# 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

N.J. Minter (✉)
School of Earth and Environmental Sciences, University of Portsmouth,
Burnaby Building, Burnaby Road, Portsmouth, Hampshire PO1 3QL, UK
e-mail: nic.minter@port.ac.uk

L.A. Buatois • M.G. Mángano
Department of Geological Sciences, University of Saskatchewan,
114 Science Place, Saskatoon, SK S7N 5E2, Canada

R.B. MacNaughton
Geological Survey of Canada (Calgary), Natural Resources Canada,
3303–33rd Street NW, Calgary, AB T2L 2A7, Canada

N.S. Davies
Department of Earth Sciences, University of Cambridge,
Downing Street, Cambridge, Cambridgeshire CB2 3EQ, UK

M.R. Gibling
Department of Earth Sciences, Dalhousie University, Halifax, NS B3H 4R2, Canada

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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

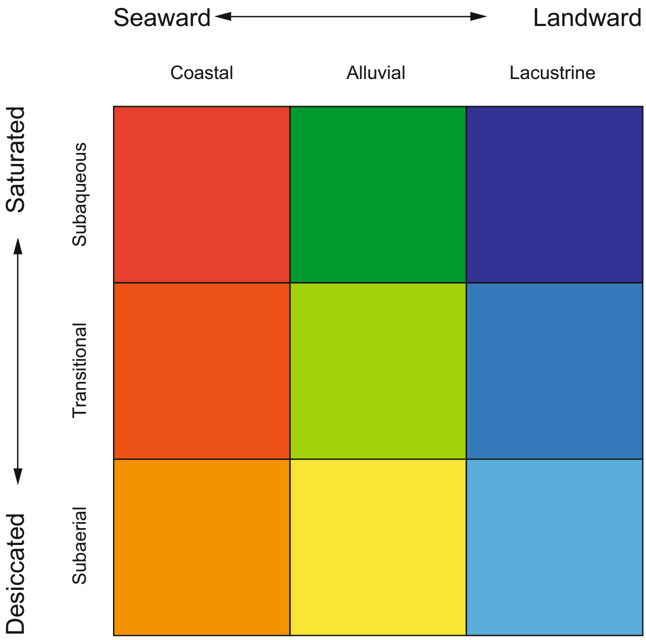

**Fig. 5.1** Environmental framework for analysis of depositional settings

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

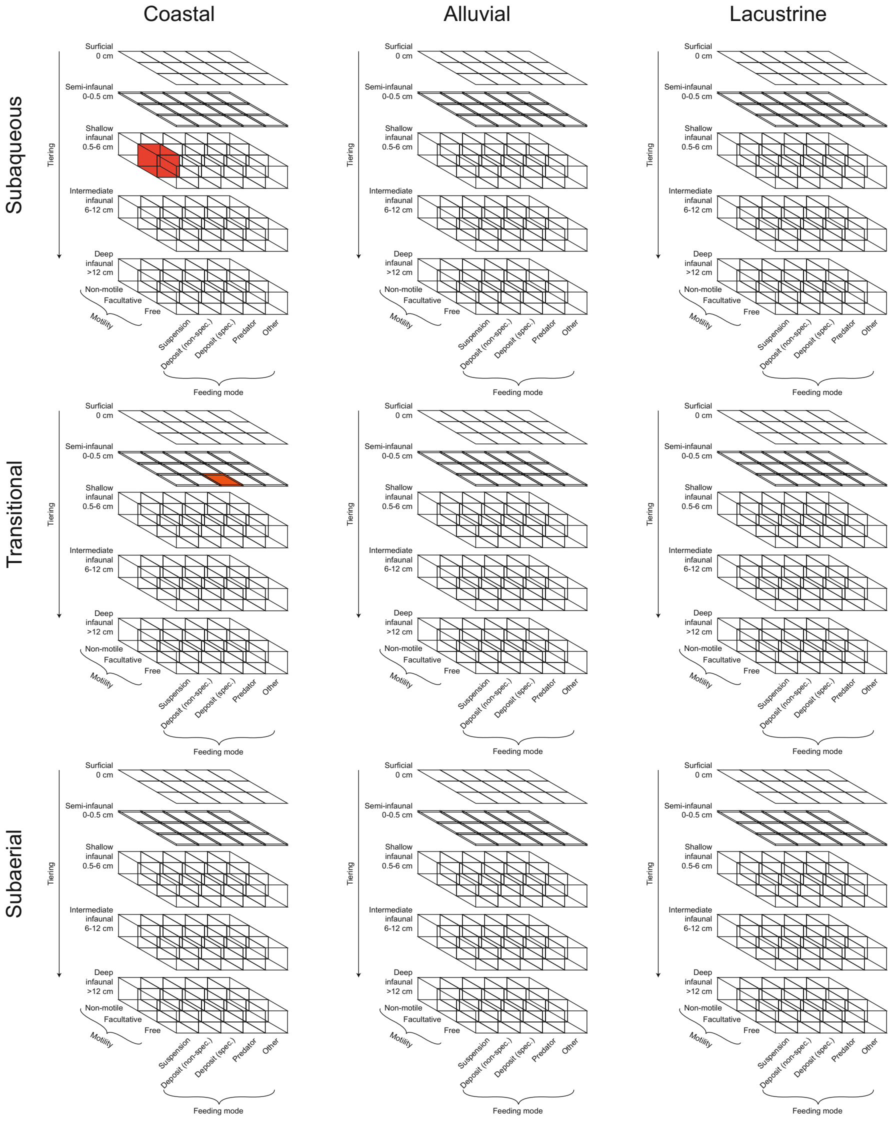

