Chapter 4
The Great Ordovician Biodiversification Event

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4.1 Introduction

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

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

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

4.2 Patterns of Environmental Colonization

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

4.2.1 Shallow-Marine Siliciclastic Environments

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

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

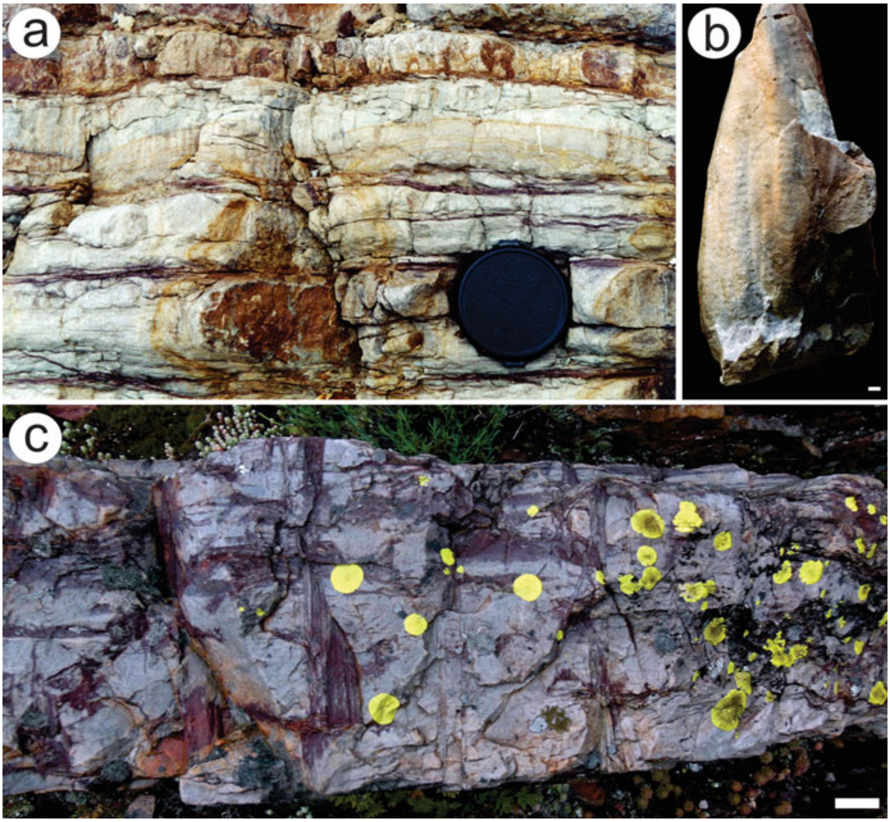

Fig. 4.1 Typical Ordovician nearshore trace fossils. (**a**) *Skolithos* pipe rock in storm deposits. Tremadocian, Alfarcito Member, Santa Rosita Formation, Quebrada de Casa Colorada, northwest Argentina. Lens cover is 5.5 cm wide; (**b**) *Daedalus desglandi*. Floian–Darriwilian, north of Muscat, Oman.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

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

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

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

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

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

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

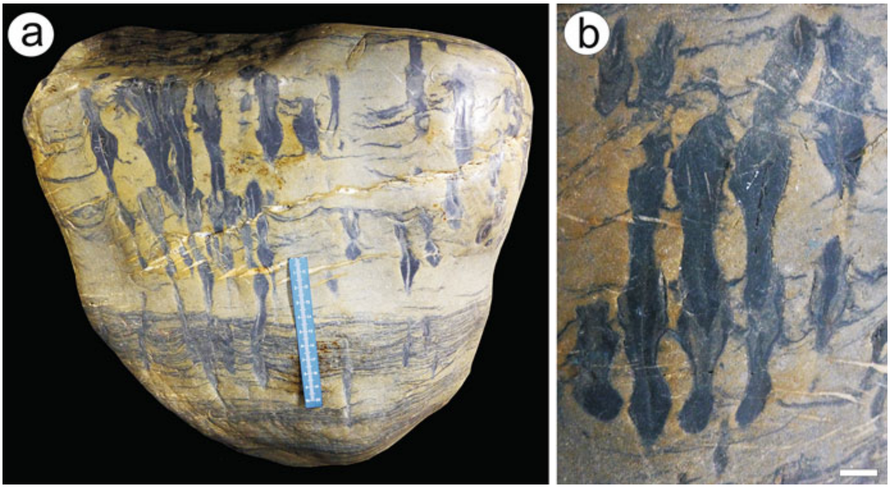

Fig. 4.2 Crowded synchronous *Rosselia* ichnofabrics from the Middle to Upper Ordovician Castro Formation of Cabo de Peñas, Asturias, Spain. (**a**) General view in cross section; (**b**) close-up showing several stacked specimens. Scale bar is 1 cm

