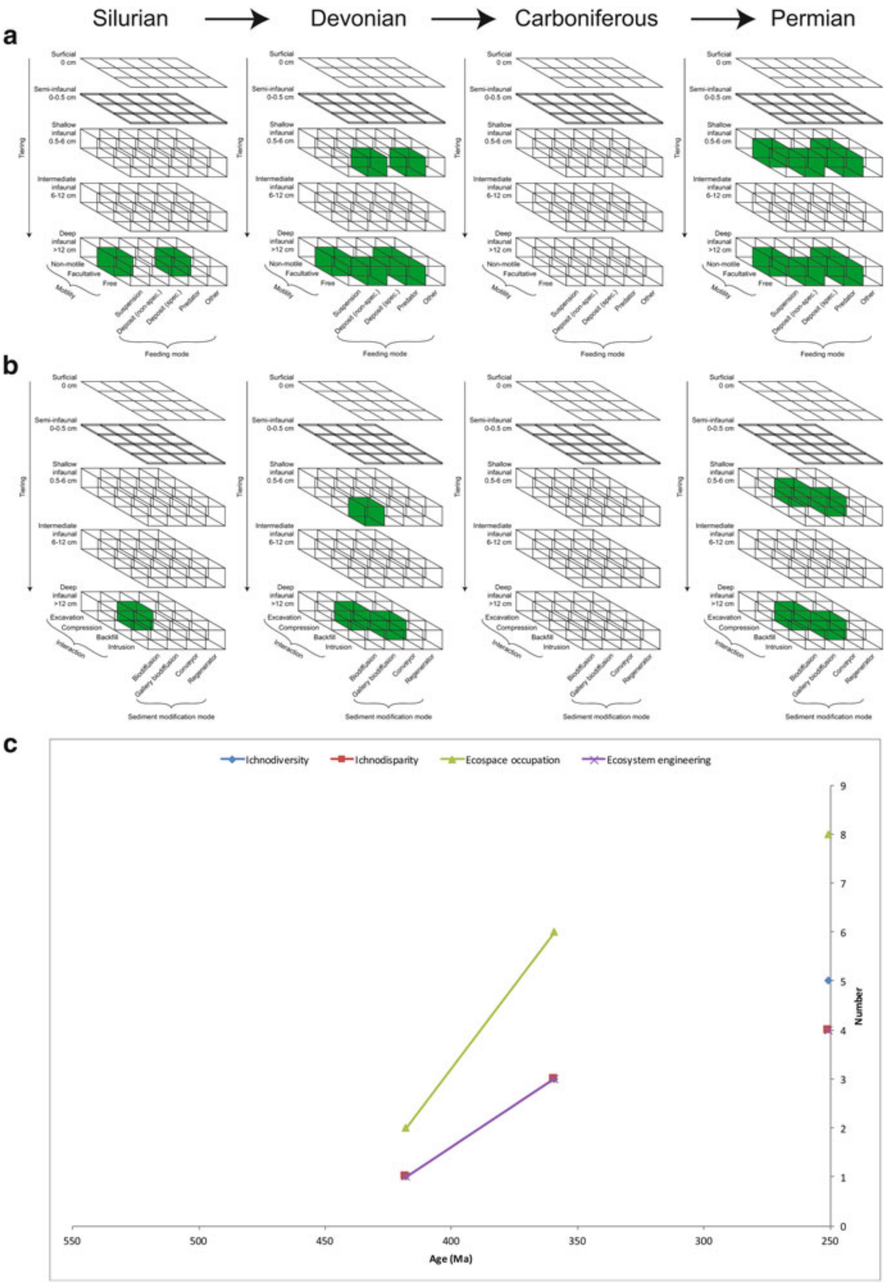

**Fig. 6.19** Colonization of subaqueous alluvial environments. (**a**) Ecospace occupation; (**b**) ecosystem engineering; (**c**) plot of ichnodiversity, ichnodisparity, ecospace occupation in terms of number of modes of life, and ecosystem engineering in terms of number of modes of sediment modification for the Ediacaran to Permian

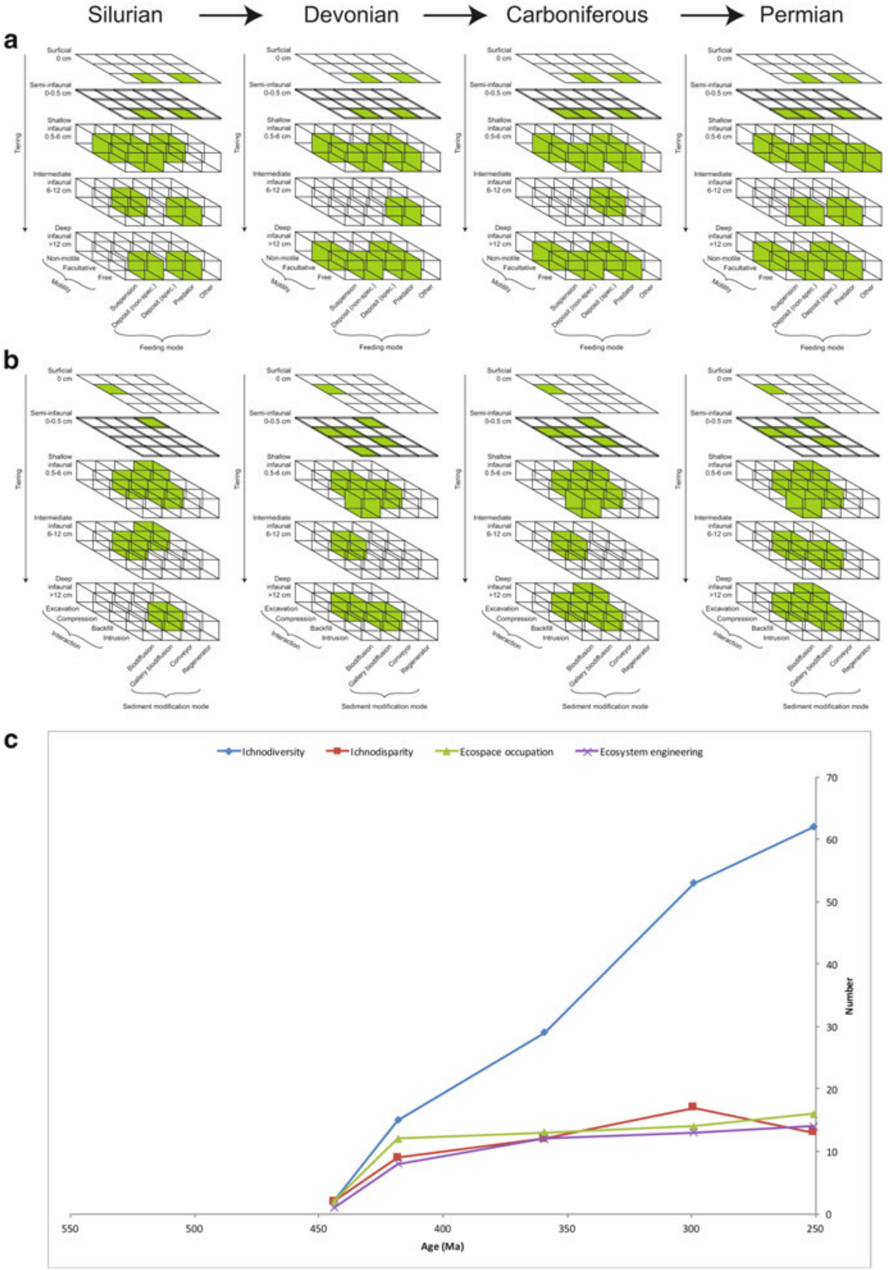

**Fig. 6.20** Colonization of transitional alluvial environments. (**a**) Ecospace occupation; (**b**) ecosystem engineering; (**c**) plot of ichnodiversity, ichnodisparity, ecospace occupation in terms of number of modes of life, and ecosystem engineering in terms of number of modes of sediment modification for the Ediacaran to Permian

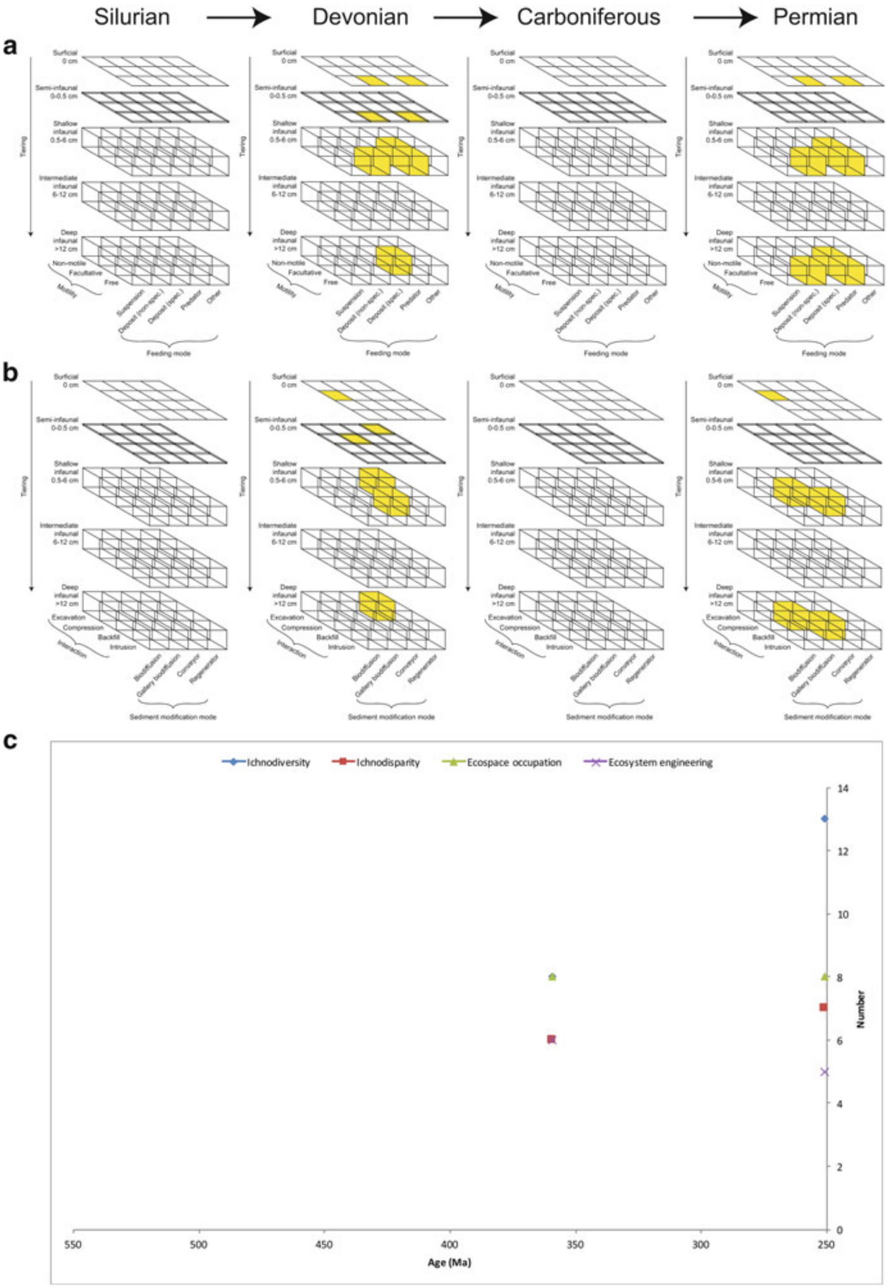

**Fig. 6.21** Colonization of eolian environments. (**a**) Ecospace occupation; (**b**) ecosystem engineering; (**c**) plot of ichnodiversity, ichnodisparity, ecospace occupation in terms of number of modes of life, and ecosystem engineering in terms of number of modes of sediment modification for the Ediacaran to Permian

