Chapter 16
Recurrent Patterns and Processes: The Significance of Ichnology in Evolutionary Paleoecology

Luis A. Buatois and M. Gabriela Mángano

16.1 Introduction

Gould (1980) established a distinction between idiographic and nomothetic paleobiology. Whereas the former deals with individual evolutionary events, the latter attempts to find regularities in the history of life. This book is rooted in an idiographic approach because most chapters review a single major evolutionary event. However, after gathering such a wealth of information on specific events, it is worth to close the book with a brief attempt at exploring the nomothetic perspective by trying to find recurrent patterns and processes in evolutionary paleoecology using ichnologic data. In fact, as noted by Gould (1980) himself regarding J. J. Sepkoski's (1978, 1979, 1984) kinetic model of diversification, the approach employed here attempts to reach a balance between nomothetics and idiographics by producing a nomothetic model which is empirically grounded (see D. Sepkoski 2012 for an insightful review). Therefore, this chapter compares several evolutionary events, searching for common themes. In order to do so, we will compare organism-substrate interactions during evolutionary radiations, benthic fauna response to mass extinctions, patterns of ecospace colonization, and environmental shifts through time.

L.A. Buatois (✉) • M.G. Mángano
Department of Geological Sciences, University of Saskatchewan,
114 Science Place, Saskatoon, SK, Canada
e-mail: luis.buatois@usask.ca

M.G. Mángano, L.A. Buatois (eds.), *The Trace-Fossil Record of Major Evolutionary Events*, Topics in Geobiology 40,
DOI 10.1007/978-94-017-9597-5_16

16.2 Evolutionary Radiations

Evolutionary radiations are dramatic proliferations of taxa within clades (Erwin 1992; Simões et al. 2016). From an ichnologic perspective, three major events in marine settings are compared in this book and are, therefore, addressed in this chapter, the Cambrian Explosion (see Chap. 3), the Great Ordovician Biodiversification Event (see Chap. 4) and the Mesozoic Marine Revolution (see Chap. 9). Figures 16.1 and 16.2 summarize changes in ichnodiversity and ichnodisparity through time, respectively. Only invertebrate trace fossils were considered. Ichnogeneric occurrences were compiled on a case-by-case basis, therefore summarizing actual occurrences. However, the curves were plotted as "range-through" data, and therefore they are based on lower and upper appearances for each ichnogenus/category of architectural design and then extrapolating their presence through any intervening gap in the continuity of its record. This allows eliminating the noise generated by small-scale fluctuations in ichnodiversity and ichnodisparity that may result from the uneven number of studies for each time span. However, a disadvantage of this approach is that it is not particularly useful to detect potential drops in ichnodiversity and ichnodisparity as a result of mass extinctions (see Sect. 16.3).

Compilation of ichnogeneric diversity through geologic time indicates that the Cambrian Explosion, the Great Ordovician Biodiversification Event and the Mesozoic Marine Revolution, all evolutionary radiations established based on body fossils, are associated with increases in ichnodiversity (Fig. 16.1). This pattern shows a remarkable consistency with our knowledge derived from the analysis of diversity based on the body-fossil record. In fact, similarities between the curve of

Fig. 16.1 (continued) were compiled at the ichnogenus level because the taxonomy is more firmly established than for ichnospecies. Total number of ichnogenera is 523 ichnogenera (417 for bioturbation structures and 106 for bioerosion structures). Synonymies have been checked to make ichnotaxonomy consistent. Individual curves were constructed for continental, shallow-marine and deep-marine bioturbation ichnotaxa, and marine and continental bioerosion. In turn, separate ichnodiversity curves were compiled for all marine bioturbation ichnogenera, all marine ichnogenera (bioerosion plus bioturbation), and all continental ichnogenera (bioerosion plus bioturbation). In order to differentiate between shallow marine, deep marine and continental occurrences, original paleoenvironmental interpretations in the literature, as well as personal data, were considered. Curves plotted as "range-through" data, and therefore based on lower and upper appearances for each ichnogenus, extrapolating their presence through any intervening gap in the continuity of its record. Temporal resolution is at Epoch rank. Because there are no formal subdivisions for the Ediacaran Period, this bin has been further divided using the informal subdivision of Vendian (560–550 Ma) and Namibian (550–541 Ma) (*sensu* Jensen et al. 2006). Biogenic structures recorded in modern sediments have been included in the Holocene. Although it occurs in both hardgrounds and firmgrounds, *Gastrochaenolites* was considered under bioerosion. The record of mirobioerosion ichnotaxa extends further into the Precambrian with *Granulohyalichnus* and *Tubulohyalichnus* ranging into 3.5 Ga (Furnes et al. 2004, 2007; Banerjee et al. 2006, 2007; McLoughlin et al. 2009), representing in fact the oldest trace fossils. Because these two ichnogenera are produced by microbial activity and our analysis is centered on invertebrates, they have not been considered in the discussion presented in the text

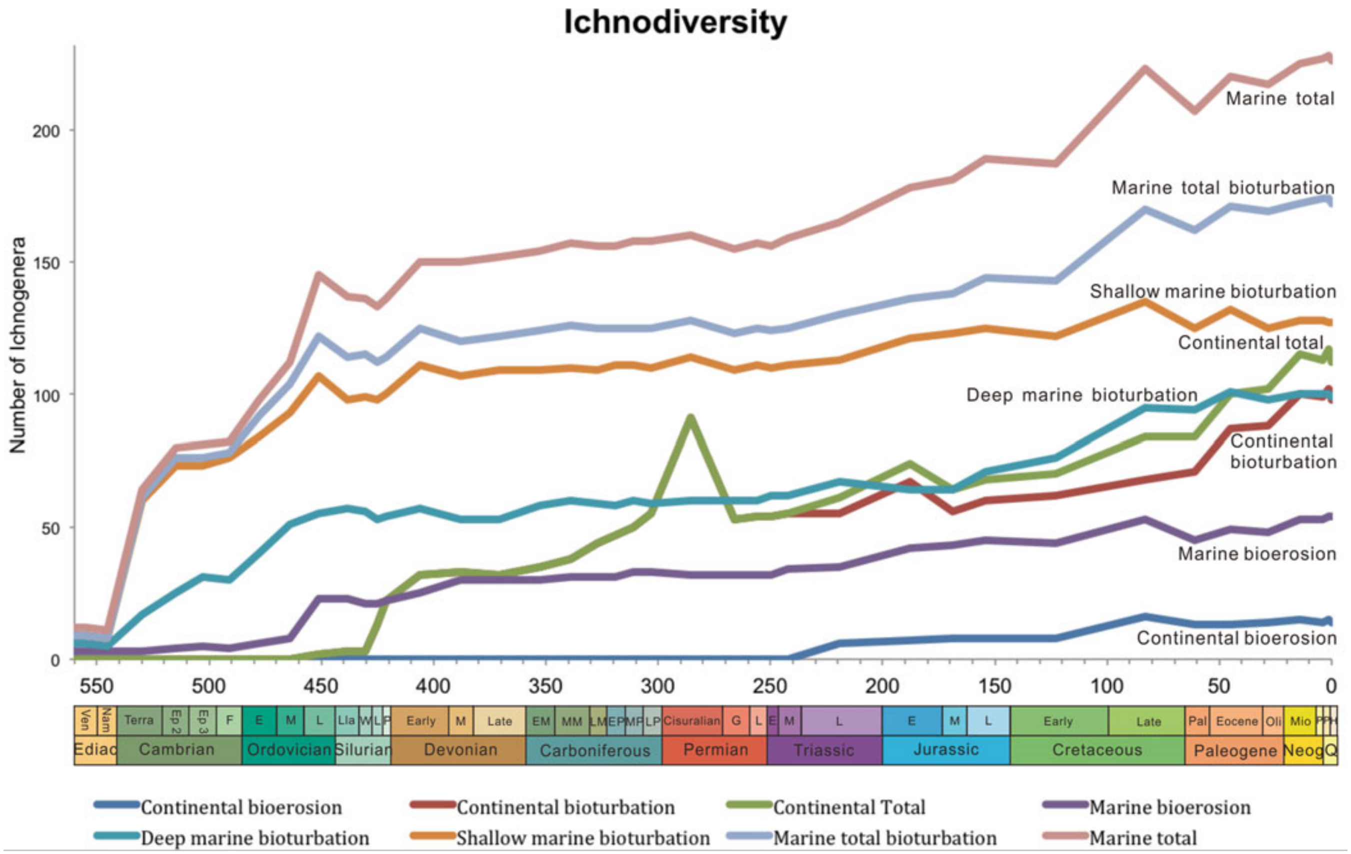
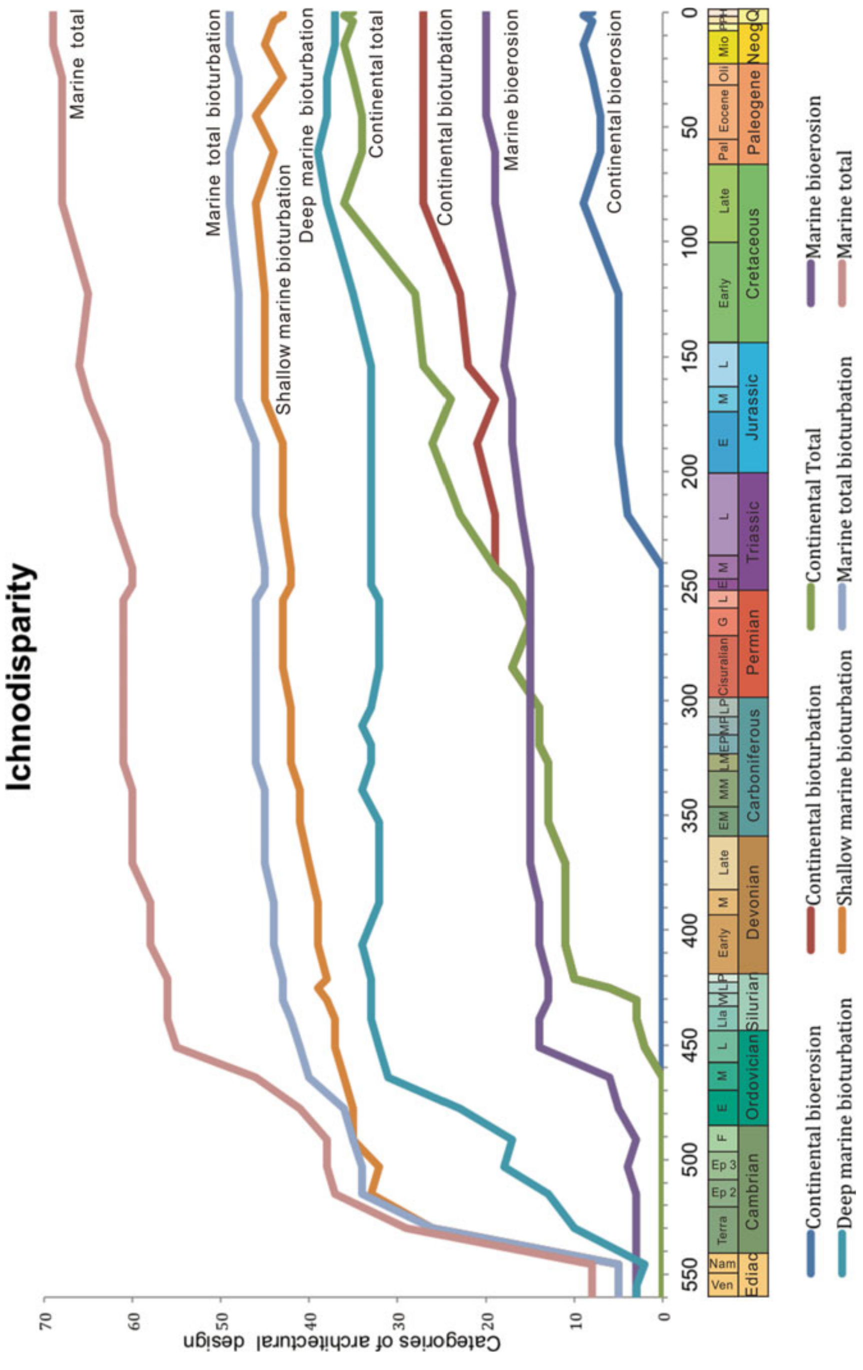