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

4.2.1.3 Faunal Turnovers in the *Cruziana* Ichnofacies

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

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

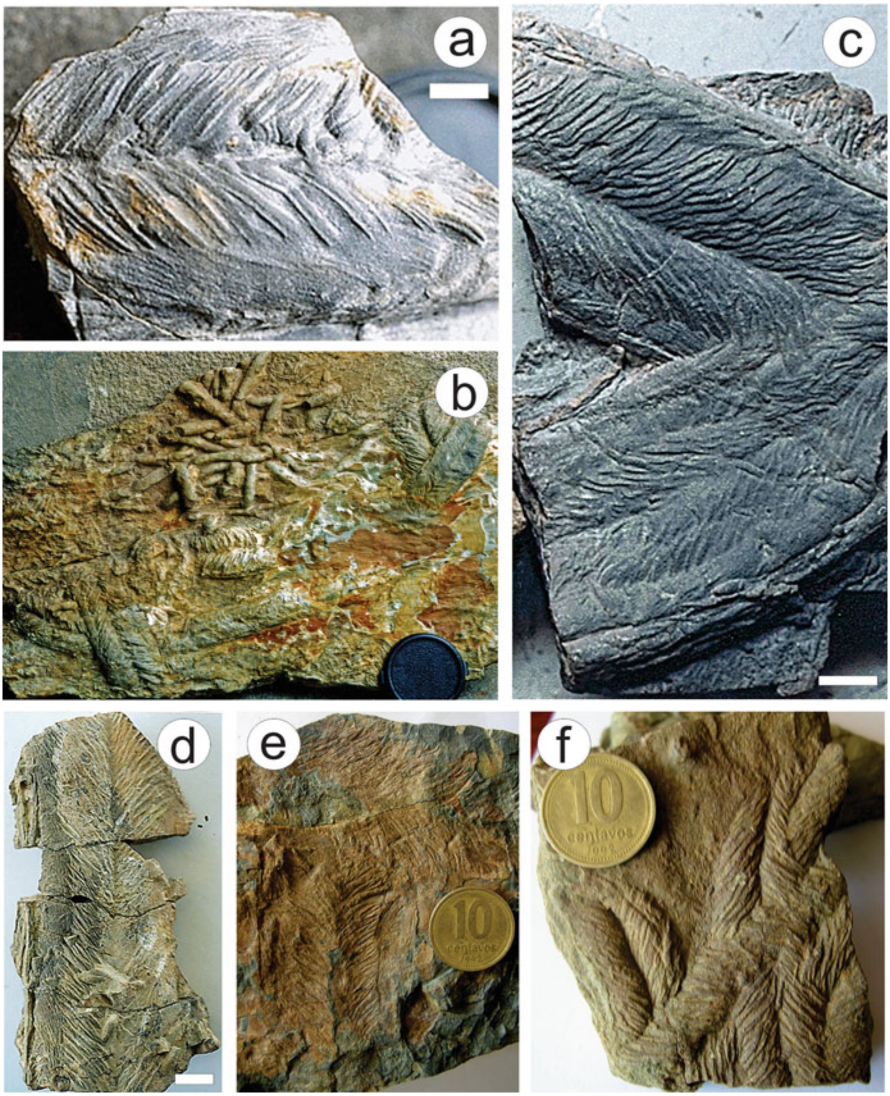

Fig. 4.3 Examples of the Furongian–Tremadocian *Cruziana semiplicata*. (**a**) Furongian, Olenus Beds, Wiśniówka Quarry, Holy Cross Mountains, Poland; (**b**) several specimens cross cut by *Phycodes* isp. and *Palaeophycus tubularis*. Furongian, Festiniog Beds, Lingula Flags, North Wales. Lens cap diameter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