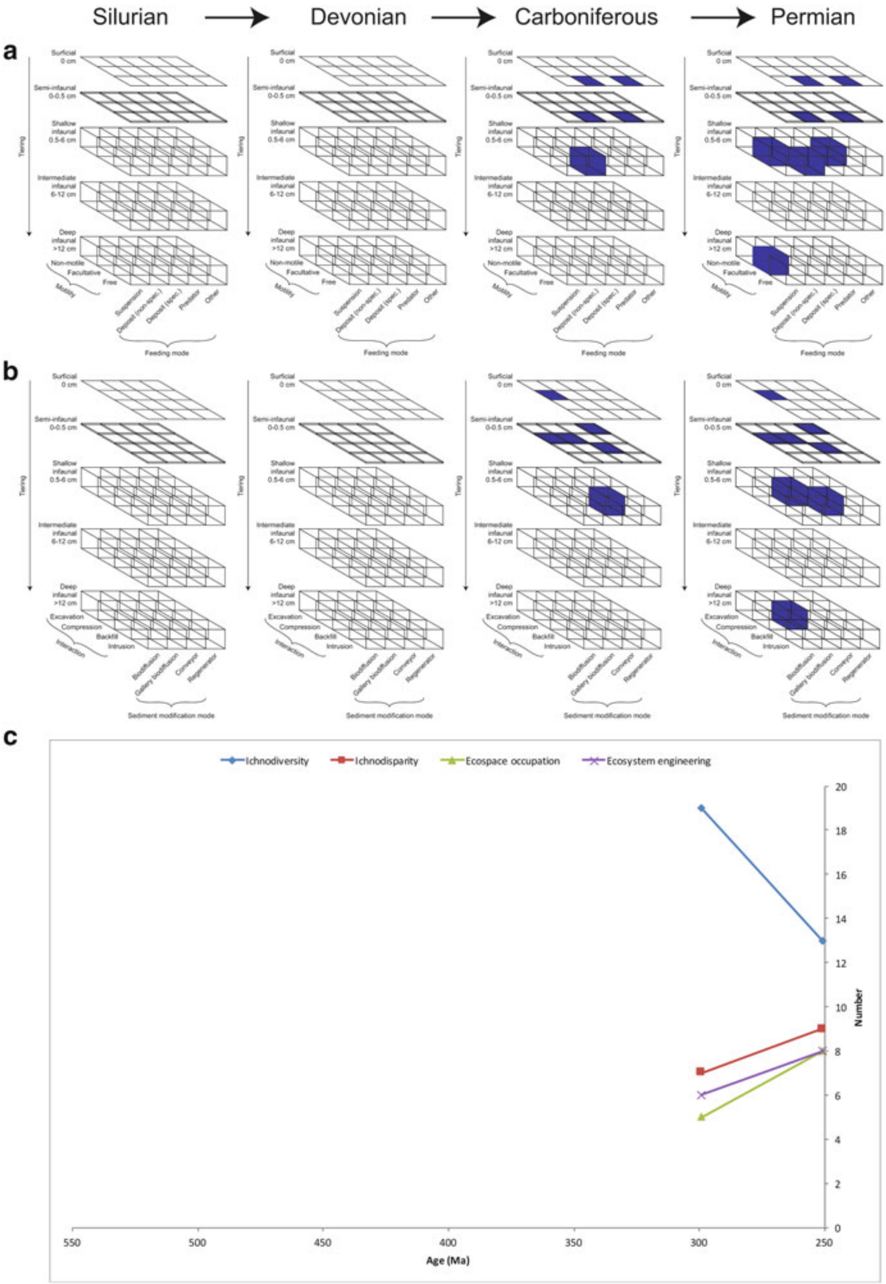

**Fig. 6.22** Colonization of subaqueous lacustrine environments. (**a**) Ecospace occupation; (**b**) ecosystem engineering; (**c**) plot of ichnodiversity, ichnodisparity, ecospace occupation in terms of number of modes of life, and ecosystem engineering in terms of number of modes of sediment modification for the Ediacaran to Permian

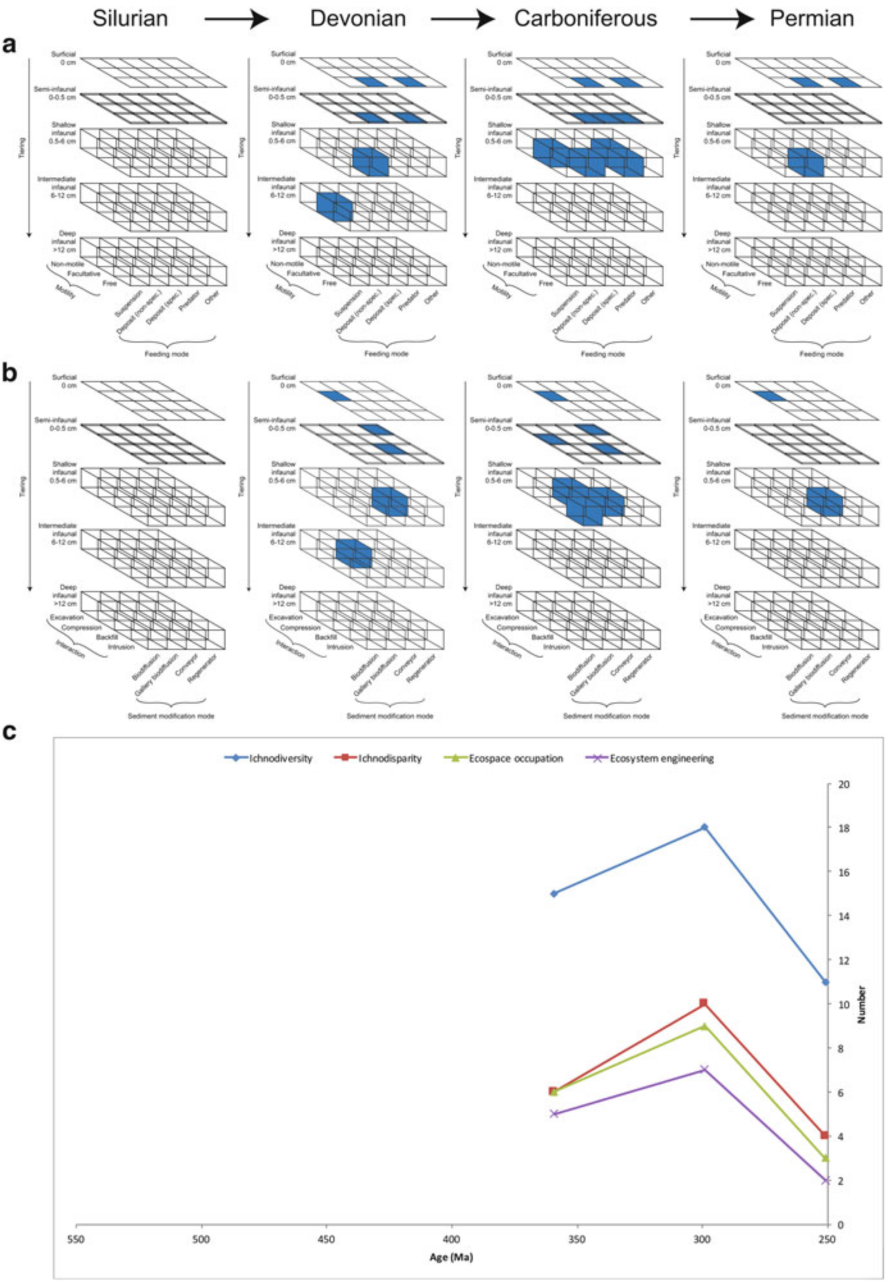

**Fig. 6.23** Colonization of lacustrine margin environments. (**a**) Ecospace occupation; (**b**) ecosystem engineering; (**c**) plot of ichnodiversity, ichnodisparity, ecospace occupation in terms of number of modes of life, and ecosystem engineering in terms of number of modes of sediment modification for the Ediacaran to Permian

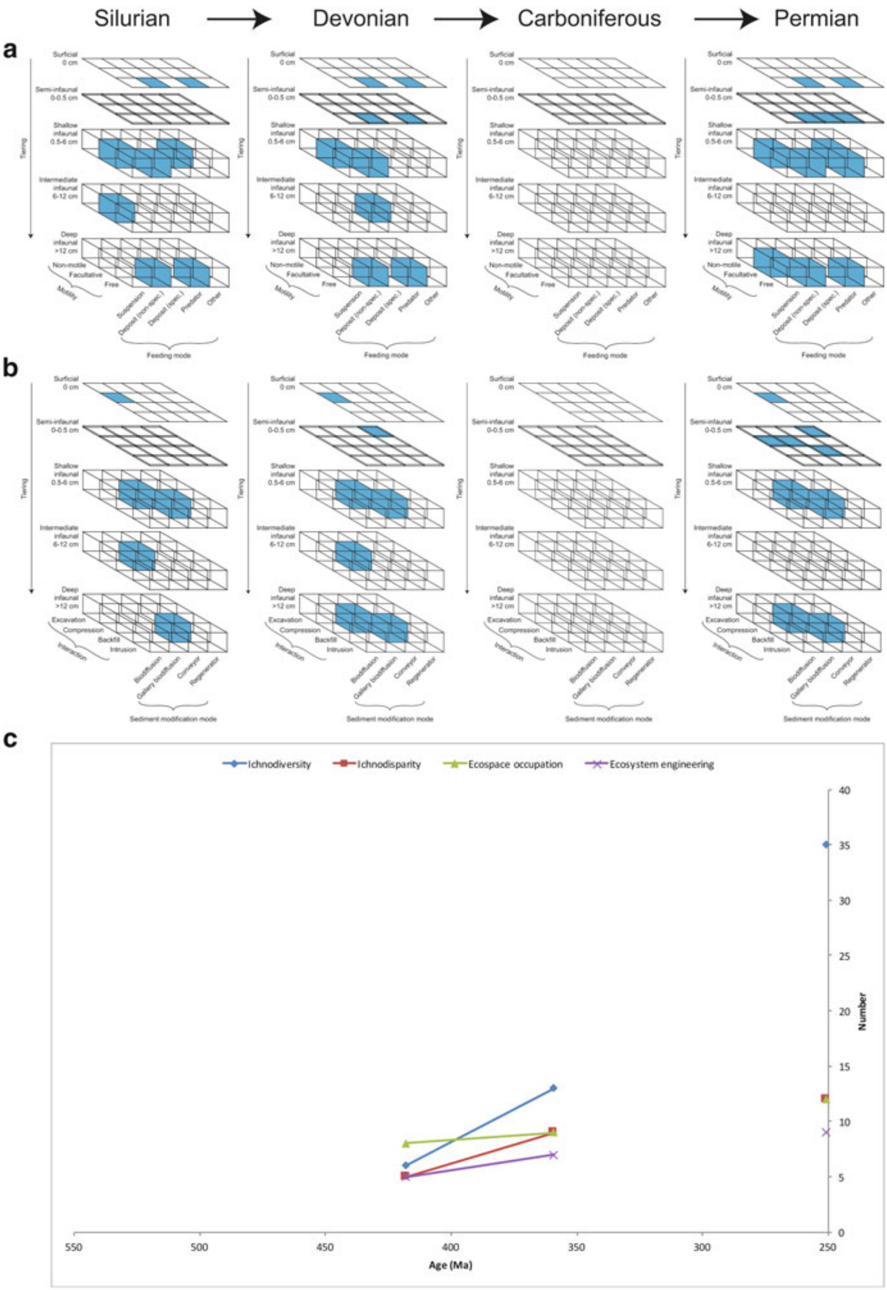

**Fig. 6.24** Colonization of ephemeral lacustrine environments. (**a**) Ecospace occupation; (**b**) ecosystem engineering; (**c**) plot of ichnodiversity, ichnodisparity, ecospace occupation in terms of number of modes of life, and ecosystem engineering in terms of number of modes of sediment modification for the Ediacaran to Permian

ichnoassemblages. Comparison of observed ichnodiversity to the null models reveals that the residuals all fall outside the (standard error) 95 % confidence intervals. This supports the notion that the observed trends cannot be explained by sampling alone and there must be some true signal within the data.

### 6.6.2 The Initial Colonization of Terrestrial Environments

The prelude to terrestrial invasion demonstrates limited colonization of subaqueous and transitional coastal environments during the Ediacaran (Figs. 6.16 and 6.17). Deeper infaunal tiers within these environments were occupied during the Cambrian and surficial organisms made amphibious forays into subaerial coastal environments (Fig. 6.18). The volume of occupied ecospace and level of ecosystem engineering increased in those environments that first had been colonized during the Ediacaran (Figs. 6.16–6.18). These features, as well as ichnodisparity, remained similar and reached a plateau in the Ordovician and across the remainder of the Paleozoic (Figs. 6.16–6.18). Transitional alluvial environments also were colonized for the first time during the Ordovician (see Chap. 5). During the Paleozoic, ichnodisparity, ecospace occupation, and ecosystem engineering in these environments reached a plateau across the Devonian to Carboniferous (Miss issippian + Pennsylvanian), but ichnodiversity shows a linear increase from the Ordovician to Permian (Fig. 6.20).

Following colonization of transitional alluvial environments during the Ordovician, trace fossils present evidence for expansion into subaqueous alluvial and ephemeral lacustrine environments during the Silurian (Figs. 6.19 and 6.24). The Devonian records the first trace-fossil evidence of organisms inhabiting eolian environments and the margins of lakes (Figs. 6.21 and 6.23). The permanently subaqueous center of deep lakes was not colonized until the Carboniferous (Fig. 6.22). This sequence of events indicates a combined landward colonization and expansion from transitional environments into permanently subaqueous and largely subaerial conditions. Colonization of the deep infaunal tier occurred in most environments during the initial invasion. For lake margins and fully subaqueous regions of lakes, the depth of initial infaunalization was limited to the intermediate and shallow tiers respectively. The extent of infaunal colonization then retreated to the shallow tier in lake margins across the Carboniferous and Permian (Fig. 6.23). Subaqueous regions of lakes show increasing infaunalization of the deep infaunal tier in the Permian (Fig. 6.24).

In general, ichnodisparity, the volume of occupied ecospace, and level of ecosystem engineering reach a plateau soon after colonization of a new environment (Figs. 6.16–6.24). The trend for ichnodiversity is more complex. It takes longer to reach a plateau, with the number of ichnogenera found globally across subaqueous and transitional coastal environments increasing from the Devonian to Carboniferous and decreasing toward the Permian (Figs. 6.16c and 6.17c). In transitional alluvial environments, ichnodiversity increases in a linear fashion throughout the Paleozoic, whereas ichnodisparity, occupied ecospace and ecosystem engineering reach an asymptote from the Ordovician to Silurian (Fig. 6.20c). Subaqueous lacustrine environments show an increase in ichnodisparity, occupied ecospace and ecosystem engineering from their initial colonization in the Carboniferous through the Permian but decrease thereafter in ichnodiversity (Fig. 6.22c). For all parameters, lacustrine-margin environments show an increase from the Devonian to Carboniferous but then exhibit a decrease to below initial levels by the Permian (Fig. 6.23c). The remaining environments do not show complete records following their colonization. Subaerial coastal environments record limited ichnodiversity and ichnodisparity and organisms are limited to the surficial tier (Fig. 6.18c). The volume of occupied ecospace and level of ecosystem engineering remained the same in the Cambrian, Silurian and Devonian. Ichnodisparity decreased, while the number of ichnogenera decreased from the Cambrian to Silurian and then increased to the Devonian. All parameters increased slightly through time in subaqueous alluvial (Fig. 6.19c) and ephemeral lacustrine environments (Fig. 6.23c), with a large increase in ichnodiversity during the Permian for the latter environment. The volume of occupied ecospace remains the same in the Permian as in the Devonian in eolian environments (Fig. 6.21c). Both ichnodisparity and the level of ecosystem engineering decreased, whilst ichnodiversity increased.