Fig. 16.1 Ichnodiversity changes through geologic time. Compilation based on literature and personal data. The main literature sources used to compile the ichnogeneric list were the Treatise volume on trace fossils (Häntzschel 1975) and the more recent revision by Knaust (2012). In addition, we have checked each ichnogenus by consulting the original ichnologic literature and pertinent reviews in order to revise its validity and potential synonyms. The ichnodiversity curves


Ichnodisparity
Categories of architectural design
0
10
20
30
40
50
60
70
0
50
100
150
200
250
300
350
400
450
500
550
Marine total
Marine total bioturbation
Shallow marine bioturbation
Deep marine bioturbation
Continental total
Continental bioturbation
Marine bioerosion
Continental bioerosion
Ven
Nam
Ediac
Terra
Ep 2
Ep 3
F
Cambrian
E
M
L
Ordovician
Lla
W
L
P
Silurian
Early
M
Late
Devonian
EM
MM
LM
EP
MP
LP
Carboniferous
Cisuralian
G
L
Permian
E
M
L
Triassic
E
M
L
Jurassic
Early
Late
Cretaceous
Pal
Eocene
Oli
Paleogene
Mio
P
P
H
Neog
Q
Continental bioerosion
Deep marine bioturbation
Continental bioturbation
Shallow marine bioturbation
Continental Total
Marine total bioturbation
Marine bioerosion
Marine total

marine ichnodiversity and that of marine animal genera produced by Sepkoski (1997) are striking with regards to the Cambrian Explosion and the Great Ordovician Biodiversification Event (Buatois et al. 2016a). A 433 % increase in ichnodiversity took place in marine environments during the Terraneuvian (12 and 64 ichnogenera in the Ediacaran and Terraneuvian, respectively), whereas a 77 % occurred as a result of the Great Ordovician Biodiversification Event (82 ichnogenera in the Furongian and 145 ichnogenera by the Late Ordovician). Whereas the Cambrian Explosion is essentially restricted to bioturbation structures, the Great Ordovician Biodiversification Event is expressed by bioerosion structures as well, an event that has been referred to as the Ordovician bioerosion revolution (Wilson and Palmer 2006). Ichnogeneric compilations show that the explosion in bioerosion took place approximately 80 my after the Cambrian Explosion in bioturbation (Buatois et al. 2016a). The explosive diversification of the early Cambrian supports an exponential model for the early phases of diversification as advocated originally by Sepkoski (1978) based on shelly fossils. Despite these similarities, two main differences are apparent. First, trace-fossil data indicate that the rapid diversification took place in the early Cambrian, rather than in the late early Cambrian as indicated by shelly fossils, suggesting that the Fortunian may be regarded as part of the phylogenetic fuse (Mángano and Buatois 2014; see Chap. 3). Second, marine animal genera show minor diversity fluctuations during the middle to late Cambrian, but ichnodiversity reached a plateau that spanned from the middle Cambrian to the onset of the Great Ordovician Biodiversification Event (Buatois et al. 2016a).

The ichnodiversity curve for marine trace fossils shows another, but more modest, increase in the Early Jurassic (8 %; 165 and 178 ichnogenera in the Late Triassic and Early Jurassic, respectively) and a more important one in the Late Cretaceous (19 %; 187 and 223 ichnogenera in the Early and Late Cretaceous, respectively) (Fig. 16.1). A more limited, but constant, increase took place between the Early Jurassic and Early Cretaceous. These changes in ichnodiversity are expressed by both bioerosion and bioturbation structures. This increase is undoubtedly a reflection of the Mesozoic Marine Revolution. Comparing ichnodiversity levels between the Late Triassic (164 ichnogenera) and the Late Cretaceous (223 ichnogenera) reveals a total 35 % ichnodiversity increase that is attributed to this evolutionary radiation. Ichnologic data indicate that the Early Jurassic experienced a change in ichnotaxonomic composition and the complexity of infaunal tiering, which is consistent with the timing of the Mesozoic Marine Revolution as revealed by our compilations (see Chap. 9).