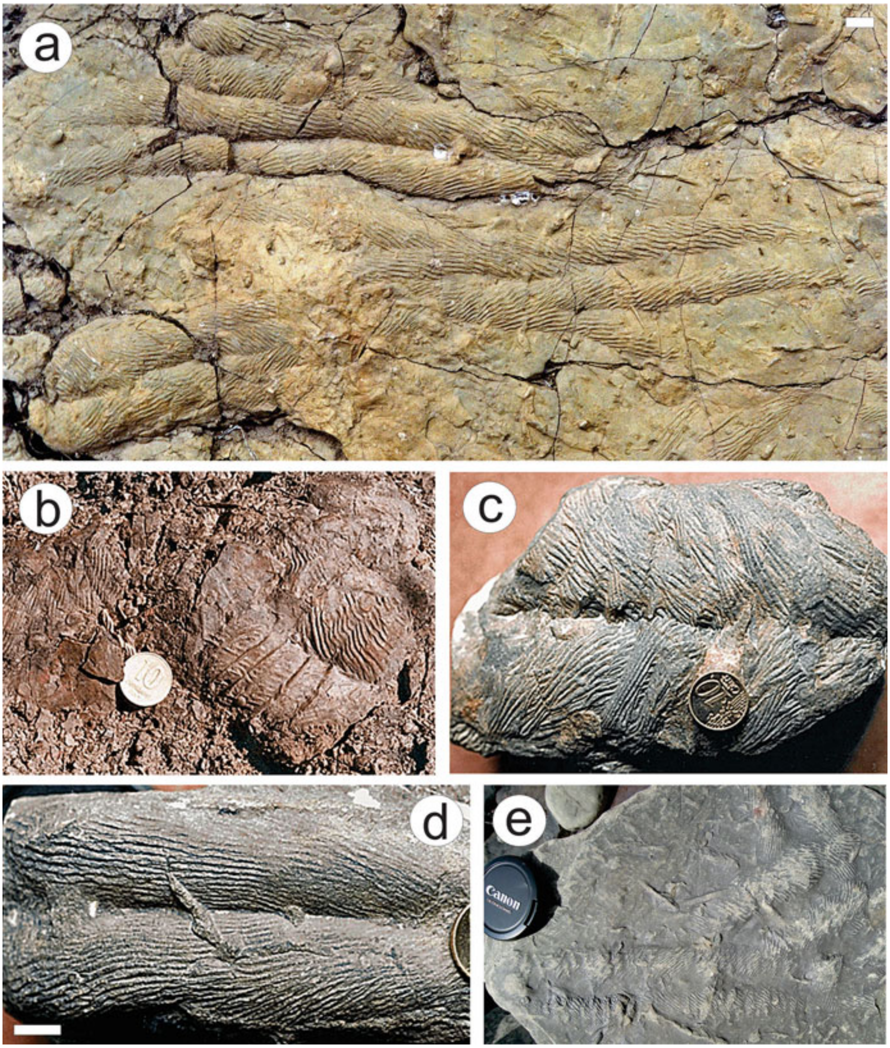

Fig. 4.4 Examples of the Floian–Darriwilian *Cruziana rugosa* group. (**a**) *Cruziana rugosa furcifera* showing sharp, regular scratch marks forming a highly variable V-angle. Floian–Darriwilian, Mojotoro Formation, Quebrada del Gallinato, northwest Argentina. Scale bar is 1 cm; (**b**) highly asymmetrical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