Decoupling between ichnodiversity and ichnodisparity is the result of increasing numbers of ichnogenera relative to architectural designs within the surficial tier (Fig. 6.25). An analysis of the number of ichnogenera per architectural design by tier shows that this trend remains fairly constant through time for the infaunal tiers. However, for the surficial tier, the number of architectural designs remains similar through time across different environments, but the number of ichnogenera increases, reflecting a greater rate of increase in ichnodiversity compared to ichnodisparity (a limited number of architectural designs) (Fig. 6.25). Such architectural designs include trackways and scratch marks. Trace fossil morphology is a product of three factors: producer, behavior and substrate (Minter et al. 2007c). The morphologies of trackways and scratch marks are more strongly influenced by, and therefore more reflective of, the anatomy of the producer and substrate conditions than that of behavior. The morphologies of other architectural designs of trace fossils such as simple and U- and Y-shaped burrows, and backfilled burrows are more influenced by, and therefore reflective of, behavior and substrate conditions as opposed to the anatomy of the producer. Increasing diversity of trace-making organisms therefore leads to a greater increase in ichnodiversity of surficial trackways and scratch marks than infaunal burrows. The diversity of infaunal trace-making organisms may well increase, but trace fossil records of their activity are more conservative in their morphology. As such, trends in ichnodiversity reflect an increase in diversity of producers as opposed to an increase in the number of kinds of behaviors. The number of architectural designs and ichnodisparity reflects increases in behavioral repertoires.

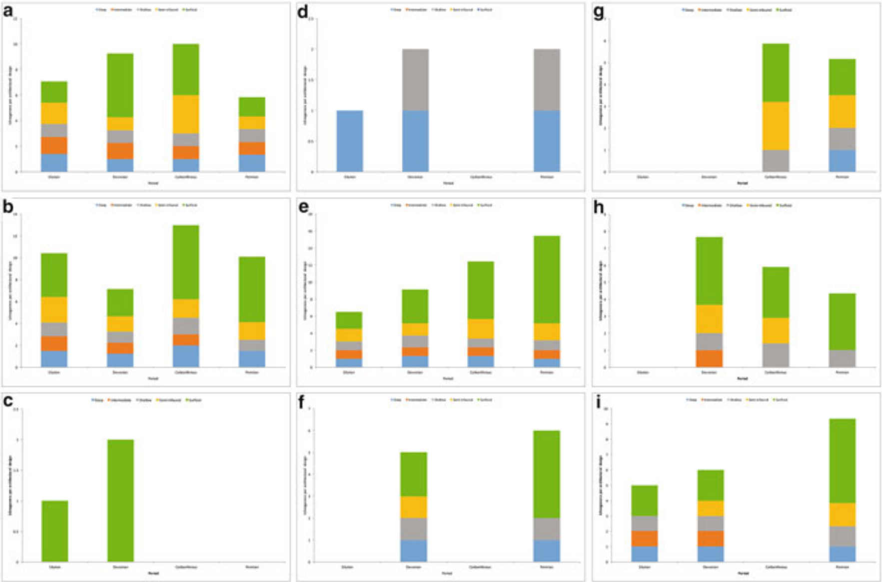

**Fig. 6.25** Number of global ichnogenera per global architectural design occupying different tiers through time in different environments. (**a**) Subaqueous coastal; (**b**) transitional coastal; (**c**) subaerial coastal; (**d**) subaqueous alluvial; (**e**) transitional alluvial; (**f**) eolian; (**g**) subaqueous lacustrine; (**h**) lacustrine margin; (**i**) ephemeral lacustrine

### *6.6.3 Emergence of the Mid Paleozoic Aquatic and Terrestrial Biota*

Many of the body fossils of terrestrial arthropod, fungal and plant lineages initially appear during the latter half of the Silurian (DiMichele and Hook 1992; Labandeira 2005). At least five groups of continental aquatic and terrestrial arthropods possessing diverse feeding habits make their first appearance at this time. These lineages include representatives from most of the major groups of arthropods that become prominent later in the Paleozoic. They are scorpions, trigonotarbid arachnids, arthropleurids, kampecarid millipedes, and centipedes (Shear and Kukalová-Peck 1990). Notably, the sixth major group, the hexapods occur shortly thereafter during the Early Devonian. Two of these groups, scorpions and kampecarid millipedes, were thought to be primitively aquatic, respiring by gills (Selden and Jeram 1989; Jeram 2001), but several lines of evidence now support terrestrial aerial respiration (Dunlop et al. 2008). Collectively, these arthropod groups are associated with a variety of aquatic, littoral and terrestrial habitats, indicated in part by trackways that have been produced by a presumed *Eoarthropleura* myriapod (Wright et al. 1995), a possible eurypterid (Marriott et al. 2009), and the ichnogenus *Paleohelcura*, which is produced by a scorpion-like arthropod (Batchelor and Garton 2013). More broadly, however, freshwater trace-fossil assemblages are referred to several ichnogenera that represent a diversity of infaunal and epifaunal habits. Commonly, these animal body-fossil and trace-fossil records occur with bacterial crusts, and land-plant debris (Trewin et al. 2012). Although inauspicious, this "phytodebris" (Gensel et al. 1990) provides evidence for major anatomical innovations in plant lineages that became important in their establishment on land during the Devonian (Wellman and Richardson 1993; Kenrick and Crane 1997).

Continental lacustrine ecosystems during the Devonian underwent major evolutionary shifts, propelled by profound changes associated with the gradual increase in the extent and reach of vegetative cover on the landscape. The increased greening of the land resulted in byproducts such as the formation of new and more vertically stratified soils, major changes in the erosion, transportation, and deposition of sediment and increased nutrient availability to colonizing plants (Algeo and Scheckler 1998; Algeo et al. 2001). These physiographic alterations match the increasing diversity and trophic complexity of emergent lacustrine and land biotas. Trophic differentiation shifted from ecosystems based dominantly on consumption largely of debris and other arthropods, to later biotas in which fungivory, saprophytism, omnivory, and especially herbivory (Labandeira et al. 2013) were added to the dietary mix (Trewin and Davidson 1996; Wilson 2006).

The Rhynie Chert of the Windyfield Chert Hydrothermal Complex in northern Scotland preserves a series of sinter lakes, features that are rarely preserved in the fossil record (White et al. 1989). The silica-rich hot-spring deposits that comprise the Rhynie Chert contain a freshwater and terrestrial biota that is diverse in plants, arthropods, fungi, and a variety of microorganisms that provide the most complete glimpse into a self-contained Devonian ecosystem. The spatiotemporally confined Rhynie Chert preserves evidence of several, major land-plant lineages, and 17 arthropod species that include crustaceans, chelicerates, myriapods, hexapods, and a euthycarcinoid (Anderson and Trewin 2003). The preservational quality of this ecosystem allows for the best assessment of the types of organisms that would have made ichnofossils in other lacustrine environments.

There are several lacustrine deposits of early Middle Devonian age preserved in northern Scotland, some of which represent deeper, more completely stratified lakes whereas others have strata that define shallower lakes. Those deposits that indicate deeper water stratification contain a rich, nektonic, vertebrate fauna and are rich in organic laminae, presumably algal derived, but lack arthropods. This spectrum of organisms in the deeper-water lakes, together with the presence of nonarthropodan invertebrates, strongly suggests the dominance of the detritivores and carnivores to the exclusion of herbivores. This heavily bimodal trophic specificity (Donovan 1980), is in stark contrast to Cenozoic and modern food webs (Dunne et al. 2014). Other lakes of the Devonian, and into the Carboniferous, include varied ichnological evidence that suggest mid-trophic-web dietary categories, such as herbivory and omnivory, were largely absent. A related issue are trackways of apterygote insects, such as *Stiaria* (Mángano et al. 1997, 2001; Minter and Braddy 2006a), and their body fossils (Shear et al. 1984; Labandeira et al. 1988), that typically occur in shallow, tidally dominated or lacustrine pond deposits of the Devonian, and extend detritivore-driven insect diets to the earlier Devonian (Labandeira 2006).

Perhaps the best example of a Mississippian lacustrine setting and its fauna is East Kirkton, in southern Scotland. This lake, persisting up to 40,000 years, harbored a rather diverse biota of stromatolites, molluscs, diverse arthropods, temnospondyl amphibians and reptile-grade tetrapods, but is bereft of fish and insects (Jeram and Selden 1993). The surrounding vegetation contained a rich assemblage of spore-bearing and seed plants. This ecosystem was characterized by an absence of active, nektonic animals within the water column, and thus its imbalance was different than that of the earlier stratified lakes of the Devonian that lacked mid-trophic-web taxa.

It has been recently argued that, because of the effects of the Late Devonian mass extinction, this initial invasion of the land ultimately failed (McGhee 2013). This view emphasizes the fact that the Late Devonian extinction event resulted in either dramatic diversity reduction or disappearance of many groups of terrestrial invaders, delaying the course of vertebrate evolution on land for approximately seven million years and, most importantly, dramatically changing the direction of vertebrate evolution. Although the impact of the Late Devonian mass extinction was definitely critical in shaping the ultimate fate of the invasion of the land, particularly regarding vertebrate communities, ichnologic information seems to suggest a continuation of the terrestrialization process across the Devonian–Carboniferous transition.

### *6.6.4 Consolidation of the Aquatic and Terrestrial Biota in the Late Paleozoic*

The earliest, well documented, terrestrial and freshwater to brackish ecosystem complex is the Wet Biome of the Pennsylvanian. This widespread, equatorial series of biotas that occupied most of Euramerica and part of Cathaysia's island continents included the noted swamp forests and other wetlands, in addition to varied lacustrine and estuarine aquatic habitats. The iconic coal-swamp vegetation was distinctive, and consisted of herbaceous plants, vines, shrubs, and a variety of trees with varied growth architectures. This vast tropical to subtropical biome also was diverse in its invertebrate (particularly arthropodan), fungal, and vertebrate taxa, consisting of virtually all of the major nonmarine lineages at that time. Notably, whereas the terrestrial component of the Wet Biome exhibited expansion of herbivory and new modes of feeding throughout the entire ecosystem (Labandeira 2001; Stull et al. 2013), the aquatic component remained as it had been since the Early Devonian. Specifically, there was an absence of herbivores, omnivores and perhaps fungivores in lacustrine and other aquatic communities that would have constituted the mid-trophic links and nodes (Dunne et al. 2014; see Chap. 13).

If the lower Permian deposits at Elmo, Kansas, and Chekarda, in Uralian Russia, are any guide, there was minimal difference in aquatic ecologic structure of the Wet Biome (Shabica and Hay 1997) and the succeeding and partly time-overlapping Dry Biome (Opluštil et al. 2013). These two deposits—Elmo and Chekarda—constitute the western and eastern margins, respectively, of the Euramerican Dry Biome that originated during the Early Pennsylvanian (Falcon-Lang et al. 2009; Falcon-Lang and DiMichele 2010; Bashforth et al. 2014). The Dry Biome was well established during the Middle Pennsylvanian, evidenced by multiple time intervals characterized by the prominence of cordaite dominated vegetation in regional floras in the Illinois Basin (Phillips and Peppers 1984; Looy et al. 2015) and xeric-dominated vegetation, including conifers, along the Variscan Deformation Front in northern Europe (van Hoof et al. 2014). This regional biome expanded considerably during the Permian. Meanwhile, the Wet Biome significantly diminished in Euramerica, where it was extinguished sometime during the mid Permian but survived in Cathaysia (D'Rozario et al. 2011), and persisted as a major element until its disappearance at, or somewhat before, the Permian–Triassic boundary. An increasing trace-fossil literature documents the expansion of ichnological diversity (Buatois and Mángano 1993a; Buatois et al. 1998a; Miller and Labandeira 2002) in lentic and lotic environments for both the Wet and Dry Biomes. This rise in ichnodiversity is paralleled by significant biotal developments, such as the earliest freshwater decapods (Babcock et al. 1998), the emergence of several new aquatic insect lineages (Novokshonov 1998), the early establishment of xeric-adapted vegetation (Falcon-Lang et al. 2009; Falcon-Lang and DiMichele 2010; van Hoof et al. 2014; Bashforth et al. 2014; Looy et al. 2015) and the expansion of plant–insect interactions (Schachat et al. 2015).

The Elmo locality documents the presence of several new insect lineages in which at least one life stage was aquatic, and occupied a playa lake along the coast of an epicontental sea (Dunbar and Tillyard 1924). This remarkable deposit, representing almost 200 hexapod species, surrounded by a rather xeric-adapted, arborescent woodland, contains the first, significantly diverse, aquatic insect biota (Sinitshenkova 2002). The terrestrial biota was well represented by herbivores (Novokshonov 1998; Shcherbakov 2000; Schachat et al. 2015; Schachat and Labandeira 2015), given studies of insect damage, insect lineages and insect faunas at relevant localities. Nevertheless, it appears that the detritivore-based Elmo and Chekarda aquatic insect faunas had not ecologically changed appreciably from the limited, earlier aquatic insect fauna of the Pennsylvanian Wet or Dry Biomes. Whereas it appears that there was greater partitioning of detritivorous resources, including possible microvores that targeted aquatic microorganisms, the aquatic component of the early Permian Dry Biome fundamentally lacked the mid-trophic-web elements of herbivores and omnivores discussed in Chap. 13.