Fig. 16.2 Ichnodisparity changes through geologic time. Compilation based on literature and personal data. Total number of categories of architectural designs is 79 (58 for bioturbation structures and 21 for bioerosion structures). Curves were constructed for ichnodisparity following the same environmental subdivision used for ichnodiversity. Curves plotted as "range-through" data, and therefore based on lower and upper appearances for each category of architectural design, extrapolating their presence through any intervening gap in the continuity of its record. Ichnodisparity was compiled following the approach of Buatois and Mángano (2013; see also Chap. 1) and categories of architectural designs summarized by Buatois et al. (2016b). Table 16.1 summarizes the different categories and the ichnogenera included. For further information, see caption of Fig. 16.1

Table 16.1 Categories of architectural designs and their ichnotaxa in alphabetical order (after Buatois et al. 2016b)

Architectural designs	Ichnogenera
1-Simple horizontal trails	*Archaeonassa, Circulichnis, Cochlichnus, Gordia, Helminthoidichnites, Helminthopsis, Herpystezoum, Mermia, Talitrichnus*
2-Trilobate flattened trails	*Curvolithus, Trisulcus*
3-Chevronate trails	*Protovirgularia, Rhadhostium*
4-Trails with undulating transverse bars and furrows	*Climactichnites, Steinsfjordichnus*
5-Bilobate trails and paired grooves	*Carpatichnis, Cruziana, Davichnia, Didymaulichnus, Diplopodichnus, Taphrhelminthoides, Tumblagoodichnus*
6-Trackways and scratch imprints	*Acanthichnus, Acripes, Allocotichnus, Angulichnus, Arachnomorphichnus, Arcichnus, Asaphoidichnus, Biformites, Bifurcatichnus, Bifurculapes, Climacodichnus, Coenobichnus, Conopsoides, Copeza, Danstairia, Dendroidichnites, Dimorphichnus, Diplichnites, Etterwindichnus, Euproopichnus, Foersterichnus, Glasbachichnium, Glaciichnium, Hamipes, Harpepus, Harpichnus, Heftebergichnus, Heteropodichnus, Heterotripodichnus, Hexapodichnus, Homopodichnus, Irichnus, Ixalichnus, Kalnaichnus, Keircalia, Kivanichnus, Konbergichnium, Kouphichnium, Lineatichnus, Lithographus, Lusatichnium, Maculichna, Megapodichnus, Merostomichnites, Mirandaichnium, Mitchellichnus, Monomorphichnus, Multipodichnus, Octopodichnus, Oklahomaichnus, Oniscoidichnus, Orchesteropus, Paleohelcura, Palmichnium, Parahamipes, Pentapodichnus, Petalichnus, Pirandikus, Protichnites, Pterichnus, Punctichnium, Siskemia, Stiallia, Stiaria, Striatichnium, Tambia, Tarichnus, Tarsichnus, Taslerella, Tasmanadia, Telsonichnus, Teratichnus, Terricolichnus, Tortilichnus, Trachomatichnus, Umfolozia, Vadichnites, Warvichnium*
7-Bilaterally symmetrical short, scratched imprints	*Avolatichnium, Arborichnus, Chagrinichnites, Cheliceratichnus, Gluckstadella, Huilmuichnus, Kingella, Orbiculichnus, Pollichianum, Ramosichnus, Rotterodichnium, Solusichnium, Surculichnus, Tonganoxichnus, Tripartichnus*

(continued)

Table 16.1 (continued)

8-Bilaterally symmetrical short, scratched impressions and burrows	*Aglaspidichnus, Alph, Cardioichnus, Cheiichnus, Craticulichnum, Crescentichnus, Faciemichnus, Limulicubichnus, Raaschichnus, Rusophycus, Selenichnites, Svalbardichnus*
9-Fan-shaped to radiating scratched imprints	*Kimberichnus, Radichnus*
10-Passively filled horizontal burrows	*Didymaulyponomos, Palaeophycus*
11-Simple actively filled (massive) horizontal to oblique structures	*Furculosus, Macaronichnus, Nenoxites, Planolites, Sericichnus, Torrowangea,*
12-Simple actively filled (meniscate) horizontal to oblique structures	*Ancorichnus, Beaconites, Compaginatichnus, Entradichnus, Imponoglyphus, Jamesonichnites, Scoyenia, Squamichnus, Taenidium*
13-Simple, actively filled (pelletoidal) horizontal burrows	*Alcyonidiopsis, Castrichnus, Edaphichnium, Quebecichnus, Sphaerapus, Tubotomaculum, Tubularina*
14-Complex actively filled horizontal structures	*Bichordites, Bolonia, Nereites, Paramargaritichnus, Parataenidium, Psammichnites, Rutichnus, Scolecocoprus, Scolicia, Tylichnus*
15-Armored burrows	*Crininicaminus, Diopatrichnus, Ereipichnus, Ichnospongiella, Lepidenteron, Nummipera*
16-Horizontal branching burrow systems	*Agrichnium, Arachnostega, Korymbichnus, Labyrintichnus, Multina, Paracanthorhaphe, Pilichnus, Saportia, Shanwangichnus, Taotieichnus, Vagorichnus, Virgaichnus*
17-Horizontal burrows with horizontal to vertical branches	*Arthrophycus, Caugichnus, Ctenopholeus, Intexalvichnus, Microspherichnus, Phycodes, Phymatoderma, Polykampton, Saerichnites, Streptichnus, Treptichnus, Tuberculichnus, Vitichnus*
18-Surface-coverage branching burrows	*Oldhamia*
19-Radial to rosetted structures	*Arenituba, Asterichnites, Asterichnus, Bifasciculus, Capodistria, Cladichnus, Clematischnia, Cycloichnus, Dactyloidites, Dactylophycus, Guanshanichnus, Gyrophyllites, Haentzschelinia, Hartsellea, Heliochone, Monocraterion, Parahaentzschelinia, Phoebichnus, Radiichnus, Rotamedusa, Scotolithus, Sphaerichnus, Stelloglyphus, Taxichnites, Volkichnium*
20-Sheaf burrow of thickly lined tubes	*Bornichnus, Schaubcylindrichnus*
21-Horizontal burrows with serial chambers	*Halimedides, Omanichnus, Sidichnus, Solanichnium, Strobilorhaphe*
22-Horizontal burrows with simple vertically oriented spreiten	*Halopoa, Teichichnus, Trichophycus*
23-Horizontal spiral burrows	*Multilaqueichnus, Pramollichnus, Spiralites, Spirodesmos, Spirophycus*
24-Horizontal helicoidal burrows	*Augerinoichnus, Avetoichnus, Helicodromites*

(continued)

Table 16.1 (continued)

25-Burrows with complex vertically oriented spreiten	*Caridolites, Daedalus, Dictyodora, Euflabella, Gyrochorte, Heimdallia, Paradictyodora, Stellavelum, Syringomorpha, Tursia*
26-Burrows with horizontal spreiten	*Criophycus, Falcichnites, Fuersichnus, Hydrancylus, Lamellaeichnus, Lobichnus, Lophoctenium, Multilamella, Phycosiphon, Rhizocorallium*
27-Burrows with helicoidal spreiten	*Echinospira, Spirophyton, Zoophycos*
28-Basal axial tubes with feather-like and spreite-like structures	*Hillichnus*
29-Mound-shaped structures	*Amanitichnus, Chomatichnus, Trusheimichnus*
30-Isolated and serial oval to almond-shaped burrows	*Calceoformites, Lockeia, Oravaichnium, Ptychoplasma*
31-Pentameral-shaped imprints and burrows	*Asteriacites, Pentichnus*
32-Oval-shaped imprints	*Astacimorphichnus, Corpusculichnus, Epibaion, Ichnocumulus, Musculopodus*
33-Dumbbell- and arrow-shaped burrows	*Arthraria, Bifungites, Monofungites*
34-Vertical plug-shaped burrows	*Amphorichnus, Astropolichnus, Bergaueria, Conichnus, Conostichus, Lithoplaision, Mammillichnis, Metaichna, Solicyclus*
35-Vertical unbranched burrows	*Altichnus, Bathichnus, Caletichnus, Cylindricum, Digitichnus, Felderichnus, Funalichnus, Guerraichnus, Laevicyclus, Lingulichnus, Lunatubichnus, Oikobesalon, Pustulichnus, Scalichnus, Siphonichnus, Skolithos*
36-Vertical single U- and Y-shaped burrows	*Arenicolites, Balanoglossites, Catenichnus, Diplocraterion, Glyphichnus, Liholites, Loloichnus, Paratisoa, Parmaichnus, Pholeus, Polarichnus, Psilonichnus, Solemyatuba, Tisoa*
37-Vertical multiple U- and Y-shaped burrows	*Kauriichnus, Lanicoidichna, Polykladichnus*
38-Vertical simple J-shaped burrows	*Artichnus, Keilorites, Naviculichnium*
39-Burrows with vertical tubes and stacked discs	*Tasselia*
40-Vertical helicoidal burrows	*Gyrolithes, Lapispira*
41-Burrows with shaft or bunch with downwards radiating probes	*Chondrites, Fascifodina, Lennea, Pragichnus, Saronichnus, Skolichnus, Trichichnus*
42-Vertical concentrically filled burrows	*Cylindrichnus, Rosselia*
43-Horizontal, branched concentrically filled burrows	*Asterosoma, Patagonichnus*
44-Spiral graphoglyptids	*Spirorhaphe*
45-Guided meandering graphoglyptids	*Cosmorhaphe, Helminthorhaphe, Spirocosmorhaphe*
46-Uniramous meandering graphoglyptids	*Belocosmorhaphe, Belorhaphe, Dendrotichnium, Helicolithus, Helicorhaphe, Punctorhaphe, Ubinia, Urohelminthoida*