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

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

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

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

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

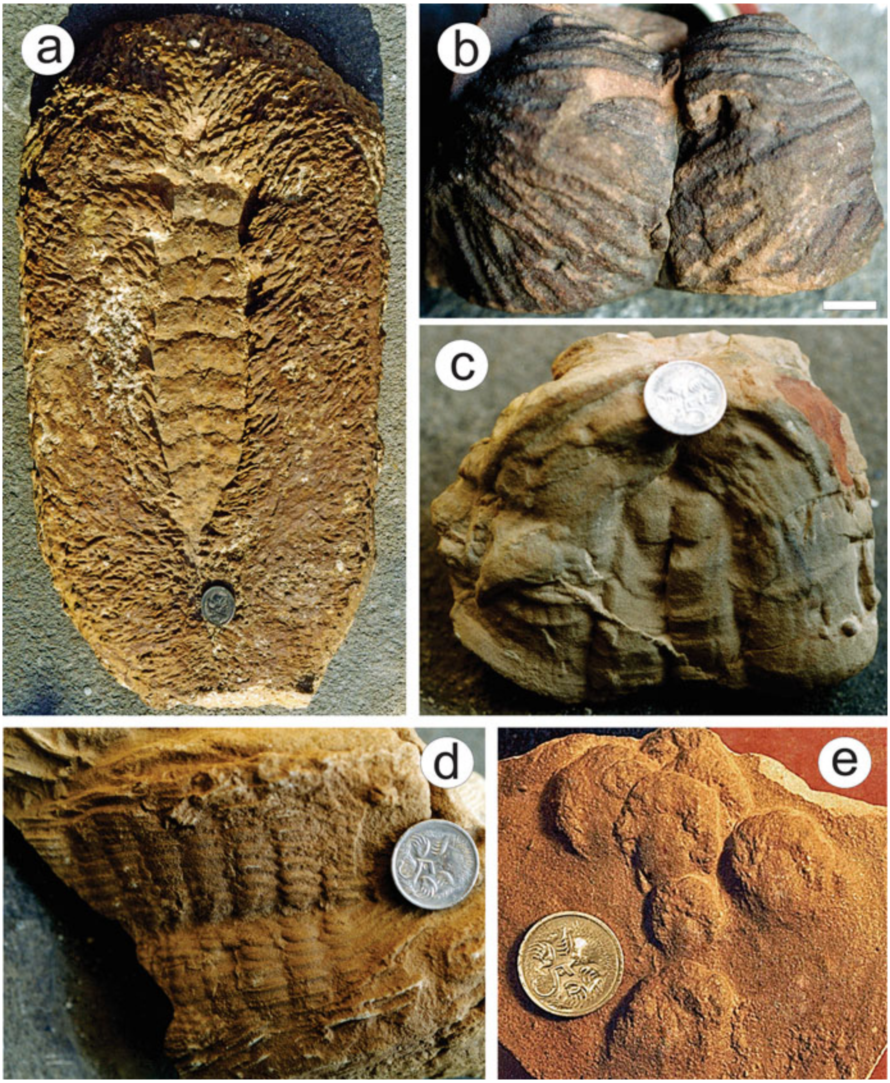

Fig. 4.5 Examples of Sandbian–Hirnantian trilobite trace fossils. (**a**) *Rusophycus radialis* characterized by large size, radial scratch pattern, and well-developed coxal impressions. Upper Ordovician, Mithaka Formation, Toko Range, Queensland, Australia. Coin diameter 1.9 cm; (**b**) *Cruziana petraea*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

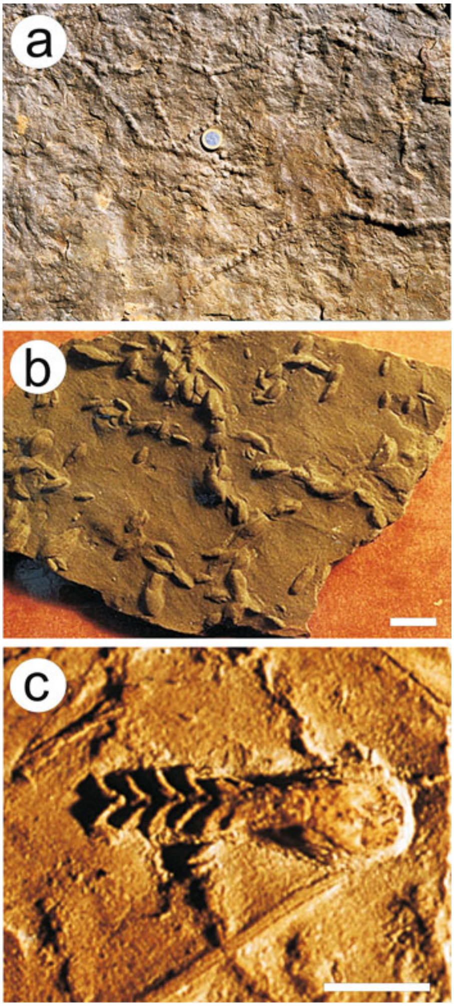

Fig. 4.6 Examples of morphologic variability of Middle–Upper Ordovician trace fossils. (**a**) *Parataenidium monoliformis*. Darriwilian-Katian, First Bani Group, Jbel Gaiz succession, Morocco. Coin diameter is 2.1 cm; (**b**) *Lockeia siliquaria*, Katian, Cincinnati, Ohio, USA. Scale bar is 1 cm; (**c**)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