**Fig. 5.2** Ediacaran ecospace occupation

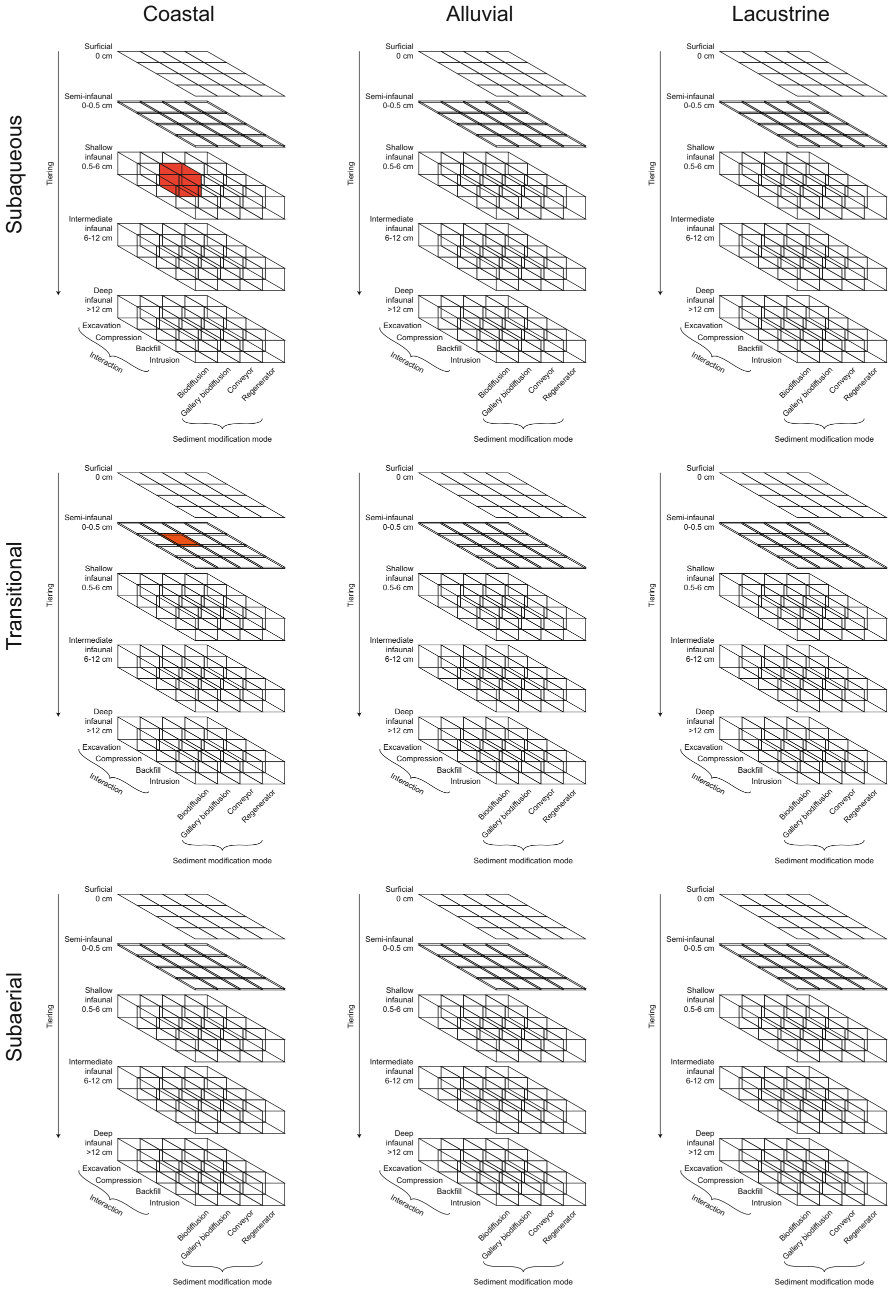

**Fig. 5.3** Ediacaran ecosystem engineering

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.

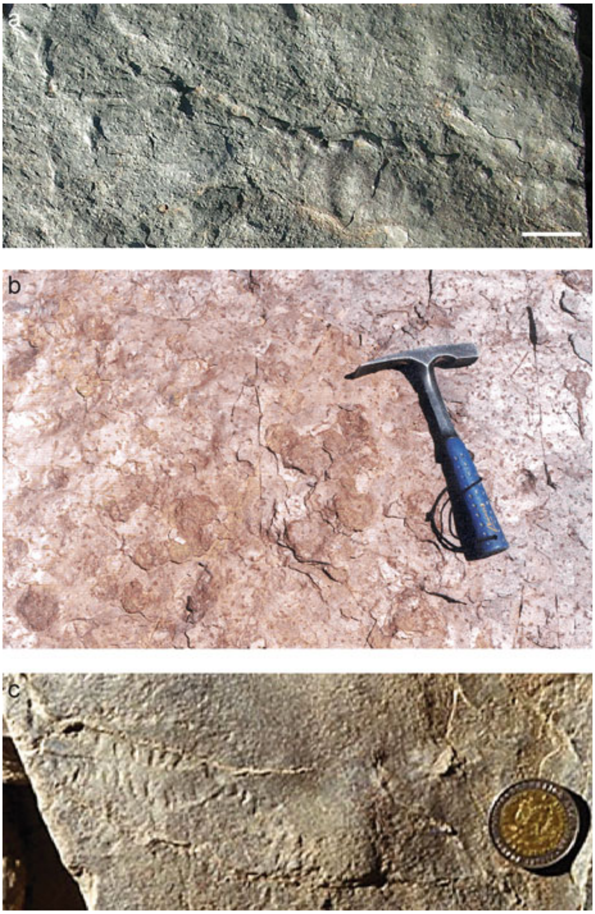

**Fig. 5.4** Selected Cambrian trace fossils from transitional settings within coastal environments. (**a**) *Treptichnus pedum* from Fortunian tidal-flat deposits of the Kalk Gat Formation, Vanrhynsdorp Group, South Africa. Scale bar is 10 mm; (**b**) Bedding plane view (*top*) of a concentration of *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