(continued)

Table 16.1 (continued)

47-Radial graphoglyptids	*Arabesca, Chondrorhaphe, Dendrorhaphe, Estrellichnus, Fascisichnium, Glockerichnus, Lorenzinia, Persichnus, Tuapseichnium, Yakutatia*
48-Biramous meandering graphoglyptids	*Desmograpton, Oscillorhaphe, Paleomeandron*
49-Regular to irregular network graphoglyptids	*Acanthorhaphe, Megagrapton, Paleodictyon, Protopaleodictyon*
50-Maze and boxwork burrows	*Ardelia, Ophiomorpha, Sinusichnus, Spongeliomorpha, Thalassinoides*
51-Vertical to oblique simple ornamented burrows	*Capayanichnus, Liticuniculatus, Lunulichnus, Spirographites*
52-Simple to complex burrows with terminal chambers	*Camborygma, Egbellichnus, Katbergia, Macanopsis, Platicytes*
53-Chambers surrounded by burrows	*Maiakarichnus, Dagnichnus*
54-Isolated, clustered or interconnected cells	*Cellicalichnus, Celliforma, Corimbatichnus, Elipsoideichnus, Palmiraichnus, Rosellichnus, Uruguay*
55-Chambers with discrete thick linings	*Chubutolithes, Coprinisphaera, Eatonichnus, Feoichnus, Monesichnus, Quirogaichnus, Rebuffoichnus, Teisseirei*
56-Excavated chambers with thin linings undetachable from rock matrix	*Fictovichnus, Pallichnus, Scaphichnium*
57-Interconnected chambers and boxworks	*Attaichnus, Barberichnus, Coatonichnus, Daimoniobarax, Fleaglellius, Krausichnus, Masrichnus, Microfavichnus, Parowanichnus, Socialites, Syntermesichnus, Tacuruichnus, Termitichnus, Vondrichnus*
58-Holes, pits and galleries in walls and fillings	*Lazaichnus, Tombownichnus*
59-Cylindrical vertical to oblique borings	*Carporichnus, Flagrichnus, Linkichnus, Pecinolites, Stipitichnus, Trypanites, Tubulohyalichnus*
60-Borings with elliptical to sub-rectangular cross sections	*Osprioneides, Xylonichnus*
61-Winding borings	*Lapispecus, Maeandropolydora*
62-U-shaped borings	*Canaliparva, Caulostrepsis, Diorygma, Pseudopolydorites, Sertaterebrites*
63- Circular holes and pit-shaped borings	*Circolites, Curvichnus, Dipatulichnus, Lamniporichnus, Oichnus, Planavolites, Polydorichnus, Stellatichnus, Tremichnus*
64-Globular to spherical borings	*Granulohyalichnus, Planobola*
65-Pouch borings	*Asthenopodichnium, Aurimorpha, Bascomella, Cuenulites, Cubiculum, Petroxestes, Rogerella, Umbichnus*
66-Clavate-shaped borings	*Cavernula, Cylindricavus, Gastrochaenolites, Palaeosabella, Phrixichnus, Ramosulcichnus, Sanctum, Teredolites, Xylokrypta*

(continued)

Table 16.1 (continued)

67-Fracture-shaped bioerosion traces	*Belichnus, Bicrescomanducator, Caedichnus, Mandibulichnus*
68-Branched tubular borings	*Calciroda, Clionoides, Cunctichnus, Dekosichnus, Ichnoreticulina, Paleobuprestis, Paleoipidus, Paleoscolytus, Runia, Scolecia, Talpina*
69-Non-camerate network borings	*Anobichnium, Filuroda, Orthogonum, Rodocanalis*
70-Camerate network borings	*Feldmannia, Haimeina, Ichnogutta, Iramena, Pennatichnus, Pinaceocladichnus, Rhopalia, Saccomorpha*
71-Non-camerate boxwork borings	*Chaetophorites, Cycalichnus, Eurygonum*
72-Camerate boxwork borings	*Entobia, Unellichnus*
73-Spiral borings	*Helicotaphrichnus, Spirichnus*
74-Radial borings	*Fascichnus, Polyactina*
75-Dendritic and rosetted borings	*Abeliella, Calcideletrix, Clionolithes, Dendrina, Dictyoporus, Megascolytinus, Nododendrina, Pyrodendrina, Scolytolarvariumichnus*
76-Single circular to tear-shaped attachment bioerosion traces	*Anellusichnus, Centrichnus, Kardopomorphos, Lacrimichnus, Ophthalmichnus*
77-Multiple attachment bioerosion traces	*Finichnus, Flosculichnus, Podichnus*
78-Elongate or branched attachment bioerosion traces	*Camarichnus, Canalichnus, Renichnus, Stellichnus, Sulcichnus*
79-Groove bioerosion traces	*Ericichnus, Gnathichnus, Osteocallis, Radulichnus*

Analysis of ichnodiversity changes from the Ediacaran to the Holocene supports the three-phase kinetic model of Sepkoski (1984) based on analysis of marine body fossils. According to this model, the three main evolutionary radiations in the marine biosphere display an early exponential growth followed by subsequent slowing of growth. In the case of the Cambrian and Ordovician radiations there was very rapid growth of diversity in their initial stages until a plateau was reached later, whereas diversity rose slowly during the onset of the Mesozoic Marine Revolution and continues to do so. Controversies regarding this model have essentially revolved around potential geologic and paleontologic biases, such as increased exposure of sedimentary rocks, uneven number of studies per interval, and increased ease of fossil extraction (Raup 1976; Peters and Foote 2001; Alroy et al. 2008; Alroy 2010). For our interest here, the most serious controversy is the one on the diversity levels attained in the post-Paleozoic world. It has been argued that standardized curves show a final diversity only slightly higher than the Paleozoic maximum (e.g., Alroy et al. 2008; Alroy 2010, 2014) in sharp contrast with the much higher diversity levels shown by Sepkoski's curves (see also Bambach et al. 2004). However, new standardized curves show that Cenozoic diversity doubles Paleozoic values, supporting sustained marine diversification during the Mesozoic–Cenozoic (Bush and Bambach 2015), a pattern more consistent with the original Sepkoski's curves.

In particular, one of the potential biases affecting estimation of post-Paleozoic diversity levels is the so-called Pull of the Recent (Raup 1979). This effect operates in two ways. First, there is an increase in the volume of Cenozoic (and to a lesser extent Mesozoic) outcrops. Second, because the modern is much better sampled that the rest of the fossil record, taxa that occur in just one stratigraphic interval and have a modern representative will be plotted as occurring through the whole interval, resulting in an inflation of diversity levels in post-Paleozoic strata. Interestingly, the trace-fossil record is not biased in the same way. Certainly, neoichnologic studies are instrumental in recognizing some biogenic structures in the modern, helping to extend the stratigraphic range of some ichnotaxa. However, at the same time, modern counterparts of some trace fossils are lacking not because these behaviors have gone extinct, but because identification of modern traces is typically much more difficult than with fossil material, particularly in the case of bioturbation structures (Bromley 1996; Buatois and Mángano 2011a). Trace fossils tend to be enhanced by diagenetic processes that assist in their recognition (Magwood 1992) and many biogenic structures are cumulative structures, which consist of both abandoned and active components (Bromley and Frey 1974); casts of modern representatives of cumulative structures would only reflect the morphology of the open components occupied by the producer, resulting in a simpler morphology than the actual overall architecture, making identification of the ichnotaxon virtually impossible (Frey 1975; Frey and Seilacher 1980; Magwood 1992). The practical result of this would be an artificial drop in ichnodiversity in the modern. This more complex pattern exhibited by the trace-fossil record is referred herein as the Push and Pull of the Recent. To avoid this problem, we have plotted in the final curves together the Holocene and the modern.

Similar to Sepkoski's curves, ichnologic data show a phase of exponential growth in ichnodiversity followed by an equilibrium stage during the Cambrian Explosion and the Great Ordovician Biodiversification Event. Identical to body fossils, the Mesozoic Marine Revolution is associated with a slower increase in ichnodiversity. The overall coincidence between Sepkoski's curves and those presented in this chapter indicates similar diversity trajectories for animal diversity and their behaviors. However, in the case of post-Paleozoic faunas, whereas the curve for marine animals does not show any evidence of a plateau, ichnologic information seems to suggest that a plateau may have been reached for both marine bioturbation and bioerosion.