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

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

4.2.2 Shallow-Marine Carbonate Environments

4.2.2.1 Peculiarities of Carbonate Ichnology

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

4.2.2.2 The *Thalassinoides* Conondrum

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

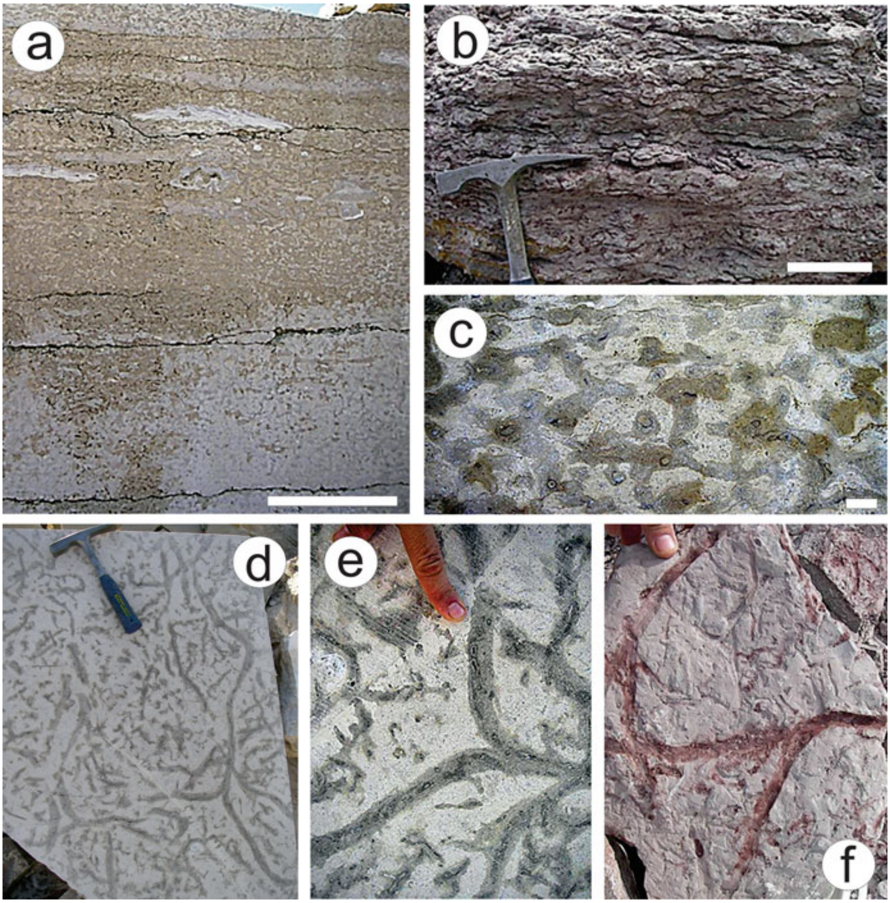

Fig. 4.7 *Thalassinoides*-like ichnofabrics in Upper Ordovician carbonates. (**a**) Katian, Selkirk Member, Red River Formation, Gillis Quarries, Garson, Manitoba, Canada. Scale bar is 40 cm; (**b**) Katian, Gunton Member, Stony Mountain Formation, Stony Mountain Quarries, Stony Mountain, Manitoba, Canada.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