### *6.6.5 Marine–Nonmarine Interfaces*

The concept of the "invasion of the land" may sometimes presuppose that the "land" being invaded was a passive blank space available for colonization. This formulation entails an unchanging spectrum of physical habitats, represented by those found in our modern world, combined with the idea of a clearly defined (and implicitly identifiable) physical and ecological boundary between the marine and nonmarine realms. The sedimentary record illustrates that such suppositions are categorically untrue; evidence for non-actualistic (i.e., unique to the past and evolving through time) Precambrian and early Paleozoic sedimentary environments is increasingly apparent, and the land–sea boundary is demonstrably in flux even in modern sedimentary environments and at human timescales. The physical, chemical, and biological signatures preserved in the stratigraphic record may be too opaque in some successions to decisively determine whether the environment of deposition was "marine" or "nonmarine." Nevertheless, even in locations where more clarity of interpretation is permitted, it is apparent that such prescriptive terms underplay the gradational boundary between, and the evolving internal complexity of, the two realms.

The terrestrial invasion took place during an interval of Earth history when landscapes were being fundamentally and irreversibly altered by the evolution of land plants. The dominance of unconfined, sheet-braided alluvial systems of the pre-Silurian evolved towards a greater disparity of fluvial styles, including self-organizing, mixed sand–mud meandering rivers toward the end of the Silurian (Davies and Gibling 2010a, b). Previously, pluvial events were accompanied by rapid sedimentation in rivers, with the effect that coastal fluvial environments were prone to rapid progradation into the marine realm during depositional events. By contrast, re-encroachment of the sea occurred during quiescent intervals. This two-fold pattern is analogous to modern coastlines in south Icelandic glacio-fluvial coastal plains (Davies et al. 2011). Such a scenario illustrates inherent problems with definitively identifying subaerial trace fossils in Silurian and older strata, where the land-sea interface was in constant flux and sediments were deposited in the distal coastal reaches of fluvial systems, resulting in a tendency toward marine reflooding. As such, many of the coastal trace fossil assemblages summarized here may represent composites of those emplaced under fluctuating marine and nonmarine conditions. One example of this is potentially illustrated by the *Heimdallia* horizons of the Tumblagooda Sandstone.

The dawn of more perennially stable fluvial and coastal landscapes, and the attendant increase in geomorphic complexity, such as meandering point bars, corresponds with a marked increase in ichnodiversity of alluvial environments at the Silurian–Devonian boundary interval. Davies and Gibling (2013) demonstrated that this ichnodiversity increase presaged a similar increase in alluvial ichnodiversity at the transition from the Mississippian to Pennsylvanian. In the latter instance, the significant increase in ichnodiversity coincided with another diversification in global sedimentary facies: the first evidence of avulsive fixed-channel ("anabranching") alluvial facies. Through modern analogy, it can be argued that an increasingly prevalent arborescent vegetation promoted anabranching by creating more stable landscapes and by creating potential avulsion triggers, in part through the abundance of logs in channels (Ielpi et al. 2014). Davies and Gibling (2013) also suggested that these coincident pulses in diversification of trace fossils, vegetation and sedimentary facies may be attributable to the development of new physical and chemical microhabitats. These microhabitats proliferated as the geomorphic complexity of terrestrial landscapes rose under the influence of increasingly persistent land vegetation. Ecological studies of modern alluvial environments have shown that biodiversity increases in more geomorphologically complex reaches of river systems as the sheer diversity of available physicochemical habitats dampens competitive exclusion (Ward et al. 2002). The sedimentary record suggests that analogous, stepwise, evolutionary increases in ichnodiversity are stratigraphically correlatable with the diversification of alluvial geomorphic elements (sedimentary facies) at a global scale (Davies and Gibling 2013; Corenblit et al. 2014).

## 6.7 Conclusions

The colonization of land was a major evolutionary transition. The trace fossil record for the Silurian to Permian demonstrates an explosion of ichnodiversity and expansion of benthic biotas into new environments, accompanied by the creation of new niches. Accordingly, there was a progressive expansion from coastal settings into riparian environments, paralic lacustrine to lake center environments, deserts, and the establishment of the Wet and Dry Biomes. Coupled with this were increases in diversity in animal, plant and fungal lineages. Analyses of trace-fossil data illustrate that following initial colonization of a new environment, there is a rapid filling of available ecospace and establishment of new behavioral programs represented by the creation of original architectural designs. The trends for global ichnodiversity are decoupled from this, continuing to increase for a period of time before reaching an asymptote after ichnodisparity, number of modes of life, and methods of sediment modification all have reached a plateau. The exception is in transitional alluvial environments, where global ichnodiversity increases linearly from the Silurian to Devonian and showed no sign of abating. The explanation for this is an artifact, such that trace-fossil morphology, and hence number of ichnogenera, is a function of the anatomy of the producer, its behavior, and the substrate. The increase of trace-making organisms in the surficial tier is therefore responsible for the creation of a large number of ichnogenera belonging to the architectural design of trackways and scratch marks. Lakes show a progressive infaunalization, a pattern that now will be tracked through to the Mesozoic Lacustrine Revolution (see Chap. 11).

**Acknowledgements** We thank Bill DiMichele and Ken McNamara for reviewing this manuscript, offering highly useful comments. Minter acknowledges receipt of a Government of Canada Postdoctoral Research Fellowship under the Canadian Commonwealth Scholarship Programme, which enabled the beginning stages of this work to be completed. Buatois, Mángano and Gibling were funded by Discovery Grants from the Natural Sciences and Engineering Research Council of Canada. Finnegan Marsh formatted Fig. 6.10. This is contribution 307 of the Evolution of Terrestrial Ecosystems consortium at the National Museum of Natural History in Washington, DC.

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# Chapter 7
# The End-Permian Mass Extinction

**Richard Hofmann**

## 7.1 Introduction

With an estimated species loss of more than 90 % in the marine realm (Raup 1979; Erwin 2006) and the most profound ecologic impact among all extinctions (McGhee et al. 2013), the end-Permian mass extinction (EPME) is widely recognized as the most devastating event in the history of metazoan life. Already since the mid-1990s, when paleontologic studies increasingly focused on the impact and consequences of the EPME using actual field data (e.g., Wignall and Hallam 1992; Schubert and Bottjer 1995), ichnology was recognized an important tool to reconstruct ecologic conditions during the extinction and its aftermath (e.g., Twitchett and Wignall 1996; Twitchett 1999). Today, trace-fossil data such as bioturbation indices, ichnodiversity, burrow size, or the presence of certain ichnotaxa are used as integral part of models to assess ecologic recovery (Twitchett et al. 2004; Pietsch et al. 2014). Twitchett (1999), Twitchett and Barras (2004), and Morrow and Hasiotis (2007) gave some substantial overviews on the consequences of the EPME as evidenced by trace fossils. New studies from a number of localities, as well as some new developments in the post-extinction research allow for a furthering of the discussion on ecologic consequences of this severe event and the controls of its recovery.

This chapter first reviews ichnologic studies that focused on the extinction and post-extinction interval and gives an overview on previous interpretations of this record. It is centered on the shallow-marine realm because this is the most compre-

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M.G. Mángano, L.A. Buatois (eds.), *The Trace-Fossil Record of Major Evolutionary Events*, Topics in Geobiology 39,
DOI 10.1007/978-94-017-9600-2_7

hensively studied facies range with respect to the ichnologic record of the EPME. Secondly, this chapter aims at reviving a debate that has been abandoned for some time. Recent geochemical studies linked secular changes in element-cycles as recorded in deep time to the global establishment or cessation of bioturbation. Derived from studies on modern environments, bioturbation is known to directly control geochemical pathways in host sediments on a local scale. Applied to the EPME, both perspectives reflate the debate on the extent and the impact of environmental stress during the recovery period. Using the ichnologic record of this time interval, a more intrinsically controlled scenario for the extinctions aftermath in the tradition of Erwin (1993) is underscored. Instead of interpreting the depauperate ecology, and hence, simple bioturbation to express ongoing environmental stress (Wignall and Hallam 1992; Twitchett and Wignall 1996; Wignall and Twitchett 1996; Chen and Benton 2012; Pietsch and Bottjer 2014), it is emphasized that the extinction itself may account for many characteristics observed in Early Triassic ecosystems. This change in perspective may help to revisit potential consequences of the loss in biodiversity and structural complexity at the end of the Permian, which after all, remains the best documented historical extinction scenario analogue to modern global change. Ichnology here serves as an approach that truly bridges paleobiology, geochemistry, and modern-day ecology and establishes itself as core discipline of geobiology.

## 7.2 The End-Permian Mass Extinction—A Brief Review

Whereas the loss in biodiversity (see Fig. 7.1 for latest estimates) and the huge faunistic turnover across the Permian–Triassic transition has been recognized quite early (Newell 1952; Schindewolf 1954), its causes remained dubious for a long time. With respect to crucial aspects, like timing, selectivity, and geochemical signatures, available data were too scant to distil truly testable hypotheses (see Payne and Clapham 2012). This situation changed dramatically during the eighties of the last century. Global diversity curves based on the compendium of Sepkoski (1982) became available to study taxonomic effects of extinctions. Around the same time, geochemical evidence has been increasingly implemented in paleontological research to reveal chronological constraints and underlying processes. Several trigger mechanisms were proposed for the EPME. These include global regressions (Holser et al. 1989), flood basalt volcanism (Renne et al. 1995; Payne and Kump 2007), and extraterrestrial impact (Becker et al. 2004). Given the close stratigraphic affinity of the main extinction pulses there is now some consensus that the Siberian Trap volcanism was the main driver behind the EPME (Fig. 7.2; see also Knoll et al. 2007; Bond and Wignall 2014 and references therein). Direct kill-mechanisms, however, remain debated. Mainly as a consequence of the emission of greenhouse gases during the eruptions, several have been invoked (Fig. 7.2), namely global marine anoxia (Hallam 1991; Wignall and Twitchett 1996; Isozaki 1997), hypercapnia (Knoll et al. 2007), euxinia (Grice et al. 2005; Meyer and Kump 2008), and ocean acidification (Payne et al. 2010).

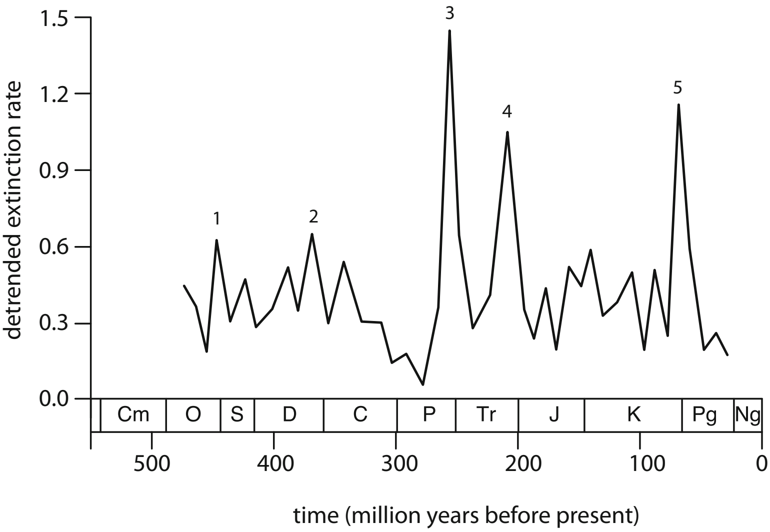

**Fig. 7.1** Extinction rates among Phanerozoic marine invertebrate genera (after Alroy 2008). *Cm* Cambrian, *O* Ordovician, *S* Silurian, *D* Devonian, *C* Carboniferous, *P* Permian, *T* Triassic, *J* Jurassic, *K* Cretaceous, *Pg* Palaeogene, *N* Neogene. *Numbers* indicate peak extinction rates that are commonly referred to as the "Big Five" mass extinctions; (*1*) end-Ordovician, (*2*) Frasnian–Famennian (Upper Devonian), (*3*) end-Permian, (*4*) end-Triassic, (*5*) end-Cretaceous

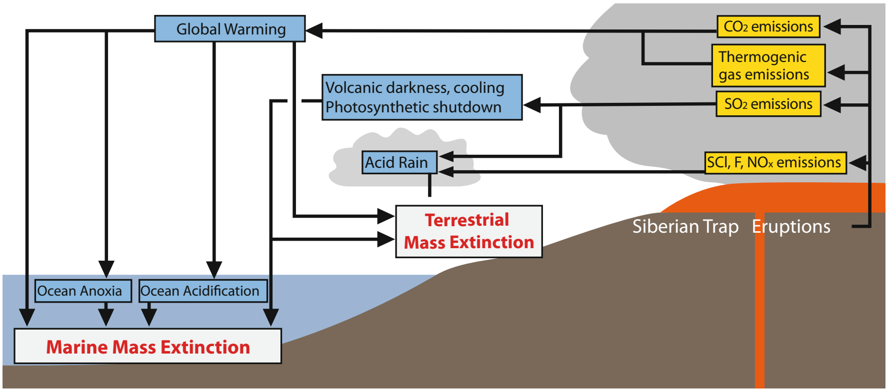

**Fig. 7.2** Schematic overview summarizing proposed main causes and effects during the end-Permian mass extinction. *Yellow boxes* indicate direct products of volcanic activity that trigger several kill mechanisms (*blue boxes*). After Bond and Wignall (2014)

Although virtually all animal groups experienced tremendous loss in diversity, extinction peaks among largely immobile, heavily calcifying clades, such as articulated brachiopods, corals, bryozoans, and echinoderms. This pattern provides some evidence that high $p\mathrm{CO}_2$ or hypercapnia would have had the most devastating effect (Knoll et al. 2007) or at least left a fingerprint in the biosphere which is easier to interpret. Yet other kill mechanisms, such as anoxia and global warming, would represent general stress factors that affected many groups alike which would explain encompassing effects on the biosphere.