In contrast, trends in ichnodisparity reveal a more complicated picture (Fig. 16.2). Whereas the Cambrian Explosion is associated with an increase in both ichnodisparity and ichnodiversity (Mángano and Buatois 2014; see Chap. 3), the Great Ordovician Biodiversification Event and the Mesozoic Marine Revolution display different trends. A 263 % increase in ichnodisparity took place during the Terraneuvian as a result of the Cambrian Explosion (8 and 29 categories of architectural designs in the Ediacaran and Terraneuvian, respectively), but only a 45 % is associated with the Great Ordovician Biodiversification Event (38 categories of architectural design in the Furongian and 55 by the Late Ordovician). In addition, if bioturbation and bioerosion structures are considered separately, it is clear that bioerosion is responsible for the overall increase (17 % increase in ichnodisparity for bioturbation structures and 367 % for bioerosion structures). Whereas the Cambrian Explosion was the main event in the Phanerozoic for large-scale innovations in animal-sediment interactions, it is the Great Ordovician Biodiversification Event that played this role regarding bioerosion (Buatois et al. 2016a). If bioturbation structures are considered separately for shallow- and deep-marine environments, it is apparent that ichnodisparity in shallow-marine settings remained very close to Cambrian levels, whereas an increase took place in the deep sea (88 %; 17 categories of architectural design in the Furongian and 32 by the Late Ordovician). In the same fashion that broad innovations in bioerosion lagged behind those in bioturbation, the establishment of the main types of animal-sediment interactions in the deep sea took place later than in shallow-marine settings, as originally envisaged in models of deep-sea colonization (e.g., Uchman 2004). Because approximately half of the architectural categories that typify Ordovician deep-sea ichnofaunas first occurred in shallow-marine settings during the Cambrian, the overall impact of Ordovician deep-sea categories in global marine ichnodisparity levels is limited (Buatois et al. 2016a).

In turn, although an increase in ichnodisparity is apparent as a result of the Mesozoic Marine Revolution, distinguishing between bioturbation and bioerosion structures shows that the increase is restricted to the latter (19 % increase between the Late Triassic and the Late Cretaceous). Ichnodisparity of bioturbation structures in both shallow- and deep-marine settings does not display any significant increase in connection to the Mesozoic Marine Revolution.

A main conclusion of our analysis of secular changes in ichnodiversity and ichnodisparity during the Cambrian Explosion, the Great Ordovician Biodiversification Event and the Mesozoic Marine Revolution is that, although increases in ichnodiversity are invariably linked to evolutionary radiations, these are necessary but not sufficient conditions for ichnodisparity increases. In order to further explore the links between ichnodiversity and ichnodisparity and the possible underlying causes for increases in the latter, it is now useful to analyze the results of our compilations regarding continental environments.

Ichnodiversity compilations for continental environments show a more protracted process of colonization through the whole Phanerozoic as revealed by bioturbation structures (Fig. 16.1). Although the process of invasion of the continents seems to have been slow and gradual, an initial rapid increase took place by the Silurian-Devonian transition (see Chap. 6), with an impressive 967 % increase in ichnodiversity between the Wenlock and the Early Devonian (3 and 32 ichnogenera in the Wenlock and Early Devonian, respectively). As in the case of the Cambrian Explosion, this rapid diversification in continental settings is consistent with Sepkoski's (1978) exponential model for early diversification. Subsequent to that increase a plateau until the Early Mississippian is apparent. However, this may be in part simply an artifact due to the scarcity of continental outcrops of Late Devonian age (see Chap. 6). Subsequently, a slow but constant increase in ichnodiversity took place until the early Permian (Cisuralian), which displays an unusual peak (65 %, 91 ichnogenera). This peak has been noted in earlier studies and deemed controversial (Buatois et al. 1998).

It reflects the presence of a wide variety of arthropod trackways in overbank deposits, which at least in part results from a marked tendency towards oversplitting in trackway taxonomy. In particular, many arthropod are only known from the Permian of Germany (e.g., Holub and Kozur 1981; Walter 1983); many of these are considered doubtful (see Chap. 6). After a plateau that lasted the whole Triassic, another more modest peak is apparent in the Early Jurassic. This is, at least in part, a monographic effect (Raup 1976) resulting from the high number of new arthropod trackway genera introduced by Hitchcock (1858, 1865) based on his analysis of continental trace fossils from the Connecticut Valley. Many of these have never been recorded elsewhere and are now regarded as doubtful (Rainforth 2005), so they have been omitted in our compilation. However, even leaving aside these doubtful ichnotaxa and only retaining those regarded as valid, the Early Jurassic ichnodiversity peak still persists (21 %; 61 and 74 ichnogenera in the Late Triassic and Early Jurassic, respectively). Since the Middle Jurassic onwards, ichnodiversity experienced a relatively constant increase.

Bioerosion in continental environments experienced a much later development than bioturbation. Although wood borings were mentioned for the early Permian (von Kušta 1880), the earliest convincing evidence of bioerosion in continental environments is from the Late Triassic, with the recording of six ichnotaxa representing wood bioerosion (Tapanila and Roberts 2012). Notably, this record predates the earliest record of marine bioerosion in wood, which is Early Jurassic (Villegas-Martín et al. 2012). In turn, the earliest record of bioerosion in bone is from the Early Jurassic (undetermined ichnotaxon), with the ichnogenus *Cubiculum* being recorded for the first time in the Late Jurassic (Xing et al. 2015). This was followed by a plateau until the Late Cretaceous with the addition of ten new ichnogenera. Since then, ichnodiversity of bioerosion structures reached a plateau that continues until the Holocene.

After the initial rapid increase in ichnodiversity of bioturbation structures by the Silurian-Devonian transition, colonization of freshwater settings was apparently quite gradual. It has been suggested that this slow pace may have resulted from the need to develop innovative styles of reproduction and dispersal, as well as complex osmoregulatory systems (Miller and Labandeira 2002). The fact that no plateau indicating an equilibrium stage in diversification is apparent for bioturbation structures may suggest that the invasion of terrestrial environments is a still ongoing process. This is consistent with the fact that the utilization of freshwater infaunal ecospace seems to have been less complete than in their marine counterparts (Miller and Labandeira 2002). Continental bioerosion ichnogenera seem to have reached a plateau by the end of the Mesozoic, but their ichnotaxonomy is still in its infancy and it is not unexpected that this trend will change with further studies.

As with ichnodiversity, ichnodisparity in continental environments reflects the process of protracted colonization (Fig. 16.2). Ichnodisparity curves of bioturbation structures reveal a rapid increase with the onset of widespread colonization by the Silurian-Devonian transition (see Chap. 6), with a 267 % increase in ichnodisparity between the Wenlock and the Early Devonian (3 and 11 categories of architectural designs in the Wenlock and Early Devonian, respectively). This was followed by a very slow increase until the Late Cretaceous that records a hike (29 %; 28 categories of architectural design in the Early Cretaceous and 36 in the Late Cretaceous), albeit limited, reaching ichnodisparity levels that persist until the Recent. The Late Cretaceous ichnodisparity peak is also expressed by bioerosion structures. However, it should be noted that all categories of architectural designs in freshwater subaqueous environments and transitional terrestrial to subaqueous settings originated in marine environments and only subsequently occurred in continental settings. In contrast, there are six categories that are exclusive of terrestrial settings (see Chap. 11). In other words, the main innovations required to invade freshwater were already present in the marine realm, but the only true behavioral innovations in continental environments were those required to colonize subaerially exposed settings. These are mostly the architectural designs developed by insects nesting in paleosols (see Chap. 13).

To summarize, our analysis shows that the key factor in building up ichnodisparity is not the existence of an evolutionary radiation *per se*, but the colonization of empty ecospace. The Cambrian Explosion records the colonization of empty ecospace and, therefore, displayed an increase in both ichnodisparity and ichnodiversity. A similar situation is expressed by bioerosion during the Great Ordovician Biodiversification Event in connection with the colonization of hard substrates. A third increase in ichnodisparity is revealed by the colonization of paleosols which experienced dramatic evolutionary innovations by the end of the Mesozoic. Finally, the cradle of evolutionary innovations is in shallow-marine settings (see Sect. 16.5). This is revealed by the appearance in shallow seas of all the architectural designs that subsequently expanded into freshwater and a substantial number of those that later bloomed in the deep sea. In almost all these cases, the ichnodisparity increase is followed by a subsequent further increase in ichnodiversity, as it is illustrated, by the diversification of insect nesting structures during the Cenozoic, following the establishment of the basic architectural designs in the Late Cretaceous. This pattern supports analysis based on body fossils that indicates a “first disparity, then diversity” scenario (Foote 1993, 1997; Erwin 2007; see Chap. 6).