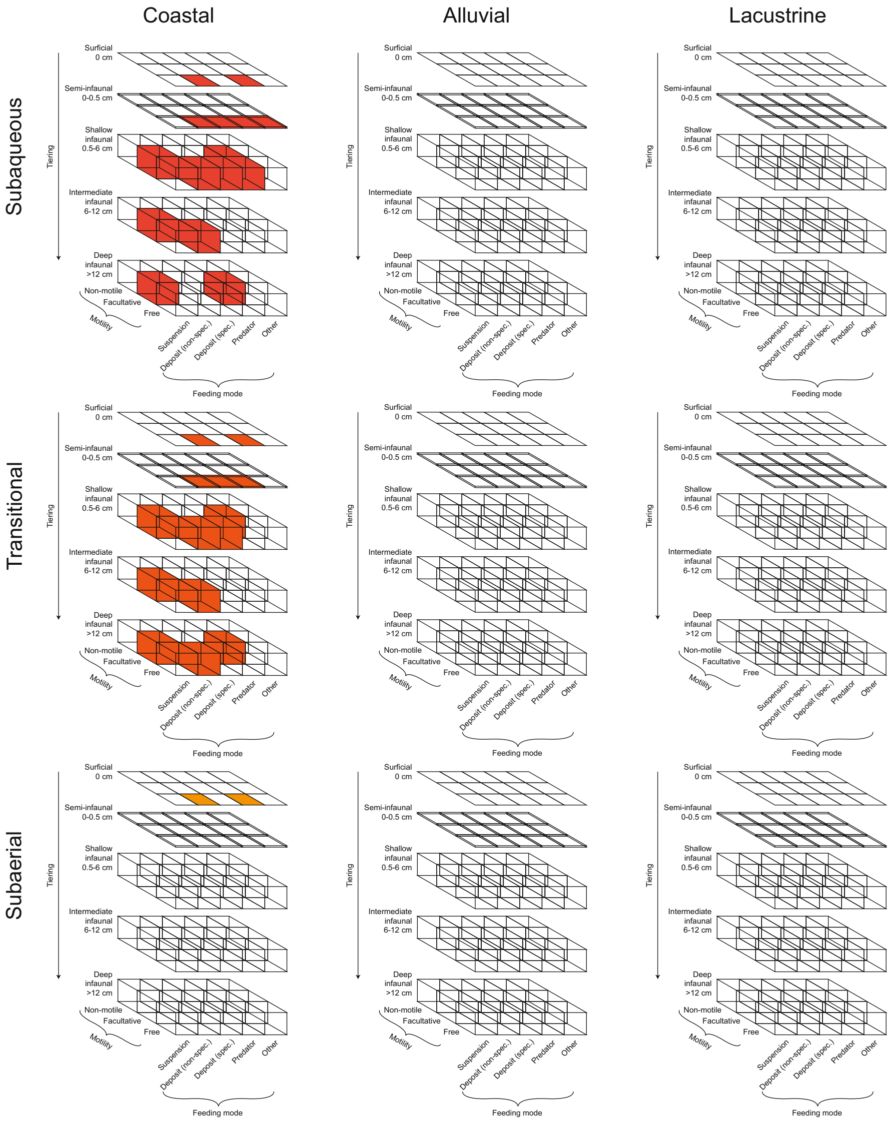

**Fig. 5.6** Cambrian ecospace occupation

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

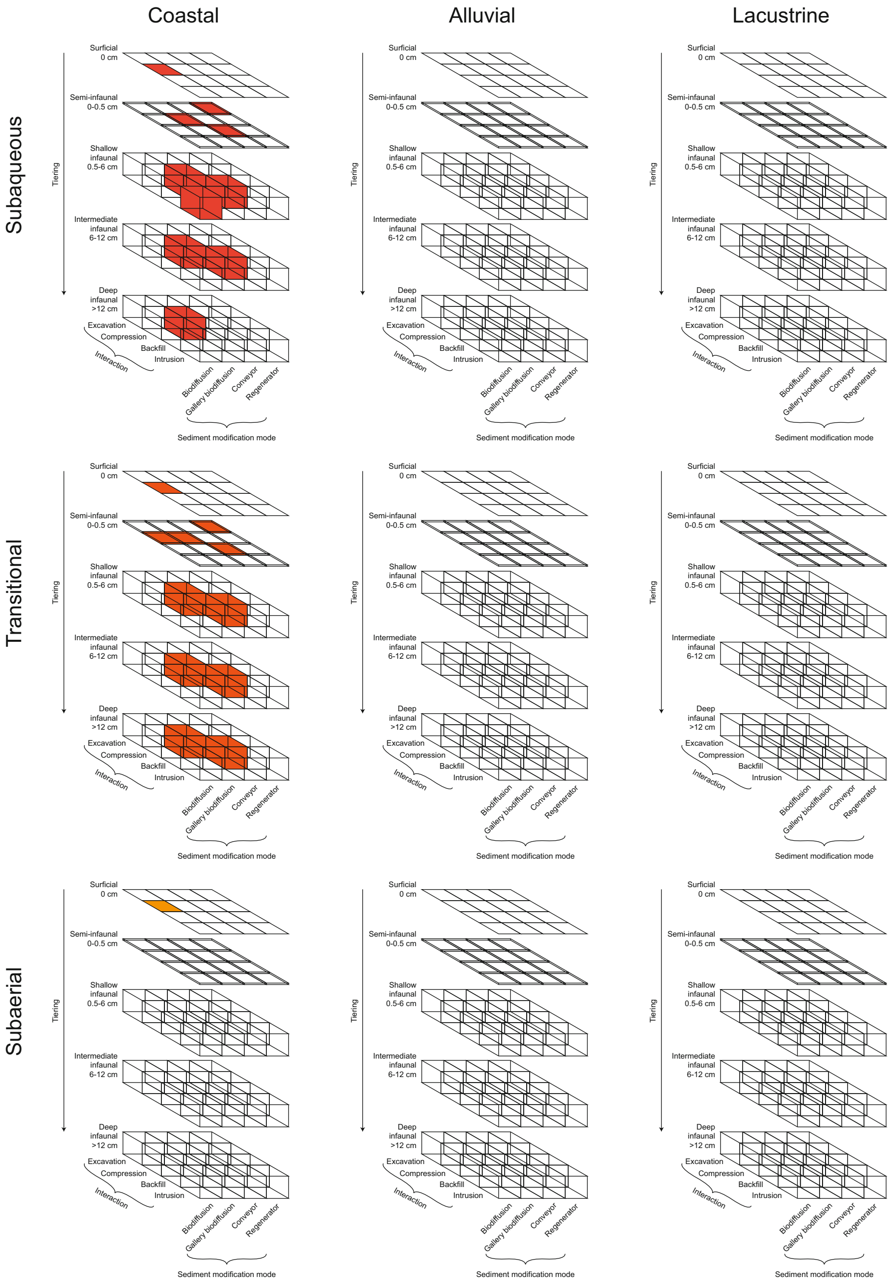

**Fig. 5.7** Cambrian ecosystem engineering