The consequences of this event were first of all a dramatic loss in biodiversity (Fig. 7.1) and the large-scale degradation of marine ecosystem networks (Erwin 2001). Possibly, together with the older end-Capitanian mass extinction which is poorly constrained (Clapham et al. 2009; Clapham and Payne 2011), the event at the end of the Permian altered the taxonomic composition and the ecologic structure of metazoan life like no other event of the Phanerozoic (Sepkoski et al. 1981; Bambach et al. 2002). The rise in the dominance of the "Modern evolutionary fauna" at the expense of the "Paleozoic evolutionary fauna" (Sepkoski et al. 1981), was presumably closely linked to extinction and ecospace vacation during the EPME. There is no marked selective loss among trace fossils, and yet extinction patterns among soft-bodied invertebrates are virtually unknown.

## 7.3 Ichnology of the Extinction

### *7.3.1 Pre-extinction Ichnofaunas*

There are rather few studies that directly described ichnofaunas from uppermost Permian strata with respect to the extinction event (but see Knaust 2009). Twitchett and Barras (2004, their Table 1) gave an overview on Permo-Triassic sections that include reports on upper Permian trace fossils. All sections include a more or less diverse assemblage found in relatively well-bioturbated strata with a well-developed infaunal tiering. Typical ichnogenera include *Diplocraterion*, *Planolites*, *Rhizocorallium*, *Skolithos*, *Zoophycos*, *Chondrites*, and *Thalassinoides* (Twitchett 1999; Wignall et al. 1998; Twitchett et al. 2001; Wignall et al. 1995). More detailed ichnological analyses reporting a considerably higher diversity on the ichnospecies level are available for some older Permian strata (e.g., Bann et al. 2004). All of them report a high ichnodiversity, complex tiering structure and bioturbation indices (Taylor and Goldring 1993), ranging from ii0–6 with higher indices (ii > 3) clearly dominating (Hofmann et al. 2015a). Such assemblages typically represent mature communities with a highly developed trophic structure (Ekdale 1985; Vossler and Pemberton 1988) that become established in stable, open-marine shelf settings. Most common shallow-tier traces are that of deposit feeders (*Planolites*) and suspension feeders or carnivores (*Palaeophycus*). Middle-tier traces are represented by dwelling burrows (*Rhizocorallium* and *Thalassinoides*), deposit-feeding structures (*Asterosoma*, *Phycosiphon*, *Teichichnus*). A wide range of strategies are present in deep-tier traces including dwelling (*Thalassinoides*), deposit-feeding (*Zoophycos*, *Macaronichnus*), suspension-feeding (*Skolithos*, *Arenicolites*), or combined behaviors (*Rosselia*, *Diplocraterion*, *Conichnus*).

### *7.3.2 The Extinction Interval*

Marine invertebrate trace fossils commonly express ecologic guilds that are widely distributed among many and also notably different clades of trace makers. This makes them unlikely to actually go extinct. This is not only true for trace fossils but applies also to guilds that are recognized in body fossils (see Foster and Twitchett 2014). In fact, there is no clear pattern of extinction seen in trace fossil taxa, at least at ichnogeneric level. Many ichnogenera returned in the course of the Early Triassic or later during the Mesozoic. To date, it is unclear for most ichnotaxa whether such reestablishments reflect the colonization of surviving lineages or the "re-inventing" of ecologic strategies by other animal groups now exploring vacant ecospace. One notable exception could be *Rhizocorallium jenense*. This ichnospecies, belonging to a long-ranging ichnogenus, is typically observed in firmgrounds and emerges in the Early Triassic (Knaust 2013). This could imply that its producer occupied an empty ecologic niche.

The differences between pre- and post-extinction strata are rather expressed in a changing style and extent of bioturbation across the boundary. In most trace fossil-bearing units that straddle the extinction interval, bioturbation usually ceases completely or drops from ii5–6 to ii0–2 (Twitchett and Barras 2004; Knaust 2010; Zhao and Tong 2010; Chen et al. 2011). If present, it is typically confined to small, deposit-feeding structures, like *Planolites* (Twitchett and Wignall 1996; Chen et al. 2011) and relatively unspecific ichnogenera, such as *Palaeophycus* (Fig. 7.3f). Suspension-feeding structures are rarely recorded (e.g., small *Diplocraterion*; Knaust 2010). In all cases, complex burrows such as *Thalassinoides*, *Zoophycos*, and *Rhizocorallium* disappear (Twitchett and Barras 2004). However, it is noted that across the Permian–Triassic transition, many settings become transgressive, shifting towards more distal deposits, in which typical shallow-marine ichnotaxa may be absent anyway. However, bioturbation remains scarce across a wide variety of environments throughout the early extinction aftermath which suggests that this is a real ecologic event triggered by the extinction. The most logical explanation for the cessation of bioturbation is the collapse of benthic ecosystems (Twitchett and Barras 2004).

### *7.3.3 The Early Triassic*

Bioturbation remains scarce for a considerable amount of time after the extinction. The consequences of this event become readily apparent if the whole Early Triassic is taken into account (for geochronological constraints see Fig. 7.4). Twitchett and Barras (2004) gave a first overview on interregional recovery trajectories of trace fossils chiefly based on data from the Dolomites (Twitchett and Wignall 1996), Svalbard (Wignall et al. 1998), and East Greenland (Twitchett et al. 2001). Twitchett and Wignall (1996) have shown that bioturbation is significantly reduced or even absent throughout the Griesbachian interval, but slightly increased in the course of

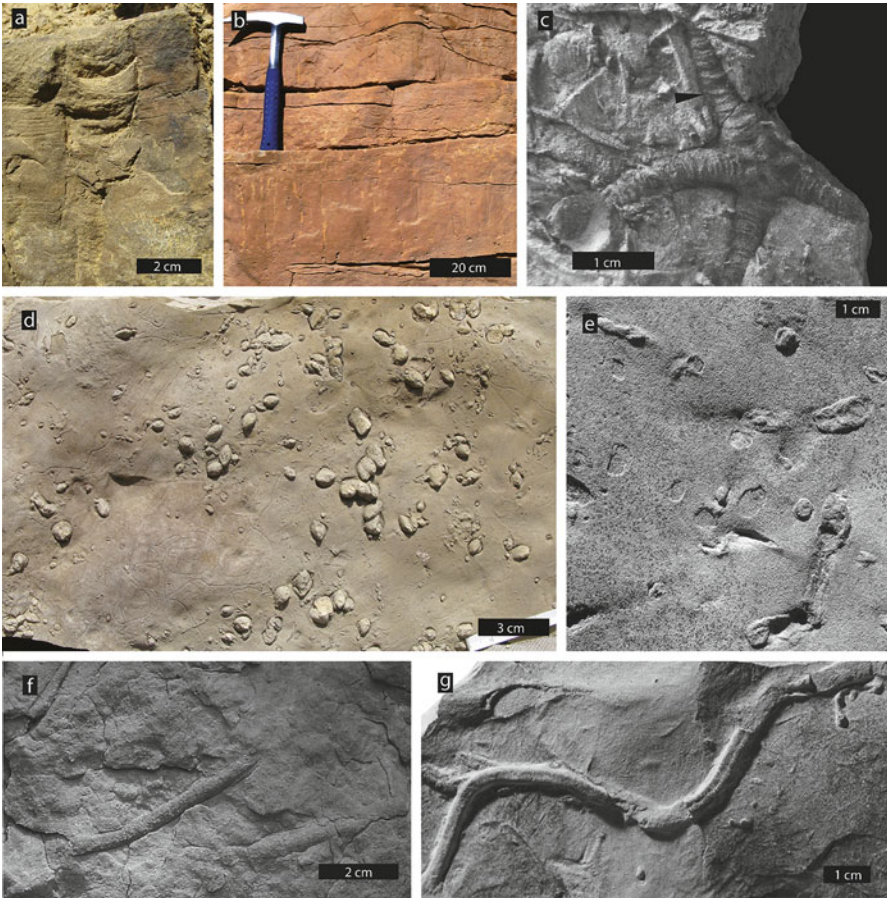

**Fig. 7.3** Some trace fossils that are commonly observed in Lower Triassic strata. (**a**) *Diplocration* isp., cross-sectional view, Dinwoody Formation, Griesbachian, Hot Springs Canyon, Idaho, USA; (**b**) *Arenicolites* isp., vertical section, Sinbad Formation, Smithian, Torrey, Utah USA; (**c**) *Asteriacites lumbricalis*, lower bedding plane view showing well-preserved transversal tube-feet scratches (*black arrow*), Campil Member, Werfen Formation, Rosengarten, Smithian, Dolomites, Italy; (**d**) *Lockeia siliquaria*, lower bedding plane view, Dinwoody Formation, Griesbachian–Dienerian, Hidden Pasture, Montana, USA; (**e**) *Diplocraterion* isp., upper bedding plane view. Virgin Formation, Spathian, St. George, Utah, USA; (**f**) *Palaeophycus tubularis* bedding-parallel view, Virgin Formation, Spathian, Hurricane, Utah, USA; (**g**) *Cruziana problematica* with well-preserved scratch traces, Virgin Formation, Spathian, Hurricane, Utah, USA

the Dienerian in the tropical Tethys (see also Knaust 2010). There is a first peak in trace-fossil diversity (five ichnogenera) around the Griesbachian–Dienerian boundary. However, earliest permanent complex burrows, such as *Rhizocorallium* (Fig. 7.5a), were firstly observed in strata not older than the Spathian (Twitchett and Wignall 1996). In contrast, permanent dwelling burrows of crustaceans (*Thalassinoides*, Fig. 7.5c), which usually indicate normal-marine conditions,

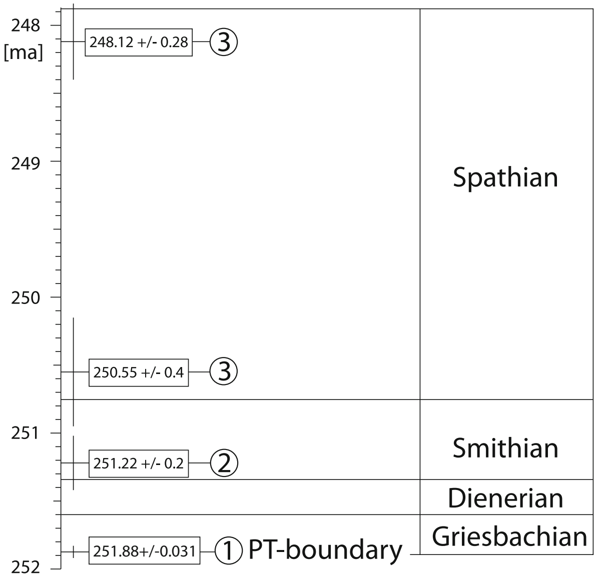

**Fig. 7.4** Geochronologic framework of Early Triassic substages. Ages in million years before present. Ages after (*1*) Burgess et al. (2014), (*2*) Galfetti et al. (2007), (*3*) Ovtcharova et al. (2006)

reappeared around the Griesbachian–Dienerian transition in higher latitudes as recorded in East Greenland and Svalbard (Wignall and Twitchett 2002; Wignall et al. 1998). This pattern led Twitchett and Barras (2004) to conclude that the recovery of tracemakers was faster in boreal marine settings when compared to those from the tropics. Data from western Canada corroborated the assertion that pace of recovery might have been largely latitude-dependent (but see Sect. 7.3.4). Several studies (Beatty et al. 2008; MacNaughton and Zonneveld 2010; Zonneveld et al. 2010) reported relatively high diversities and numerous "complex" ichnotaxa (e.g., *Spongeliomorpha*, *Rhizocorallium*, *Cruziana*, *Rusophycus*; Fig. 7.5) from mid- and high-latitude settings of the eastern Panthalassa margin during the Griesbachian. Beatty et al. (2008) have shown that these advanced ichnofaunas are confined to strata of the offshore transition zone, in which storm-waves sufficiently oxygenated bottom waters to allow oxygen-dependent trace makers to persist in an otherwise largely oxygen-deficient ocean (Wignall and Twitchett 2002). This concept of a "habitable zone" is used today (e.g., Pietsch and Bottjer 2014; Pietsch et al. 2014) to explain the presence of such diverse faunas relatively early after the extinction. Fraiser and Bottjer (2009) documented the presence of some key ichnogenera, such as *Arenicolites* (Fig. 7.3b), *Diplocraterion* (Fig. 7.3a and e) and *Rhizocorallium* (Fig. 7.5a), indicative of normal marine conditions in the Griesbachian–Dienerian Dinwoody Formation. Knaust (2010) reported well-bioturbated strata and a comparatively high ichnodiversity from upper Griesbachian deposits of the western Neotethys. Hofmann et al. (2011) described an "advanced" recovery ichnofauna,