Finally, the limitations of ichnodiversity analysis to unravel evolutionary trends need to be addressed (see Buatois and Mángano 2013 for a detailed analysis). As stated many times, the fact that ichnodiversity cannot be equated with the actual diversity of organisms represents a cautionary note (Ekdale 1985). Behavioral convergence resulting in different organisms being able to produce the same ichnotaxon may mask evolutionary trends. The opposite case, the one of several ichnotaxa resulting from the work of a single producer, also undoubtedly introduced a bias in ichnodiversity analysis through geologic time. Because of this, the different chapters exploring the ichnologic blueprints of evolutionary radiations use a plurality of conceptual and methodological tools rather than being restricted to an analysis of the number of ichnogenera or architectural designs. For example, it is clear that burrows produced by decapod crustaceans represent one of the most, if not the most, archetypal biogenic structures of the Mesozoic Marine Revolution. However, because some of its most characteristic structures, namely burrow systems included in *Thalassinoides*, are produced not only by decapod crustaceans, but by other organisms with a stratigraphic range that extends well before the Mesozoic, the importance of crustacean burrows remains undetected if only ichnodiversity is considered. In other words, the long stratigraphic range of *Thalassinoides* is misleading with respect to its key role during the Mesozoic Marine Revolution. A clearer picture emerges when, for example, abundance is considered as well (Carmona et al. 2004; see Chap. 9).

Also, in part as a result of behavioral convergence, ichnogeneric extinction rates are remarkably low. It has been noted that increases in diversity within clades may be produced from a drop in extinction rate rather that diversification *per se*, resulting in the so-called "pseudoradiations" (Simões et al. 2016). In the case of trace-fossil data, extinction rates can be regarded not only as low but also as constant, the latter at least since the Ordovician. Because of the impossibility of equating biological diversity and ichnodiversity, the trace-fossil expression of evolutionary radiations is not primarily of a phylogenetic nature, but rather reflects behavioral innovations.

Other problems are evident while dealing with ichnodiversity changes in specific environments through the Phanerozoic. Because there is a trend to increased infaunalization through time, the colonization of deeper tiers is conducive to obliteration of the more shallowly emplaced structures, which in many cases represent a substantial contribution to ichnodiversity. As a result, a decrease in ichnodiversity through time rather than an increase, has been noted in the case of tidal flats (Mángano et al. 2002; Mángano and Buatois 2015) and lakes (see Chap. 11). These cases underscore the importance of careful evaluation of taphonomic overprints.

Also, using ichnodiversity at ichnogeneric level may preclude detection of other patterns. Ichnospecies reflect minor behavioral variations and, therefore, they may help to detect more subtle trends in behavioral innovations (see Chap. 3). A large number of ichnogenera that have their first occurrence early in the Paleozoic seem to have displayed an increase in the number of ichnospecies through the Phanerozoic (see Chaps. 3 and 9). Exploring patterns of ichnospecies distribution through time is a promising line of research, although this would imply in-depth critical reevaluation of trace-fossil taxonomy at this rank, something beyond the scope of the present study.

Regardless of potential shortcomings, our review indicates that ichnologic information (including both ichnodiversity and ichnodisparity) is highly useful as an independent line of evidence to understand paleobiologic trends through geologic time.

16.3 Benthic Fauna Response to Mass Extinctions

Ichnologic information typically reveals a set of common responses to the three mass extinctions analyzed in this book, the end-Permian (see Chap. 7), the end-Triassic (see Chap. 8), and the end-Cretaceous (see Chap. 12). Most of these extinction events are characterized by a reduction in ichnodiversity, decrease in degree of bioturbation, reduction of bioturbation depth, size reduction, dominance of simple trace fossils in post-extinction strata, preferential survival of ichnotaxa produced by deposit feeders, and selective extinction in shallow-marine ecosystems. How pronounced were these effects seems to depend on the severity of the mass extinction event, with the end-Permian mass extinction clearly showing the most severe impact from an ichnologic standpoint, showing consistency with body-fossil data. In turn, this is reflected in the pattern of recovery after the extinction, with longer recovery times involved in the end-Permian mass extinction in comparison with the end-Cretaceous event. Ichnologic information on the other two major events, the end-Ordovician and late Devonian extinctions is patchy, with only a few studies available (McCann 1990; Herringshaw and Davies 2008; Buatois et al. 2013) and, therefore, any generalization remains premature.

Although these extinctions are associated to a decrease in ichnodiversity, actual extinction of invertebrate ichnotaxa is quite rare. On the contrary, ichnotaxa that disappeared after the mass extinctions for the most part reappeared during the recovery time, representing Lazarus ichnotaxa (Gibert 2003). As noted previously, trace-fossil extinction rates tend to be very low, a fact that, at least in the case of relatively simple behaviors, results from behavioral convergence. Some ichnotaxa (e.g., the undermat miner *Oldhamia*, the large trail *Climactichnites*), however, seem to reflect behaviors that have apparently disappeared by the end of the Cambrian, together with their producers.

Because the curves illustrated in Figs. 16.1 and 16.2 have been compiled as range through data, they are of limited use to detect changes in ichnodiversity as a result of mass extinctions. For example, whereas a significant drop in ichnodiversity is associated with the end-Permian mass extinction (see Chap. 7), this is not reflected by the ichnodiversity curves. Similarly, the end-Triassic mass extinction resulted in a decrease in ichnodiversity, albeit more modest (see Chap. 8), which is not recorded in our ichnodiversity curves. The absence of an ichnodiversity drop in these curves is simply an artifact resulting from the methodology employed in their construction. It is therefore surprising that a 7 % decrease in total marine ichnodiversity (5 % for bioturbation structures and 15 % for bioerosion structures) is revealed by these curves in connection with the end-Cretaceous mass extinction. The Late Cretaceous peak and subsequent drop in ichnodiversity are also present in the curves that were plotted eliminating the occurrence of singletons.

Decrease in the degree of bioturbation has been noted in connection with many mass extinction events. Although comparative analysis of mass extinctions from a trace-fossil perspective are still in their infancy, available information seems to suggest that the extent of this decrease in intensity of bioturbation tends to reflect how profound was the impact of the event. This is illustrated by the end-Permian mass extinction, which shows a collapse of the mixed layer (see Chap. 7 and Sect. 16.4; Buatois and Mángano 2011b; Hofmann et al. 2015). A similar situation has not been recorded so far associated with any of the other mass extinction events. In fact, intense bioturbation has been noted in Danian post-extinction deposits (see Chap. 12).

Reduction in the size of trace fossils has been detected in connection with many mass extinction events, most notably the end-Permian (see Chap. 7) and end-Triassic (see Chap. 8). In other cases, such as the end-Cretaceous, this trend is not apparent (see Chap. 12, although see Wiest et al. 2015 for documentation of trace-fossil size reduction in the aftermath of the end-Cretaceous mass extinction). The so-called Lilliput effect has been noted in the paleobiologic literature to explain the sharp decrease in body size, based on both the body fossil and trace-fossil records, in the aftermath of mass extinctions (Urbanek 1993; Twitchett 2007). Explanations for this size reduction are still unclear, with both externalist and internalist causes being involved. Limited oxygen and food have been invoked as likely candidates for the former (Twitchett 2007), whereas survival of small taxa; the dwarfing of larger lineages and the evolutionary miniaturization from larger ancestral stocks fall among the later (Harries and Knorr 2009).

Dominance of simple trace fossils is another typical feature in post-extinction strata. For example, simple trace fossils attributed to *Planolites* are the first in reappearing after the end-Permian mass extinction (see Chap. 7). Simple forms, such as *Planolites* and *Palaeophycus*, seem to be common in Lower Jurassic post-extinction deposits as well (see Chap. 8). The prevalence of these simple morphologies overall reflect very simple feeding behaviors, most likely reflecting opportunistic population strategies in the aftermath of mass extinctions (Fraiser and Bottjer 2009).

It has long been noted that organisms are differentially affected during extinctions according to trophic type (Jablonski and Raup 1995; Smith and Jeffrey 1998; Hansen et al. 2004; Twitchett 2006). In particular, suspension feeders tend to have been more affected than deposit feeders during mass extinctions. In this regard, it has been concluded that both selective deposit feeding and omnivory significantly enhance survivability during mass extinction events (Twitchett 2006). This is clearly illustrated by the overwhelming dominance of deposit-feeding traces in Danian post-extinction deposits (see Chap. 12). Also, post-extinction late Devonian ichnofaunas are dominated by structures produced by selective deposit feeders, whereas suspension-feeding burrows are absent (Buatois et al. 2013).