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

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

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

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

4.2.2.3 The Ordovician Bioerosion Revolution

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

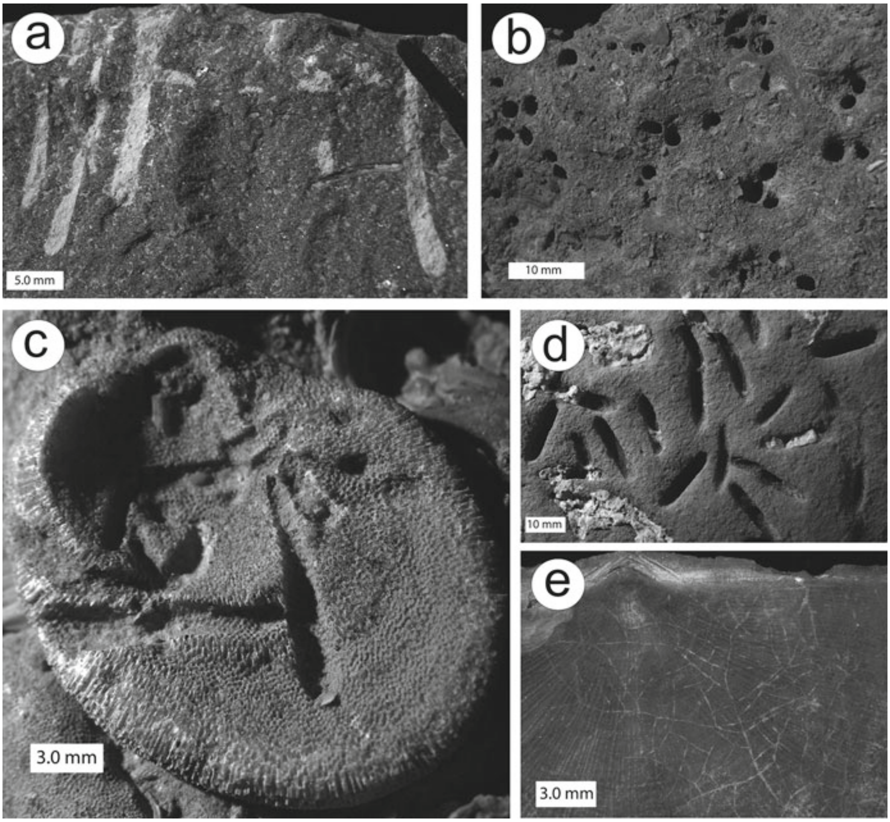

Fig. 4.8 Upper Ordovician bioerosion structures. (**a**) *Trypanites weisi* (*cross-sectional view*) in a carbonate hardground. Katian, Grant Lake Limestone, near Washington, Kentucky, USA; (**b**) *Trypanites weisi* (*bedding-plane view*) in a carbonate hardground. Katian, Grant Lake Limestone, near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

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

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

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

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

4.2.3 Deep-Marine Environments

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

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

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

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

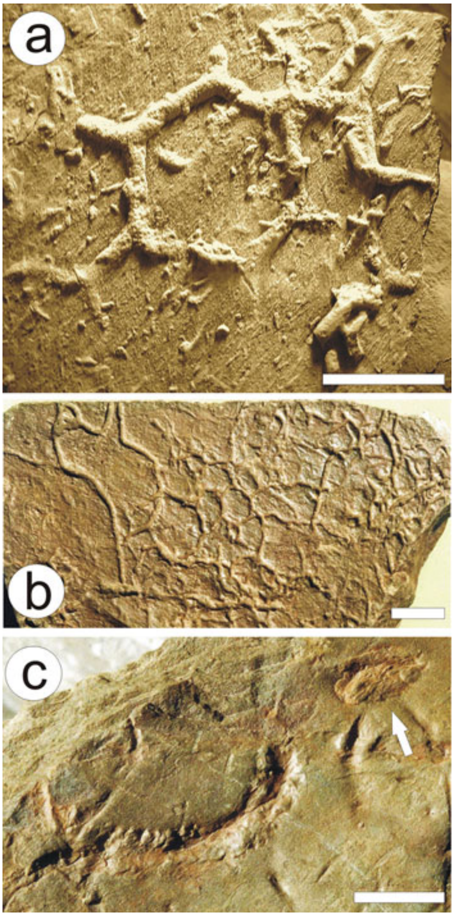

Fig. 4.9 Deep-marine ichnofaunas, Tremadocian, Chiquero Formation, Susques, northwest Argentina. (**a**) *Paleodictyon* isp.; (**b**) *Multina magna*; (**c**) *Protovirgularia* isp. and *Lockeia* isp. (*arrow*). All scale bars are 1 cm long