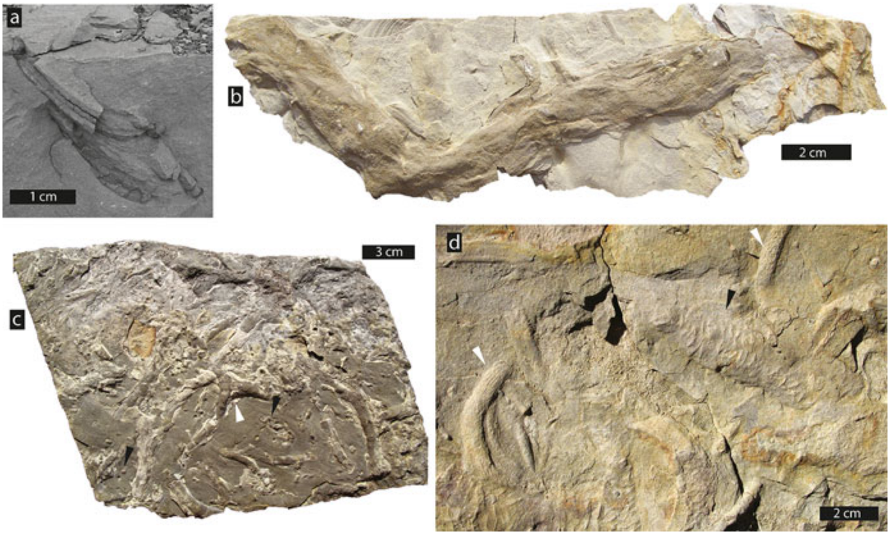

**Fig. 7.5** Some trace fossils that are usually recognized to indicate "advanced" recovery stages (sensu Twitchett 1999; Twitchett and Barras 2004). (**a**) *Rhizocorallium* isp. cross-sectional view, Virgin Formation, Spathian, Hurricane, Utah, USA; (**b**) *Spongeliomorpha* isp., bedding plane view showing preserved scratches, Seis/Siusi Member, Werfen Formation, Griesbachian–Dienerian, Rosengarten, Dolomites, Italy; (**c**) *Thalassinoides* cf. *suevicus* (*white arrow*) and *Arenicolites* sp. (*black arrow*) visible as paired circular openings, lower bedding plane view, Seis/Siusi Member, Werfen Formation, Griesbachian–Dienerian, Aferer Geisler, Dolomites, Italy; (**d**) *Rhizocorallium jenense* (*white arrows*) *Cruziana* (?*Spongeliomorpha*) *seilacheri* (*black arrow*), both showing well preserved scratch traces, lower bedding plane view, Virgin Formation, Spathian, Hurricane, Utah, USA

including *Spongeliomorpha*, *Rhizocorallium*, and *Thalassinoides* (Fig. 7.5b and c), from the upper Griesbachian of the Dolomite region in the same stratigraphic interval in which Twitchett and Wignall (1996) reported a peak in ichnodiversity. Such findings suggest that recovery of tracemakers might have been somewhat variable but was principally synchronous on a global scale with advanced ichnofaunas (sensu Twitchett 1999) becoming established in the course of the Griesbachian. The time span between the main extinction interval and the Griesbachian–Dienerian transition must be considerably less than 600,000 years (Fig. 7.4), which makes this global restoration signal even more remarkable.

During the Dienerian, ichnodiversity somewhat retreats in sections of the Dolomites (Twitchett and Wignall 1996; own observations) and western Canada (Zonneveld et al. 2010). It is currently unclear whether this is largely facies-controlled or reflects interregional setbacks in the benthic recovery. However, recent body-fossil data (Hofmann et al. 2013a, 2014, 2015b) suggest that level-bottom communities in fact experienced a notable crisis towards the end of the Dienerian. Some geochemical evidence from western Canada suggests that anoxia and dysoxia developed along the north-eastern Panthalassan shelves around this time interval (Grasby et al. 2013). Recent trace-fossil data from South China seem to corroborate such a scenario of a reset in the benthic recovery. Shi et al. (2015) reported a significant decline in ichnodiversity, burrow size, and bioturbation intensity that took place across the Dienerian–Smithian transition, followed by a rebound observed in late Smithian and Spathian deposits.

In Smithian strata, trace-fossil diversity may peak locally (see Fig. 7.6) as indicated by studies from south China (Chen et al. 2011) and Western Australia (Chen et al. 2012). Interestingly, as in the case of these two locations, relatively diverse and well-preserved trace-fossil assemblages occur in marginal-marine settings which normally impart a number of stress factors (e.g., high temperatures and strong salinity fluctuations) on benthic faunas. More open-marine settings show a considerable lower ichnodiversity during the Smithian as seen in the Dolomites (Twitchett and Wignall 1996; own observation), the western USA (Pruss and Bottjer 2004; Fraiser and Bottjer 2009, own observation), and South China (Shi et al. 2015). For the Dolomites, this is easily explained by local facies effects. The Smithian Campil Member of the Werfen Formation is almost exclusively composed of reddish siltstone and sandstone with numerous levels of contorted bedding and ball-and-pillow structures, which signal high fluvial run-off, relatively high sedimentation rates, and possibly considerable variations in salinity (Broglio Loriga et al. 1983; Twitchett and Wignall 1996). For the western USA, Pietsch and Bottjer (2014) suggested that this signal could represent different recovery patterns due to prevailing oxygen-restricted conditions in outer-shelf settings.

There are only few studies on the trace-fossil record of the Spathian. Twitchett and Wignall (1996) presented data from the Werfen Formation (Dolomites) and Pruss and Bottjer (2004) analyzed roughly coeval strata of the Virgin Formation of the Western USA. In both localities, there is an increase in infaunal tiering, burrow diameter, and trace-fossil diversity. Furthermore, fairly complex dwelling and feeding burrows, such as *Rhizocorallium* and *Thalassinoides*, become locally abundant (Twitchett and Wignall 1996; Pruss and Bottjer 2004; own observations). Hofmann et al. (2013b) mentioned a number of ichnotaxa, including *Rhizocorallium*, *Thalassinoides*, *Cruziana*, *Spongeliomorpha*, and *Ophiomorpha*, from the Virgin Formation (see also Figs. 7.3g amd 7.5a, d) which signals a certain diversification among ichnofaunas in shallow-subtidal and marginal-marine environments. Accordingly, the Spathian has been portrayed as the time interval showing the most advanced recovery as seen from both the trace-fossil (Twitchett 1999; Twitchett and Barras 2004) and the body-fossil perspective (Schubert and Bottjer 1995; Hofmann et al. 2013b). This is not surprising given the elapsed time from the extinction interval of about 1–1.5 Myr (Fig. 7.4).

### 7.3.4 Earlier Hypotheses

Twitchett and Barras (2004) suggested that some trace fossils may reappear uniformly at least among similar latitudes in the aftermath of the extinction. More recent studies, however, suggest that such patterns are ambiguous on both global and latitudinal scales (Fig. 7.6). *Rhizocorallium*, which was assumed to become

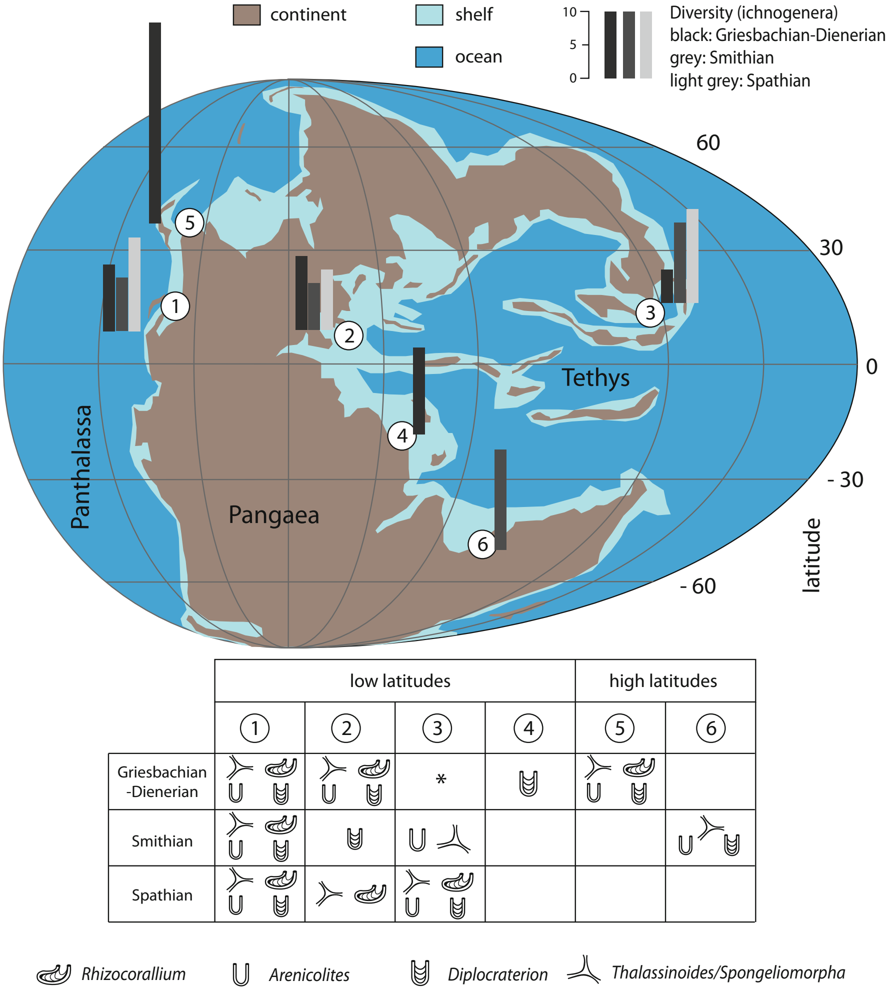

**Fig. 7.6** Global occurrences and trends in ichnodiversity throughout the Early Triassic in selected key-localities with a good trace-fossil record. Ichnodiversity and the presence of key ichnotaxa that indicate normal marine conditions are compiled from published trace-fossil reports for each localities. (*1*) Western USA (Pruss and Bottjer 2004; Fraiser and Bottjer 2009; Hofmann et al. 2013a, b). (*2*) Northern Italy (Twitchett and Wignall 1996; Hofmann et al. 2011). (*3*) Southern China (Chen et al. 2011). (*4*) Oman (Knaust 2010). (*5*) Western Canada (Zonneveld et al. 2010). (*6*) Western Australia (Chen et al. 2012). Apart from a very distinctive diversity peak observed in the Griesbachian of western Canada, trace-fossil diversities seem to change rather insignificantly with respect to latitudinal setting. Only southern China appears to be low diverse during the Griesbachian. The presence of ichnotaxa showing advanced recovery stages (Twitchett 1999) also shows no trends. *Asterisk* indicates that no traces were recorded. *Blank boxes* indicate the absence of data. Palaeogeographic restoration after Blakey (2015)

established during the Spathian in the Paleotropics, has been observed in both the western USA and the Dolomites during the late Griesbachian (Fraiser and Bottjer 2009; Hofmann et al. 2011). *Thalassinoides*, considered to be absent in the Paleotropics before the Middle Triassic (Twitchett and Barras 2004), has also been reported from the Griesbachian/Dienerian of the Dolomites and the western USA (Hofmann et al. 2011, 2013a), the Smithian of China (Chen et al. 2011), as well as the early Spathian of the western USA (Pruss and Bottjer 2004; Hofmann et al. 2013b). The occurrences of fairly deep *Arenicolites*, and *Diplocraterion* (Fig. 7.3a) recorded in the Dinwoody Formation of the western USA (Fraiser and Bottjer 2009; Hofmann et al. 2013a) and the Sinbad Formation (Fig. 7.3b) challenge the notion of deeper tiers to reappear not earlier than the Spathian (Twitchett 1999; Twitchett and Barras 2004). The stepwise fashion recovery throughout the Early Triassic, as assumed by Twitchett and Barras (2004), must be questioned. It rather seems that the first record of certain ichnotaxa is largely controlled by facies and follows no latitudinal or stratigraphic trends (Fig. 7.6). A reason for this could be that trace fossils, as highly facies dependent, may be recorded within rather narrow ranges of the lithological record. Consequently, occurrences are not uniformly distributed with respect to environment and stratigraphic position. Given the relatively few continuous Lower Triassic successions available for study, local facies effects (as in the case of the Campil Member of the Werfen Formation) may also superimpose primary recovery signals. Patterns throughout the late Griesbachian, Dienerian, and Smithian are equivocal and, besides possible global perturbation during the recovery (Hofmann et al. 2011, 2015b), governed by a multitude of factors, such as primary facies architecture and local environmental stress. What can be said with some confidence is that ichnofaunas become more complex and diverse between the early or mid-Griesbachian and the Spathian, where many ichnotaxa typical for Mesozoic shallow-marine environments have their first local first appearances.

## 7.4 Consequences

As prime evidence for animal–sediment interactions, which governs many geobiological processes, trace fossils are chief witnesses of the chain of effects set off by the extinction. Several authors (e.g., Erwin 1993, 2006; Fraiser and Bottjer 2009; Buatois and Mángano 2011; Hofmann et al. 2011, 2015a) expected that the effects of the EPME may have had tremendous impact on marine substrates and ecosystems that goes beyond the simple observation of loss in diversity and a temporary near-complete breakdown of functioning ecosystems in the marine realm on a global scale (Benton and Twitchett 2003). However, concomitant phenomena are still insufficiently explored. In the following paragraphs some potential geobiologically significant consequences of the breakdown and reorganization of benthic ecosystems caused by the EPME are discussed.