Ichnofaunas from shallow-marine environments tend to be more strongly affected than those in marginal-marine and deep-marine settings. Marginal-marine, brackish-water faunas typically consist of opportunistic animals that flourish under extreme conditions. Therefore, they are able to rapidly colonize environments after a major disturbance, such as mass extinctions. Of the five colonization phases recognized for brackish-water settings by Buatois et al. (2005), only the end of the first (Ediacaran–Ordovician) and the third (Permian–Triassic) coincide with mass extinctions (the Late Ordovician and Late Triassic mass extinctions, respectively). The remaining three of the "Big Five", the late Devonian, end-Permian, and end-Cretaceous mass extinctions, does not show any impact in marginal-marine biotas. In the same vein, ichnofaunas from deep-water settings do not seem to have been strongly affected by mass extinctions (Uchman 2004). No major crisis has been associated with any of the "Big Five" in the deep sea, other than a reduction in the diversity and abundance of graphoglyptids in the case of the end-Ordovician and end-Cretaceous mass extinctions (Uchman 2003).

16.4 Patterns of Ecospace Colonization

Having established that there are some recurrent ichnologic patterns involving evolutionary radiations and mass extinctions, we may now explore if recurrent motifs can be established in connection with colonization of empty or underutilized ecospace. In other words, is it possible to detect trace-fossil assemblages that recur through geologic time not as a response to environmental constrains (as is the case of ichnofacies), but driven by large-scale evolutionary controls instead? We have attempted to address this question in a previous paper, referring to this particular recurrence of ichnoassemblages revealing common strategies in ecospace colonization as "the Déjà vu effect" (Buatois and Mángano 2011b). In this chapter, we argue that three main types of trace-fossil assemblages can be recognized in connection with exploitation of empty or underutilized ecospace.

The first of these assemblages consists of very small grazing trails (e.g., *Helminthopsis*, *Helminthoidichnites*, *Gordia*) produced by epifaunal or very shallow infaunal vermiform animals, very shallow-tier feeding structures (e.g., *Treptichnus*, *Oldhamia*, *Pilichnus*) of infaunal vermiform organisms, and (in some cases) trackways (e.g., *Diplichnites*, *Stiaria*) of epifaunal arthropods (Buatois and Mángano 2011b). Almost invariably trace fossils occur in association with structures suggestive of microbial stabilization, such as wrinkle marks, palimpsest ripples, and old elephant skin (Noffke 2010; Buatois and Mángano 2012a). The associated primary sedimentary fabric and bedding-plane physical sedimentary structures are superbly preserved (e.g., Buatois et al. 1997). Ichnofaunas reveal superficial and shallow-tier grazing and mining of microbial mats in the absence of substantial infaunal bioturbation. The presence of microbial mats allows preservation of minute trace fossils, displaying delicate fine morphologic features (Buatois and Mángano 2011b). These trace-fossil assemblages occur across a wide range of environmental settings, such as Ediacaran-lower Cambrian shallow-marine (e.g., Gehling 1999; Buatois et al. 2014), Cambrian deep-marine (e.g., Buatois and Mángano 2003), and late Paleozoic continental to fluvio-estuarine (Buatois et al. 1997; Mángano et al. 1997) settings, invariably in connection with empty or underutilized ecospace.

The second assemblage is characterized by shallow-tier burrows (*Spongeliomorpha*, *Halopoa*), trails (*Cruziana*), and resting traces (*Rusophycus*) with well-developed ornamentation, typically bioglyphs. Very shallow-tier burrows and trackways may be present as well. The occurrence of well-preserved bioglyphs and the sharp burrow boundaries suggest emplacement in sediment that was firm at or close to the sea bottom. These trace-fossil assemblages are associated with widespread firm substrates and the virtual absence of a mixed layer (Droser et al. 2004; Jensen et al. 2005; Buatois and Mángano 2011b; Mángano et al. 2013; Hofmann et al. 2015). This is illustrated by two apparently unrelated ichnofaunas: those in Cambrian–Ordovician and Lower Triassic shallow-marine environments. Both deposits are characterized by preferential preservation of epifaunal and very shallow-tier infaunal trace fossils; paucity of mid- and deep-tier trace fossils; absence of mottled bioturbation textures; and dominance of cohesive substrates in open-marine environments (Hofmann et al. 2015). In the case of lower Paleozoic strata, the mixed layer was still incipient and poorly developed (Droser et al. 2004; Jensen et al. 2005; Callow and Brasier 2009; Mángano et al. 2013), whereas in the Lower Triassic the mixed layer may have collapsed as a result of the end-Permian extinction (Buatois and Mángano 2011b; Hofmann et al. 2015; see Chap. 9). The ichnologic responses in both situations were essentially identical.

The third assemblage is characterized by the presence of horizontal branched burrow systems (e.g., *Multina*, *Vagorichnus*) at the base of event sandstone beds (Buatois and Mángano 2011b). These burrow systems are preserved along lithologic interfaces creating virtually no disturbance in the primary sedimentary fabric. *Multina* is common at the base of lower Paleozoic marine tempestites and turbidites, where it records post-event colonization (e.g., Buatois and Mángano 2004, 2012b; Buatois et al. 2009). *Vagorichnus* has been recorded at the base of Jurassic lacustrine turbidites (Buatois et al. 1995, 1996). Although these occurrences are from disparate environments and from rocks of different ages, they are all associated with an increase in burrowing depth reflecting initial exploitation of the infaunal ecospace (Buatois and Mángano 2011b). From an evolutionary standpoint, this incipient colonization of the infaunal ecospace preceded the onset of more intense bioturbation and the establishment of a well-developed mixed layer.

The recurrent presence of these three types of trace-fossil assemblages in rocks of different ages and formed under a wide variety of environmental settings can only be understood under the light of the evolutionary prism. These assemblages reveal a limited repertoire of behavioral strategies that allow benthic faunas to colonize empty or underutilized ecospace. Fossilization of these behavioral strategies in the form of biogenic structures is mediated by a set of preservational conditions resulting from the recurrent opening of a taphonomic window. This window was responsible for the preservation of surface and shallow-tier structures which typically are obliterated by deeper-tier and more intense bioturbation (Bromley 1996).

16.5 Environmental Shifts Through Time

A number of studies published for the most part in the eighties and nineties revealed that the fossil record can be characterized by a recurrent pattern of onshore origination of evolutionary innovations and their subsequent expansion to deeper water, resulting in the proposal of the so-called "onshore–offshore model" (e.g., Jablonski et al. 1983; Sepkoski and Miller 1985; Jablonski and Bottjer 1990; Sepkoski 1991; Sepkoski and Sheehan 1983). In fact, it has been argued that an onshore–offshore pattern is displayed by Sepkoski's evolutionary faunas themselves, as illustrated by the replacement of trilobite-rich communities by mollusk-rich communities in shallow-water niches throughout the Paleozoic (Sepkoski and Miller 1985).

The trace-fossil record provides further empirical support to this model across a broad range of scales. First, an onshore–offshore pattern is evident from individual ichnotaxa, showing either evidence of expansion or retreat. In the first case, an ichnogenus occurring for the first time in shallow water subsequently extends its environmental range into deeper-marine settings without loss of onshore representatives. In the second case, migration into deeper water occurs together with loss of onshore representatives (Bottjer et al. 1988; Stanley and Pickerill 1993). Examples of expansion include *Ophiomorpha* (Bottjer et al. 1988; Tchoumatchenco and Uchman 2001), *Scolicia* (Seilacher 1986) and *Rhizocorallium commune* (Knaust 2013). An example of retreat is *Zoophycos* (Bottjer et al. 1988).

Second, entire groups of trace fossils may display the onshore–offshore pattern. The best example is graphoglyptids, which in the early Cambrian occur in shallow water, but subsequently migrated to the deep sea (Crimes and Anderson 1985; Jensen and Mens 1999), where they became the core component of the *Nereites* Ichnofacies.

Third, the onshore–offshore pattern is also displayed by ichnofabrics. For example, it has been argued that in carbonate settings intense bioturbation first took place in shallow-water settings and only later seaward (Droser and Bottjer 1989). This pattern may reflect the fact that niche partitioning within the substrate first developed in shallow water and subsequently expanded into deeper water.

Fourth, and at a larger scale, the onshore–offshore pattern is displayed in connection with the colonization of empty or underutilized ecospace. This is shown by trace-fossil evidence of original colonization of shallow-marine settings and the progressive subsequent expansion into the deep sea, marginal-marine environments and continental settings. Also, this pattern is apparent within continental environments themselves, as demonstrated by the initial colonization of lake-margin settings and later expansion into subaqueous lacustrine settings (Buatois and Mangano 1993; Buatois et al. 1998; see Chaps. 5 and 6). This is certainly analogous to the migration of plants from upland areas to the lowlands during the Carboniferous-Permian transition (DiMichele and Aronson 1992) and the origination of aquatic insects in running water and subsequent expansion into lacustrine habitats (Wooton 1988).