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

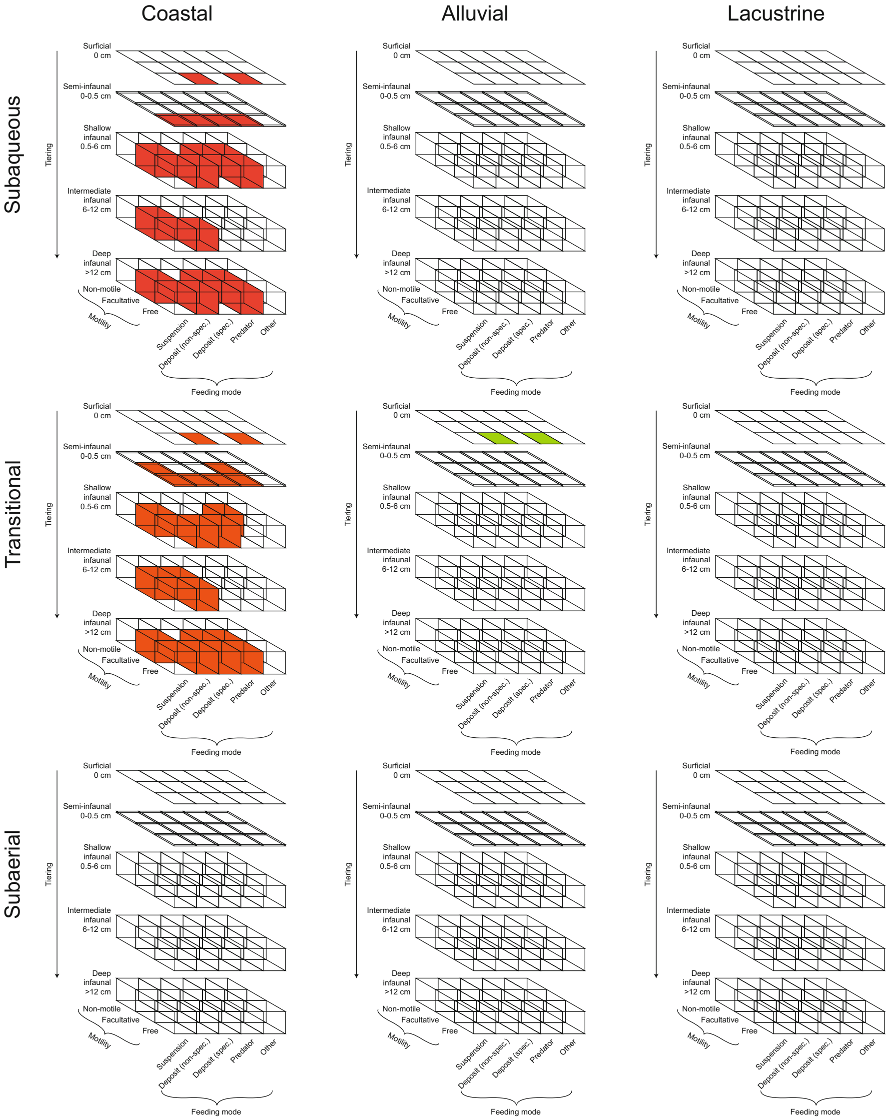

**Fig. 5.9** Ordovician ecospace occupation

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

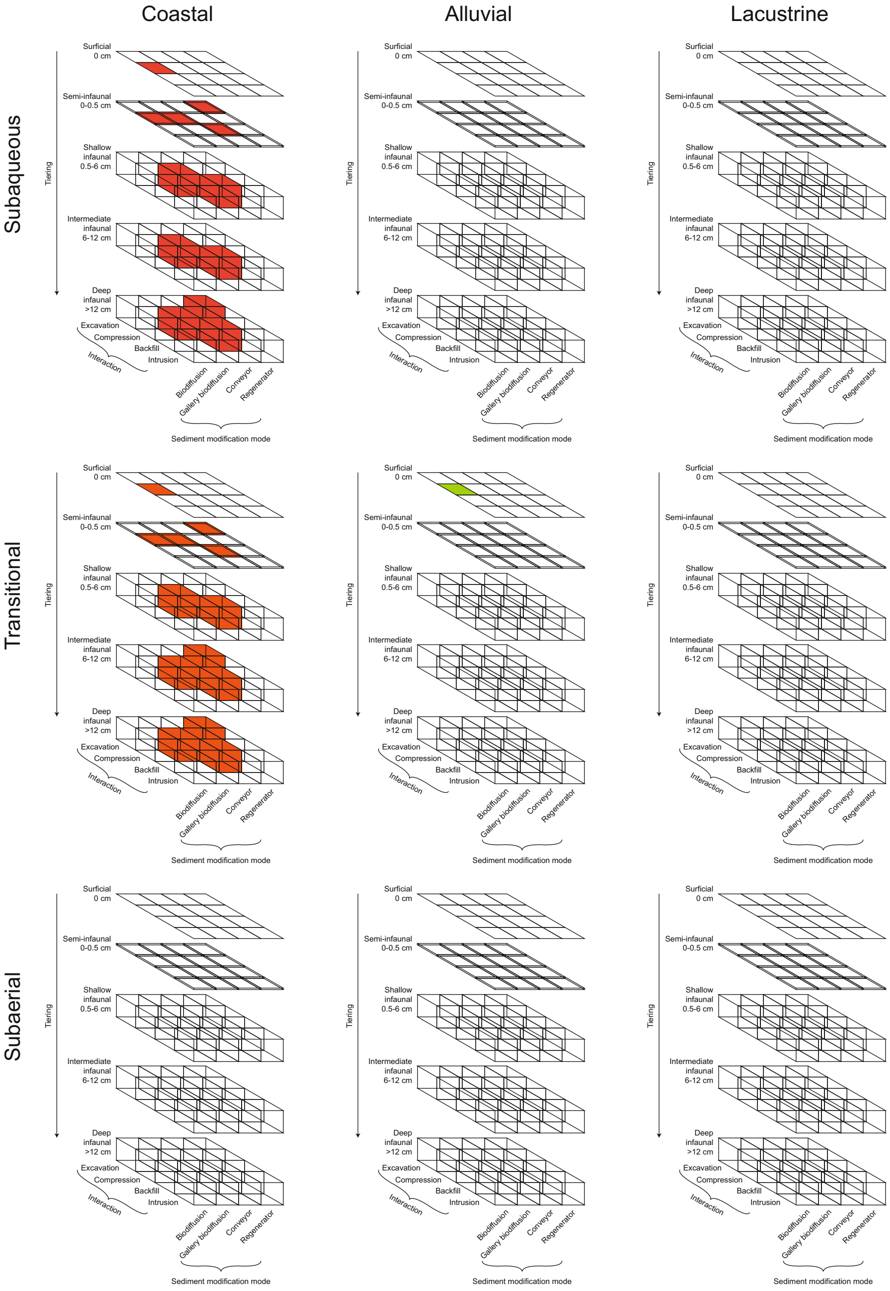