### 7.4.1 The Loss of the Mixed Layer

In modern oceanic bottoms, the mixed layer is a zone in the uppermost sediment (about 10 cm; Boudreau 1998; Teal et al. 2008), which is usually completely homogenized by infaunal activity. Biogenic mixing maintains an open interface between sediments and seawater after the depositions of sediment and thus creates a major domain of chemical recycling in the marine system (Lohrer et al. 2004). This zone "evolved" with the rise of bilaterian ecospace exploration, mainly during the Ordovician (Droser et al. 2002; Mángano and Droser 2004), and is well developed in marine shelf sediments since the mid-Paleozoic. It is usually well recognized in ancient sediments (Bromley 1996). Buatois and Mángano (2011) emphasized that the ichnologic record mirrors major evolutionary-ecologic transformations as well as setbacks with the latter being expressed by a loss of sediment reworking (Fig. 7.8). Buatois and Mángano (2011) indicated that Early Triassic trace-fossil assemblages can be viewed as far younger expressions of an ecology that is typically seen in the early Paleozoic. In fact, benthic ecosystems of the Cambro-Ordovician are notorious for their relatively simple infaunal and epifaunal tiering, prevalence of microbial mats, and relatively low rate of sediment reworking (Buatois and Mángano 2011, and references therein). By Cambrian times, such conditions mirror the true evolutionary constitution of bottom communities which are, despite the tremendous impact of the "Cambrian Explosion," characterized by restricted ecospace utilization (Droser et al. 2004; Mángano et al. 2013). During the Early Triassic, this limited use of infaunal ecospace was possibly a major result of the extinction. In fact, a number of workers have emphasized that many Lower Triassic strata show evidence of absent or very limited sediment mixing (Erwin 1993; Pruss and Bottjer 2004; Fraiser and Bottjer 2009; Buatois and Mángano 2011) in shallow-marine environments.

Following these studies and reviewing available trace-fossil material, Hofmann et al. (2015a) have shown that the mixed layer was essentially absent in most observed Early Triassic localities signified by sediments showing very low rate of bioturbation (Fig. 7.7a and b). Typical features for an absent mixed layer include: (1) evidence for cohesive substrates, (2) dominance of epifaunal and very shallow infaunal tiers, (3) absence of mottled textures, and (4) presence of microbially induced sedimentary structures. If correct, this scenario would affect the perception and the interpretation of the geological record of this time interval. Some of the potential effects of a loss of the mixed layer have been significant for many geobiological processes on a global scale (Fig. 7.8). The timing of the reestablishment of the mixed layer is currently unknown. It is likely that this process was diachronous with respect to habitat (marginal vs. shallow vs. deep marine), and was mainly controlled by the reappearance of true deep burrowers in the aftermath of the mass extinction. Hofmann et al. (2015a) noted that structures that indicate true sediment mixing begin to reappear (Fig. 7.7c and d) during the later Early Triassic (Spathian). Based on available trace-fossil material (see Hofmann

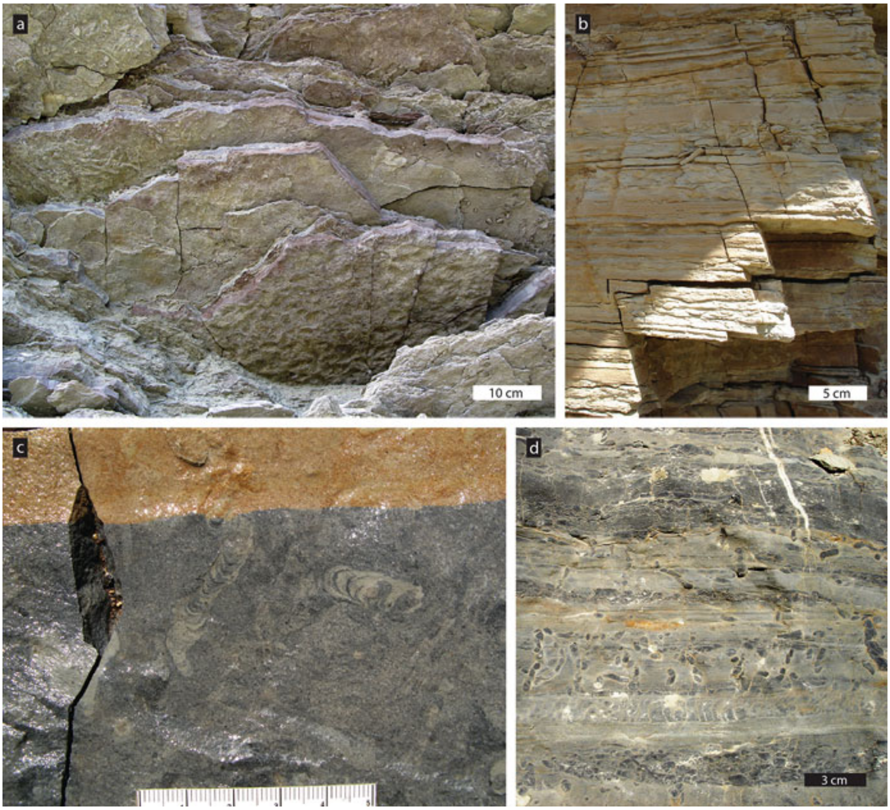

**Fig. 7.7** Typical ichnofabrics from Lower Triassic strata. (**a**) Exposed lower bedding planes showing abundant horizontal but non-penetrative, shallow-tier trace fossils. Dinwoody Formation, Griesbachian–Dienerian, Hidden Pasture, Montana, USA; (**b**) Laminated sedimentary fabric of subtidal deposits with discrete levels showing abundant horizontal bioturbation but sparse vertical reworking, late Griesbachian, lower Seis/Siusi Member, Werfen Formation, Rosengarten, Dolomites, Italy; (**c**) Mottled fabric with *Teichichnus rectus* in calcareous subtidal deposits, Early Spathian, Virgin Formation, Hurricane, Utah, USA; (**d**) Parallel-laminated and scrambled texture of calcareous subtidal deposits with abundant *Teichichnus*-type trace fossils, Spathian, Val Badia Member, Werfen Formation, Costabella, Dolomites, Italy

et al. 2015a), concomitant effects of an absent or poorly developed mixed layer are expected to have been most profound during the early aftermath of the EPME mainly involving the Griesbachian and Dienerian substages. Data from marginal-marine and terrestrial environment are relatively scarce. Thomson and Droser (2015) reported that the preferential preservation of vertebrate swim tracks associated to deltaic environments could mirror the absence of sediment mixing in the aftermath of the EPME. The impact of the loss of the mixed layer (Hofmann et al. 2015a) might have affected a much wider range of environments than the shallow marine realm.

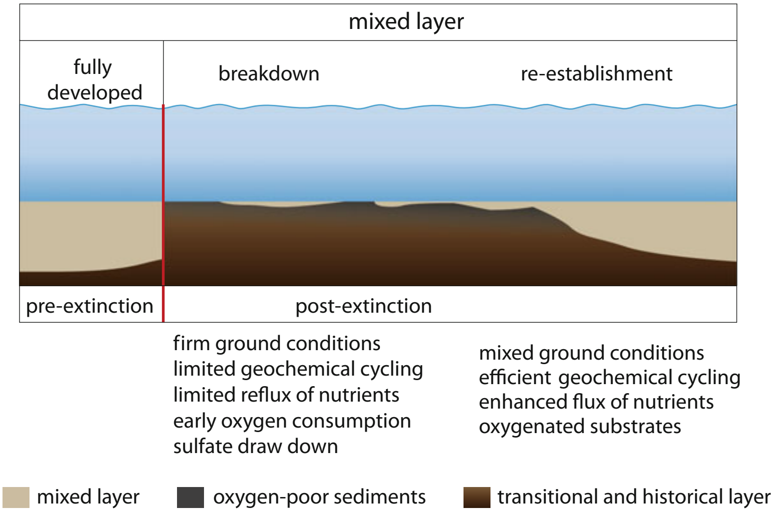

**Fig. 7.8** Geobiological effects caused by the loss of the mixed layer across the end-Permian mass extinction

## *7.4.2 The Early Triassic Anoxia Conundrum*

The question of limited bioturbation during and after the extinction is at the heart of a contentious debate that, however, has received rather little attention in recent times. Erwin (1993, p. 246) reasoned that parallel-laminated beds document the lack of bioturbators in the first place, which could have had many grounds, but essentially reflect that "most everything was dead." In contrast, Wignall and Hallam (1992) and Twitchett and Wignall (1996) regarded the absence of trace fossils (among other proxies) as evidence for anoxic seawater. It was concluded that most of the Griesbachian strata of northern Italy and the western USA signify anoxic and dysoxic seawater, which would have prevented colonization by benthic organisms. This latter view has been favored by many workers until today (see reviews in Chen and Benton 2012; Pietsch and Bottjer 2014) and much of the data have been interpreted within the context of the anoxia scenario (e.g., Beatty et al. 2008). However, studies on extant marine ecosystems demonstrate that the presence or absence of burrowing organisms has a tremendous impact on geochemical conditions of the marine sediment (see Sect. 7.4.1; Aller 1982; Solan et al. 2004) and there is a direct control of the extent and nature of bioturbation on sediment oxygenation in marine bottoms (Aller 1982; Aller and Aller 1986; Kristensen 1989). This inevitably leads to an interesting conundrum: Were Early Triassic marine bottoms anoxic due to the lack of bioturbation, or was bioturbation lacking due to anoxic conditions?

From a first glance, the seawater anoxia scenario (Hallam 1991; Wignall and Hallam 1992; Wignall and Twitchett 1996) was perceived as the leading paradigm during the last two decades. However, newer paleontologic studies have accumulated some evidence that is at variance with this anoxia model. As noted above, recent analyses on body fossils and trace fossils suggest that ecologic and partly taxonomic recovery also was much faster than previously assumed. Hautmann et al. (2011) reported a benthic fauna from microbial carbonates of South China, which well exceeded advanced recovery faunas (i.e., of the Spathian; Schubert and Bottjer 1995; Hofmann et al. 2013b) in diversity. This finding firstly questioned the idea of the resurgence of microbialites in devastated ecosystems in the presence of anoxia (Chen and Benton 2012) and, secondly, it showed that highly diverse benthic faunas (cf. Twitchett and Barras 2004) are neither restricted to Early Triassic refuges nor to younger, more advanced communities. However, it should be noted that high diversity of the Shanggan fauna and also of the Wadi Wasit block fauna from Oman (Twitchett et al. 2004) reflects a certain lagerstätten effect. In any case, this rather implies that "usual" diversities of benthic shelly faunas (e.g., Hofmann et al. 2013a) have been commonly underestimated. The body-fossil data presented by Hofmann et al. (2015b) suggest that the recovery trajectory in the Werfen Formation behaves quite the opposite of what is expected if the anoxia scenario as proposed by Wignall and Twitchett (1996) for the same localities would be correct. All these data suggest that anoxia had apparently no strong influence on the recovery trajectory as observed in concomitant faunas.

However, there has been a considerable body of geochemical evidence presented in favor of an anoxic water column during the Early Triassic. The proposed absence of profound biotic sediment reworking provides an answer to this paradox, namely that anoxic signatures in Lower Triassic sections rather reflect the shut-down of bioturbation (Hofmann et al. 2015a). If this effect of the extinction is taken into account, the interpretation of the signatures like the presence of pyrite, abundance of small-sized framboidal pyrite, $\delta^{34}S$ values, and low Th/U ratios. Pyrite is a widespread authigenic mineral phase in modern anoxic sediments (Wilkin et al. 1996), which does not necessarily require an anoxic water column, but first of all anoxic pore-waters. Also, the established relationship between seawater oxygenation and the size distribution of framboidal pyrite (Wilkin et al. 1996) may be equivocal with respect to anoxic seawater (see Roychoudhury et al. 2003). Additionally, size populations of framboids have been observed to lie well outside the strictly anoxic window (sensu Wilkin et al. 1996) in many Lower Triassic sections (Bond and Wignall 2010). Similarly, it is unclear whether or not low Th/U ratios (Wignall and Twitchett 1996) as a proxy for redox conditions apply to oxygenation of the sediment or, more strictly, the water column. Uranium usually precipitates in anoxic pore waters (Fleisher et al. 1986), which leads to low Th/U ratios. Zheng et al. (2002) have shown that Uranium is redistributed to the water column by bioturbation. Accordingly, widespread non-bioturbated sediments with anoxic pore-waters would represent a considerable sink for Uranium on a global scale. In fact, Brennecka et al. (2011) have argued the overall Th/U ratio to reflect the global signal when associated to marine carbonates. Siliclastic rocks may capture the local signal (Brennecka et al. 2011). The rocks on which Wignall and Twitchett (1996) applied the Th/U method are mainly marls possibly capturing a mixed signal. Intriguingly, their Th/U ratios seem to co-vary with bioturbation intensity, which could also suggest that bioturbation controlled Uranium release from sediments to the ocean-water column. Those signatures that are more confidently associated to seawater anoxia such as size populations of pyrite framboids (Wilkin et al. 1996; but see Roychoudhury et al. 2003) or the presence of biomarkers diagnostic for anoxic photosynthesis (Grice et al. 2005) were applied on rather short stratigraphic intervals across the extinction (e.g., Bond and Wignall 2010; Hays et al. 2007). This makes it difficult to convincingly support a catastrophic scenario involving the whole Griesbachian to be anoxic as proposed by Wignall and Twitchett (2002). Studies that investigate longer intervals demonstrate that oxygenation proxies show a rather volatile behavior throughout the Early Triassic (Grasby et al. 2013). The Cerium anomaly curve (Wright et al. 1987), which has been cited as evidence for widespread Early Triassic anoxia by Wignall and Hallam (1992), provides a very coarse resolution and thus is of little value. A more detailed study (Kakuwa and Matsumoto 2006) shows that Cerium values indicative for anoxic water are unique to levels prior to the extinction.