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

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

4.3 Trends in Ichnodiversity and Ichnodisparity

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

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

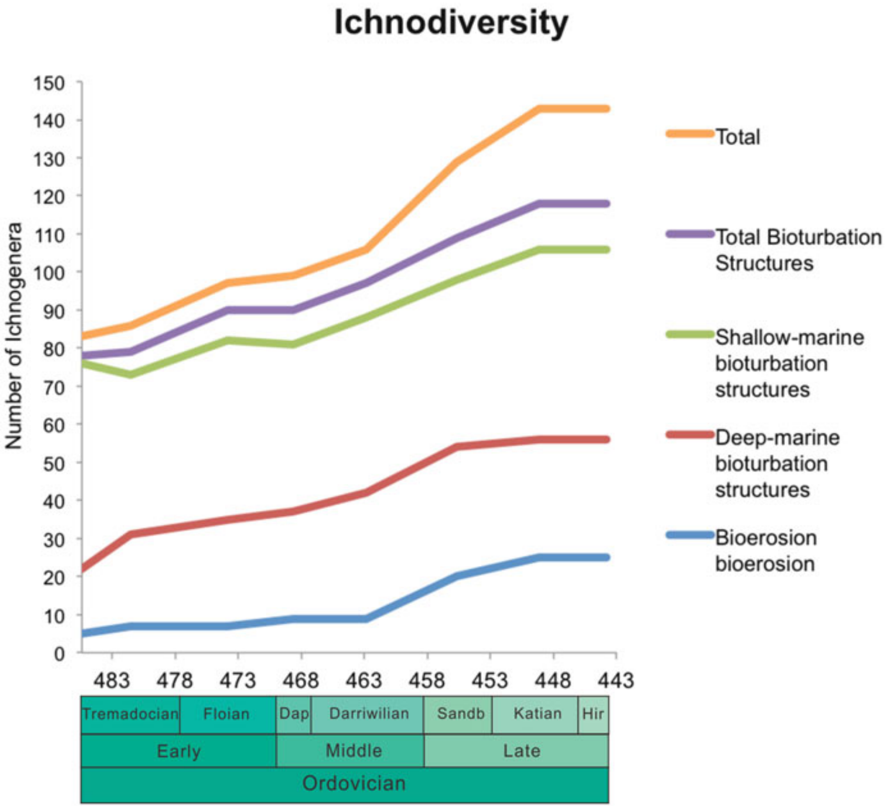

Fig. 4.10 Trends in ichnodiversity of bioturbation and bioerosion structures through the Ordovician (after Buatois et al. 2016b)

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

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

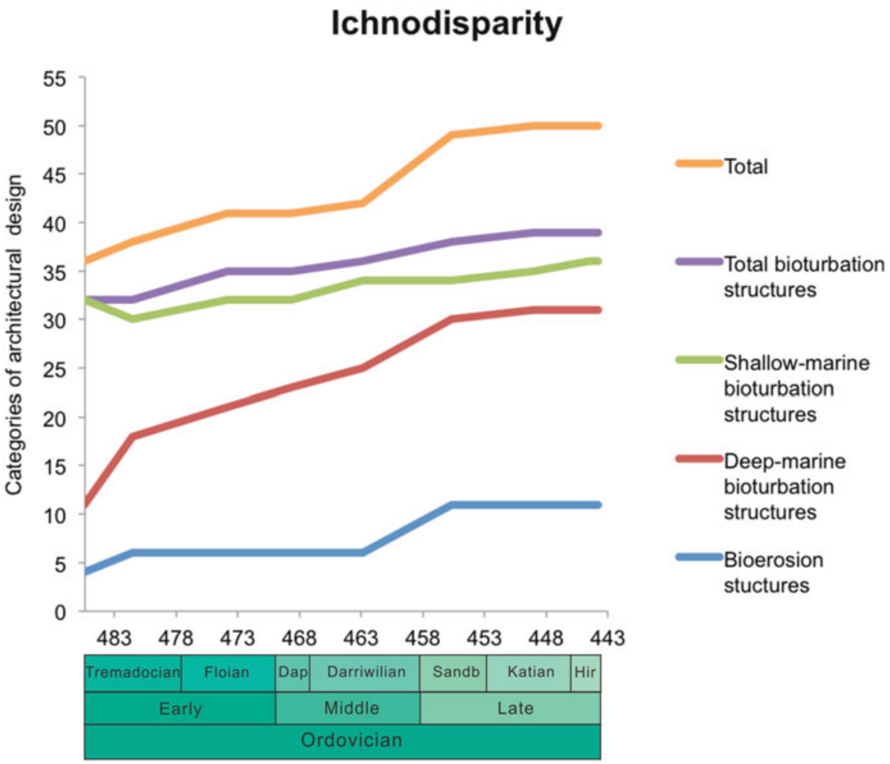

Fig. 4.11 Trends in ichnodisparity of bioturbation and bioerosion structures through the Ordovician (after Buatois et al. 2016b)