**Fig. 5.10** Ordovician ecosystem engineering

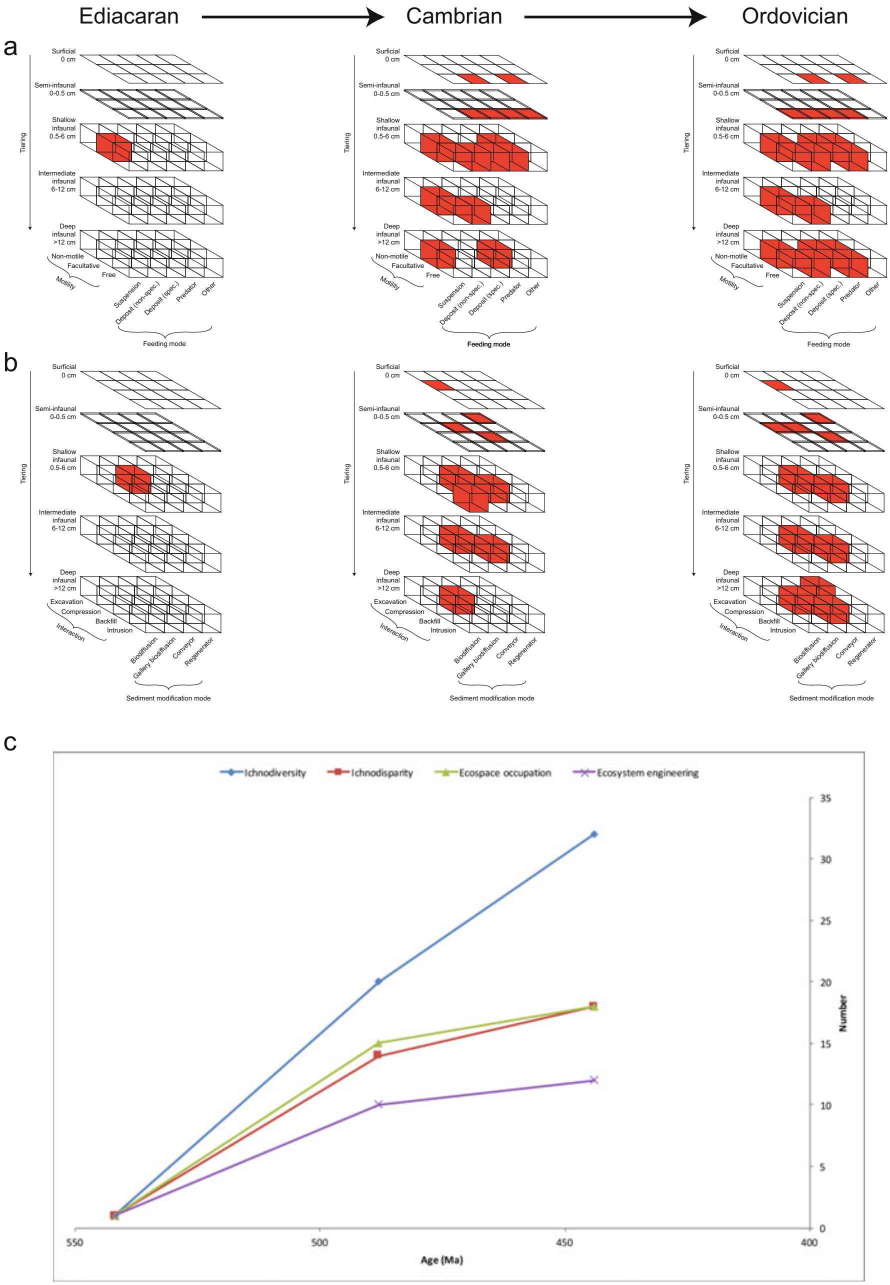

**Fig. 5.11** Colonization of subaqueous coastal environments. (**a**) Ecospace occupation; (**b**) ecosystem engineering; (**c**) plot of ichnodiversity, ichnodisparity, ecospace occupation in terms of number of modes of life, and ecosystem engineering in terms of number of modes of sediment modification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