“Wignall et al. (2016) criticized the ‘Erwin scenario’ put forward by Hofmann et al. (2015a) by noting that benthic organisms were in fact capable of creating thoroughly mixed sediments. Hofmann et al. (2015a) did not exclude possible occurrences of intense biogenic mixing but rather noted that it is, if present, restricted to the shallowest tier of trace fossils (see also Fraiser and Bottjer 2009). Wignall et al. (2016) even noted that burrow depths usually do not penetrate more than a few centimetres into the sediment – exactly what is observed by Hofmann et al. (2015a). Finally, highly bioturbated sediments reported by Wignall et al. (2016) not only fall within assumed oxic phases but they are more or less coeval to times where benthic ecosystems seem to rebound on an interregional scale. The first presumably global restoration pulse is observed across the Griesbachian-Dienerian transition and the Early Dienerian (Hofmann et al. 2011; Hofmann et al. 2015b). The most pronounced global recovery in bottom communities is observed during the Spathian (Schubert and Bottjer 1995; Twitchett and Wignall 1996; Hofmann et al. 2015b). Both time intervals in the Svalbard sections of Wignall et al. (2016) record the highest bioturbation indices. Such a pattern may also be interpreted as a local acme in the re-establishment of surviving and also newly evolved benthic clades after the main extinction pulses at the end of the Permian and the end-Dienerian respectively (Hofmann et al. 2015b), which would lag behind the actual ceasing of kill mechanisms. The Wignall et al. (2016) scenario of an anoxia-switch to eclipse benthic organisms would be highly plausible with a fully diversified and structured background biosphere at hand. However, comprehensive faunal data (e.g. Foster and Twitchett 2014, Hofmann et al. 2014) rather show that the instalment of such conditions probably took some two million years (i.e. around the Early Spathian) when all typical Mesozoic benthic guilds became firmly established across the globe. Any time before, the proper functioning of benthic ecosystems including a vital mixed layer may have been impeded by an ecologically impoverished biosphere left by the extinction.

It is beyond the scope of this contribution to settle this debate, which I hope is to be continued. Nevertheless assuming that the loss of the mixed layer after the EPME was a real phenomenon and that sediment mixing was as important for sediment oxygenation in ancient marine ecosystems as it is for modern ones, anoxic signatures in Lower Triassic marine sediments should be viewed with some caution.

### *7.4.3 Element Recycling and Isotopic Signatures: The Sulfur Example*

The “anoxia conundrum” outlined above exemplifies the potential impact of very limited bioturbation on a number of sedimentologic and geochemical features observed shelf deposits of the Early Triassic. Decreased sediment oxygenation may be just one cumulative consequence of losing a major part of marine infaunal macroinvertebrates. With reference to studies on extant ecosystems, it can be assumed that individual elemental cycles would have been affected by the proposed breakdown of bioturbation in the aftermath of the EPME. The marine sulfur cycle may be picked as an example for an elemental cycle illustrating the influenced by biogenic sediment reworking.

In recent marine bottoms, oxidation of sulfate is intimately linked to biogenic sediment mixing and irrigation. By introducing oxygen into deeper sediment layers, bioturbation lowers the overall microbial sulfate reduction rate (Berner 1982), and by disrupting the sediment–water interface, it enhances the general reflux of sulfate back into the water column (Berner and Westrich 1985). This is typically found in diffusion-dominated (i.e., fine-grained) marine bottoms (Mermillod-Blondin 2011) which are estimated to make up about 70 % of the global marine sea floor (Lohrer et al. 2004). Thus, predicted effects include a much higher sulfur withdrawal from the marine reservoir and an increasing isotopic fractionation expressed in volatile $\delta^{34}$S behavior.

There has been an increasing awareness on the role of bioturbation in deep-time geochemical studies in recent years. Canfield and Farquhar (2009) and Boyle et al. (2014) are just two studies which attributed secular changes in elemental cycles to the emerging bioturbation during the lower Paleozoic (see also McIlroy and Logan 1999). Song et al. (2014) gave a comprehensive overview on the controls of Early Triassic seawater geochemistry with respect to sulfate. The authors highlighted that many factors contribute to this sensitive geochemical marker including carbon burial, climate, and continental weathering. The potential role of bioturbation was hardly considered by Song et al. (2014). Canfield and Farquhar (2009) proposed that the loss of bioturbation during the EPME would explain some of the effects seen in the sulfur cycle and $\delta^{34}$S curve of the Early Triassic. Hofmann et al. (2015a) concluded that global scale reduction of active sediment reworking remains a plausible scenario for this very time interval and satisfied a prediction made in Canfield and Farquhar (2009). Their model predicts that a cessation of bioturbation will result in a drop in seawater sulfate concentration and an increase in $\delta^{34}$S. This is the pattern observed with the Early Triassic isotope record of seawater sulfate showing a rapid increase from low $\delta^{34}$S values of 17‰ at the Permian–Triassic boundary to up to 38‰ in the Spathian (Song et al. 2014). Values returned to pre-extinction levels by the beginning of the Middle Triassic (Kampschulte and Strauss 2004). The integration of ichnologic and geochemical datasets strongly supports the hypothesis that reduced bioturbation and temporary loss of the mixed layer at least contributed to the transient increase in the $\delta^{34}$S of seawater sulfate (Canfield and Farquhar 2009).

### 7.4.4 Paleoecologic Implications

Marine bioturbators are recognized as ecosystem engineers that directly influence not only the chemical conditions of the sediment (see above) but significantly enhance ecosystem function as they control the “roughness” of the ecologic landscape, the availability of infaunal ecospace, the efflux of nutrients (C, N, P, Fe; Fig. 7.8), as well as the rate of primary production (Jones et al. 1994; Johnson et al. 1999; Biles et al. 2002; Lohrer et al. 2004; Solan et al. 2004; Meysman et al. 2006; Caliman et al. 2007; Mermillod-Blondin 2011). Based on the proposed non-mixing scenario (Erwin 1993; Hofmann et al. 2015a; see Sect. 7.4.1), it can be assumed that, compared to other time intervals characterized by a highly structured biosphere, Early Triassic sea floors held some intricacies for benthic organisms, such as relatively high sediment shear strength, reducing conditions within the sediment (Aller 1982) and low secondary production (Foster and Twitchett 2014). Reducing conditions and high shear strength would represent barriers impeding infaunal colonization as well as opportunities for adapted biota. Admittedly, this is rather speculative but such a scenario might explain several peculiarities observed in Lower Triassic strata, such as (1) the unusual dominance of byssally attached epifaunal bivalves in many fine-grained (i.e., supposedly softground), Early Triassic bottoms (Fraiser and Bottjer 2009), and (2) the virtual absence of deep infaunal guilds (Foster and Twitchett 2014; Hofmann et al. 2015a). If correct, the reestablishment of the mixed layer may be closely linked to the recovery of organisms that invade deeper-infaunal tiers in largely cohesive substrates.

As far as bivalves are concerned, there seems to be a dominance of shallow-infaunal forms (Foster and Twitchett 2014; Hofmann et al. 2015a), which just insignificantly contribute to sediment mixing as they colonize only the upper few centimeters of the substrate just below the sediment–water interface. The radiation of siphonate, deeply burrowing bivalves, which are among the prominent sediment mixers in modern environments, is a chiefly Mesozoic affair (Stanley 1968) (see Chap. 9). Possible members of the respective families first appear in the late Early Triassic (Hautmann et al. 2013). What is also striking is the absence of infaunal deposit-feeding bivalves during the Early Triassic (Foster and Twitchett 2014)—a group which typically inhabits Mesozoic softgrounds (Aberhan 1994). Taken together, this suggests that respective biota begin to explore this adaptive zone in course of ecospace expansion during the recovery in tandem with emerging sediment mixing (Hofmann et al. 2015a).

Another group of important marine bioturbators are crustaceans that are able to colonize cohesive substrates because of their ability to modify firm sediment with their hard appendages (Savazzi 1994) (see Chap. 9). During the Early Triassic, typical crustacean-produced ichnogenera, such as *Thalassinoides* and its firmground equivalents *Spongeliomorpha*, may be locally common in shallow-marine substrates, but never penetrate deeply into the sediment (Hofmann et al. 2015a and references therein). Especially members of this group could serve as ecosystem engineers that actively irrigate marine sediments. A functional much more important group are infaunal deposit feeders that actively move through the sediment and by ingesting particles are responsible for a major part of mass and energy transfer within benthic ecosystems (Lohrer et al. 2004). First of all, respective trace fossils are virtually absent in Lower Triassic successions, and Foster and Twitchett (2014) documented a decrease and a generally low abundance of such guilds across the extinction and a first increase across the Early–Middle Triassic boundary.

Low primary productivity and a decoupling of benthic/planktonic-ecosystem function (Caliman et al. 2007) could result from limited sediment mixing. This is hard to test for the Early Triassic but it has been speculated that low primary productivity was prevalent during some Early Triassic intervals (Twitchett 2007). However, there is also some evidence presented in favor of the opposite scenario (Meyer et al. 2013). Furthermore, Foster and Twitchett (2014) noted that if bioturbation depths receded to shallow levels, this may have impacted nutrient cycling and secondary production would have been significantly reduced.

A largely ignored consequence of the near complete breakdown of bioturbation as well as the generally low biodiversity is that established paleocologic models (e.g., Savrda and Bottjer 1986) forfeit much of their predictability (see Fig. 7.9). Models that use biodiversity, ecosystem complexity, as well as ichnologic data to infer on environmental conditions may only work with a sufficiently developed "background biosphere", which is clearly not the case in the aftermath of the biggest

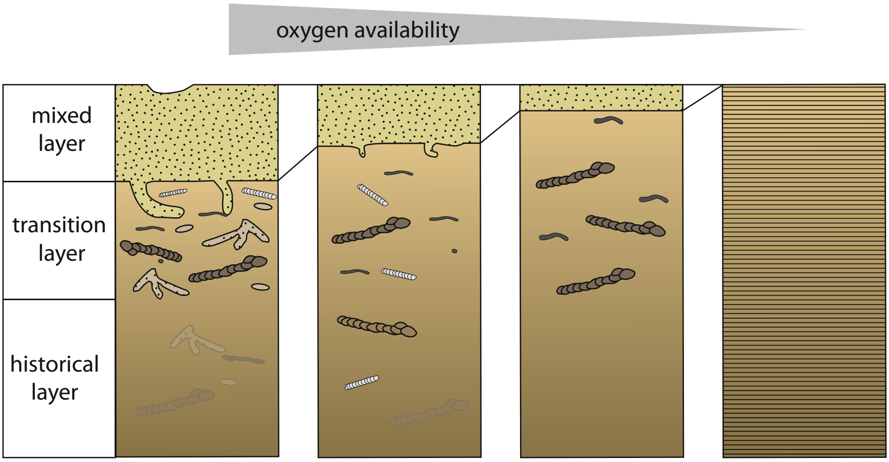

**Fig. 7.9** The oxygenation model after Savrda and Bottjer (1991). It predicts that bioturbation intensity, ichnofaunal composition, and penetration depth is a direct function of oxygen content of the near bottom water column. The model found broad agreement and is widely used for environmental analysis using trace fossils as an indicator. The problem is that it largely relies on an intact or sufficiently developed "background" biosphere, from which bioturbators can be recruited if environmental conditions allow them to colonize the substrate. However, this might be not the case for times with special macroecologic/evolutionary framework conditions such as the Ediacaran, the lower Palaeozoic (McIlroy and Logan 1999) and aftermaths of extinction events (Buatois and Mángano 2011; Hofmann et al. 2015a) when a considerable portion of the metazoan diversity is missing

mass extinction of the Phanerozoic. McIlroy and Logan (1999) noted similar feedback mechanisms between sediment oxygenation and bioturbation to be applicable with respect to expansion of biota into infaunal ecospace during the Early Paleozoic and these authors explained several geochemical anomalies and the decline of Precambrian taphonomic pathways with the absence of sediment mixing.

## 7.5 Outlook

The devastating EPME has had consequences that go well beyond the simple loss of biodiversity and ichnodiversity. Of course, some of these ideas are partly speculative as the understanding of extant ecosystem function is still limited and, probably more important; the application of such principles to ancient ecosystems is ambiguous at best. However, there has been a growing mutual interest of deep-time geochemists (Logan et al. 1995; Canfield and Farquhar 2009; Shen et al. 2011; Boyle et al. 2014), paleobiologists (McIlroy and Logan 1999; Fraiser and Bottjer 2009; Hofmann et al. 2015a), and ecologists (Meysman et al. 2006) to resolve the interconnections on an evolving planet. The analysis of trace fossils is central in bridging these disciplines. The EPME and subsequent recovery represents one of the rare deep-time test cases to reveal various feedback mechanisms between biosphere and geosphere.

**Acknowledgements** I would like to thank Gabriela Mángano and Luis Buatois for inviting me to contribute to this volume. The observations that allowed me gaining some understanding of Early Triassic ichnology were essentially made during my Ph.D. project at the University of Zurich. The funding was provided by the Schweizer National Fond awarded to my thesis advisor Michael Hautmann (SNF-projects: 200021_121774/1 and 200020_1403501/1). I thank Martin Schobben (Museum für Naturkunde Berlin, Germany) for his advice regarding clarification of geochemical issues. The comments by the reviewers Dirk Knaust (Statoil Norway) and Matthew Clapham (University of California, Santa Cruz) greatly improved the manuscript.

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© Springer Science+Business Media Dordrecht 2016
M.G. Mángano, L.A. Buatois (eds.), *The Trace-Fossil Record of Major Evolutionary Events*, Topics in Geobiology 39,
DOI 10.1007/978-94-017-9600-2