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

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

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

4.4 Trends in Tiering Structure and Diachronism in Infaunalization

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

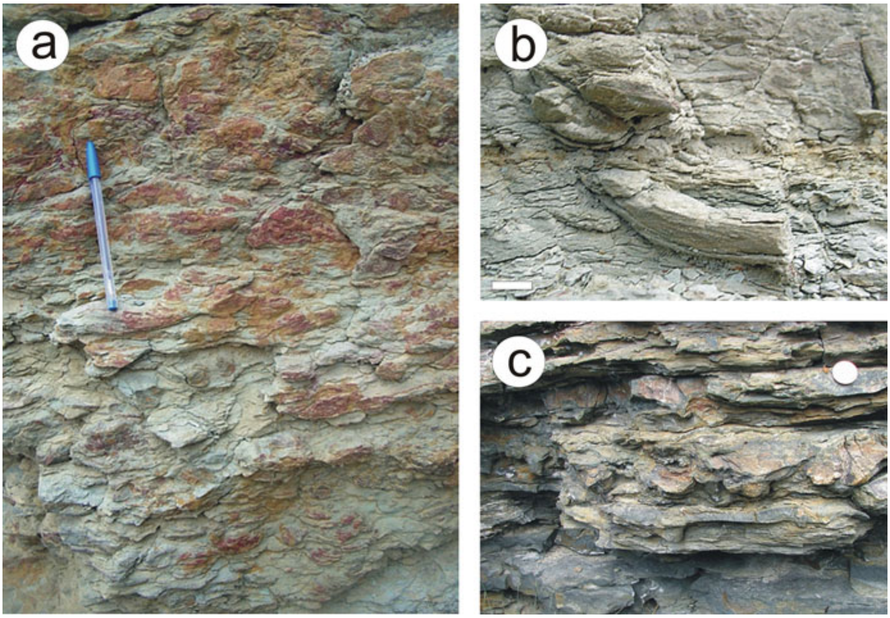

Fig. 4.12 Lower Cambrian occurrences of the *Trichophycus* ichnofabrics in Baltica and Laurentia. (**a**) Cross-sectional view from the Lower Cambrian Norretorp Member, Bornholm, Denmark. Pencil is 14 cm long; (**b**) close-up showing the overall U-shaped morphology of *Trichophycus*. Lower Cambrian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

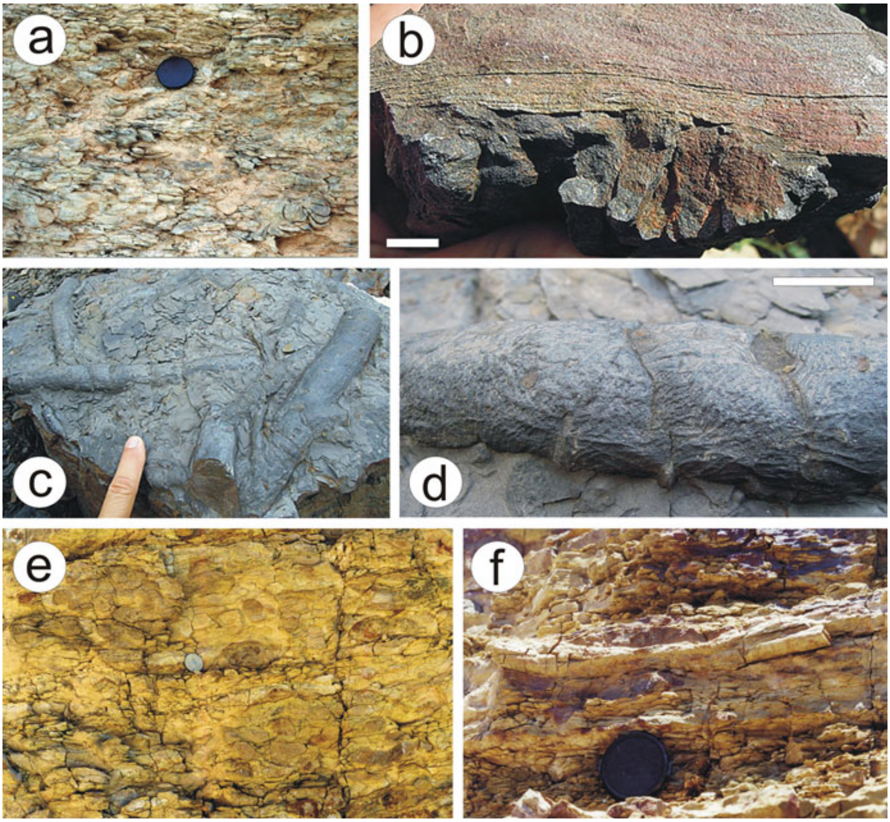

Fig. 4.13 Upper Tremadocian–Floian occurrences of the *Trichophycus* ichnofabrics in Gondwana. (**a**) Intensely bioturbated deposits. Floian, Upper Fezouta Formation, Imini succession, Central High Atlas, Morocco. Lens cover is 5.5 cm; (**b**) Dense occurrence of *Trichophycus* at the base of a sandstone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

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

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

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

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

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

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

4.5 Conclusions

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

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