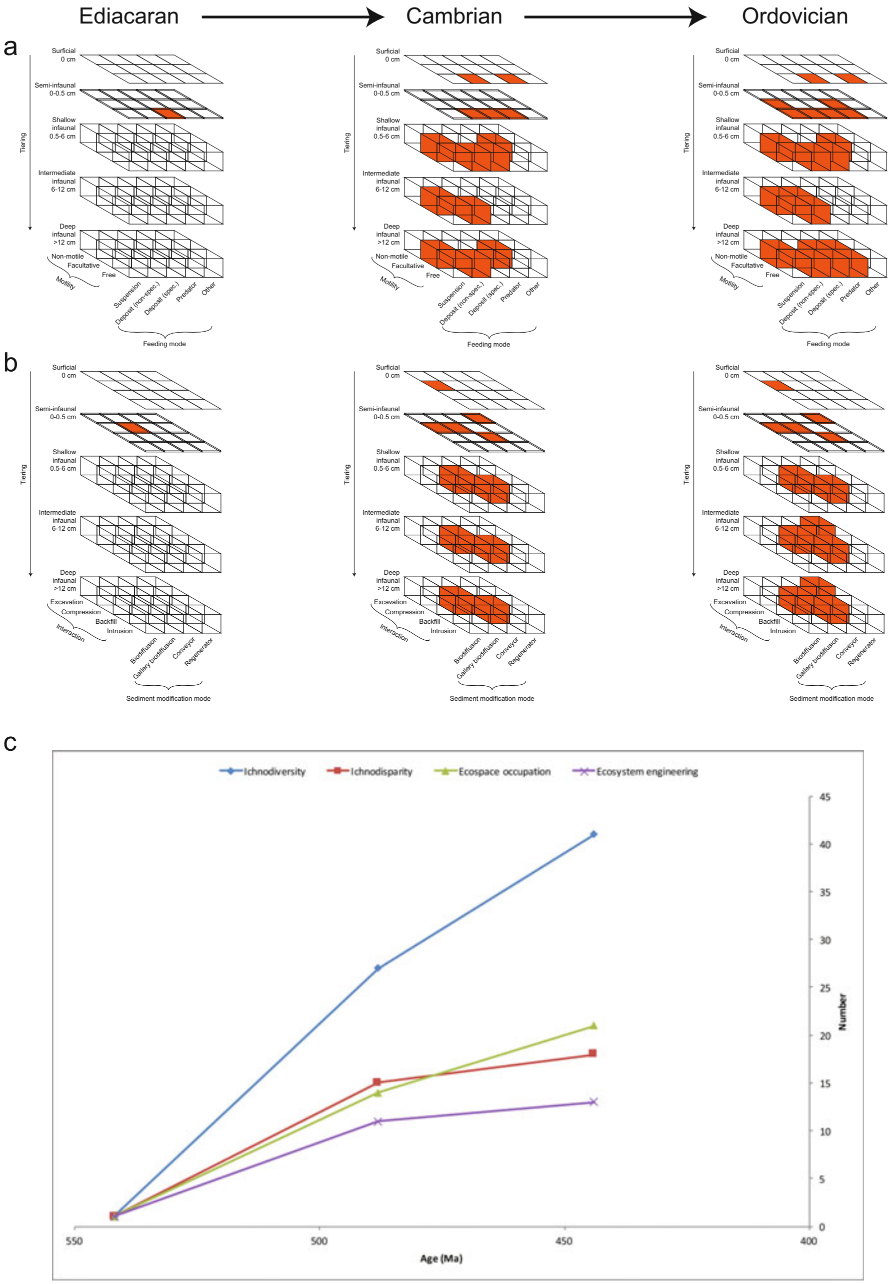

**Fig. 5.12** Colonization of transitional coastal environments. (**a**) Ecospace occupation; (**b**) ecosystem engineering; (**c**) plot of ichnodiversity, ichnodisparity, ecospace occupation in terms of number of modes of life, and ecosystem engineering in terms of number of modes of sediment modification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

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