16.6 Conclusions

Comparative analysis of the ichnologic record of major evolutionary events allows detecting recurrent patterns that may help to further increase our understanding of the underlying evolutionary dynamics of animal-substrate interactions through geologic time. In particular, we have detected recurrent patterns of organism-substrate interactions during evolutionary radiations, benthic fauna response to mass extinctions, strategies of ecospace colonization, and environmental shifts through time. Evolutionary radiations are invariably associated with an ichnodiversity increase, whereas increases in ichnodisparity are linked to the colonization of empty ecospace. Evaluation of mass extinction events suggests common responses from the perspective of animal-substrate interactions, namely a reduction in ichnodiversity, decrease in degree of bioturbation, reduction of bioturbation depth, size reduction, dominance of simple trace fossils in post-extinction strata, preferential survival of ichnotaxa produced by deposit feeders, and selective extinction in shallow-marine ecosystems. The recurrent presence of certain trace-fossil assemblages in rocks of different ages and formed under a wide variety of environmental settings seems to suggest a limited repertoire of behavioral strategies for colonization of empty or underutilized ecospace. The trace-fossil record provides further empirical support to the onshore–offshore model across a broad range of scales.

Acknowledgments We thank José Carlos Garcia Ramos, Jorge Genise, Verónica Krapovickas, Conrad Labandeira, Marisa Lopez-Cabrera, Radek Mikuláš, Nic Minter, Eduardo Olivero, Laura Piñuela, Cecilia Pirrone, Eric Roberts, Alfred Uchman, Mark Wilson, and Max Wisshak for generously providing highly useful advice and information at different stages of the compilation. Eduardo Olivero and Roy Plotnick reviewed the chapter providing highly useful feedback. Kai Zhou assisted us with plotting the information in tables and charts.

References

Alroy J (2010) The shifting balance of diversity among major marine animal groups. Science 329:1191–1194

Alroy J (2014) Accurate and precise estimates of origination and extinction rates. Paleobiology 40:374–397

Alroy J, Aberhan M, Bottjer DJ, Foote M, Fürsich FT, Harries PJ, Hendy AJW, Holland SM, Ivany LC, Kiessling W, Kosnik MA, Marshall CR, McGowan AJ, Miller AI, Olszewski TD, Patzkowsky ME, Peters SE, Villier L, Wagner PJ, Bonuso N, Borkow PS, Brenneis B, Clapham ME, Fall LM, Ferguson CA, Hanson VL, Krug AZ, Layou KM, Leckey EH, Nürnberg S, Powers CM, Sessa JA, Simpson C, Tomaovch A, Visaggi CC (2008) Phanerozoic trends in the global diversity of marine invertebrates. Science 321:97–100

Bambach RK, Knoll AH, Wang SC (2004) Origination, extinction, and mass depletions of marine diversity. Paleobiology 30:522–542

Banerjee NR, Furnes H, Muehlenbachs K, Staudigel H, de Wit M (2006) Preservation of ~ 3.4–3.5 Ga microbial biomarkers in pillow lavas and hyaloclastites from the Barberton Greenstone Belt, South Africa. Earth Planet Sci Lett 241:707–722

Banerjee NR, Simonetti A, Furnes H, Muehlenbachs K, Staudigel H, Heaman L, Van Kranendonk MJ (2007) Direct dating of Archean microbial ichnofossils. Geology 35:487–490

Bottjer DJ, Droser ML, Jablonski D (1988) Palaeoenvironmental trends in the history of trace fossils. Nature 333:252–255

Bromley RG (1996) Trace fossils: biology, taphonomy and applications. Chapman & Hall, London

Bromley RG, Frey RW (1974) Redescription of the trace fossil *Gyrolithes* and taxonomic evaluation of *Thalassinoides*, *Ophiomorpha* and *Spongeliomorpha*. Bull Geol Soc Den 23:311–335

Buatois LA, Mángano MG, Wilson MA, Wisshak M (in review) Categories of architectural designs in trace fossils: a measure of ichnodisparity. Earth Sci Rev

Buatois LA, Mangano MG (1993) Ecospace utilization, paleoenvironmental trends and the evolution of early nonmarine biotas. Geology 21:595–598

Buatois LA, Mángano MG (2003) Early colonization of the deep sea: ichnologic evidence of deep-marine benthic ecology from the Early Cambrian of northwest Argentina. Palaios 18:572–581

Buatois LA, Mángano MG (2004) Terminal Proterozoic–Early Cambrian ecosystems: Ichnology of the Puncoviscana Formation, Northwest Argentina. In: Webby BD, Mángano MG, Buatois LA (eds) Trace Fossils in evolutionary palaeoecology. Fossils & Strata 51:1–16

Buatois LA, Mángano MG (2011a) Ichnology: organism–substrate interactions in space and time. Cambridge University Press, Cambridge

Buatois LA, Mángano MG (2011b) The déjà vu effect: recurrent patterns in exploitation of ecospace, establishment of the mixed layer, and distribution of matgrounds. Geology 39:1163–1166

Buatois LA, Mángano MG (2012a) The trace-fossil record of organism-matground interactions in space and time. In: Noffke N, Chafetz H (eds) Microbial mats in siliciclastic depositional systems through time, vol 101. SEPM Spec Publ, Tulsa

Buatois LA, Mángano MG (2012b) An early Cambrian shallow-marine ichnofauna from the Puncoviscana Formation of northwest Argentina: the interplay between sophisticated feeding behaviors, matgrounds and sea-level changes. J Paleontol 86:7–18

Buatois LA, Mángano MG (2013) Ichnodiversity and ichnodisparity: significance and caveats. Lethaia 46:281–292

Buatois LA, Mángano MG, Wu X, Zhang G (1995) *Vagorichnus*, a new ichnogenus for feeding burrow systems and its occurrence as discrete and compound ichnotaxa in Jurassic lacuslrine turbidites of central China. Ichnos 3:265–272

Buatois LA, Mángano MG, Wu X, Zhang G (1996) Trace fossils from Jurassic lacuslrine turbidites of the Anyao Formation (central China) and their environmental and evolutionary significance. Ichnos 4:287–303

Buatois LA, Mángano MG, Maples CG, Lanier WP (1997) The paradox of nonmarine ichnofaunas in tidal rhythmites: integrating sedimentologic and ichnologic data from the Late Carboniferous of eastern Kansas, USA. Palaios 12:467–481

Buatois LA, Mángano MG, Genise JF, Taylor TN (1998) The ichnologic record of the invertebrate invasion of nonmarine ecosystems: evolutionary trends in ecospace utilization, environmental expansion, and behavioral complexity. Palaios 13:217–240

Buatois LA, Gingras MK, MacEachern J, Mángano MG, Zonneveld JP, Pemberton SG, Netto RG, Martin AJ (2005) Colonization of brackish-water systems through time: evidence from the trace-fossil record. Palaios 20:321–347

Buatois LA, Mángano MG, Brussa E, Benedetto JL, Pompei J (2009) The changing face of the deep: colonization of the Early Ordovician deep-sea floor, Puna, Northwest Argentina. Palaeogeogr Palaeoclimatol Palaeoecol 280:291–299

Buatois LA, Angulo S, Mángano MG (2013) Onshore expansion of benthic communities after the Late Devonian mass extinction. Lethaia 46:251–261

Buatois LA, Narbonne GM, Mángano MG, Carmona NB, Myrow P (2014) Ediacaran matground ecology persisted into the earliest Cambrian. Nat Commun 5:3544

Buatois LA, Mángano MG, Olea RA, Wilson MA (2016a) Decoupled evolution of soft and hard substrate communities during the Cambrian Explosion and Great Ordovician Biodiversification Event. PNAS 113:6945–6948

Buatois LA, Wisshak M, Wilson MA, Mángano MG (2016b) Categories of architectural designs in trace fossils: A measure of ichnodisparity. Earth Sc Rev (in press)

Bush AM, Bambach RK (2015) Sustained Mesozoic-Cenozoic diversification of marine Metazoa: a consistent signal from the fossil record. Geology 43:979–982

Callow RHT, Brasier MD (2009) Remarkable preservation of microbial mats in Neoproterozoic siliciclastic settings: implications for Ediacaran taphonomic models. Earth Sci Rev 96:207–219

Carmona NB, Buatois LA, Mángano MG (2004) The trace fossil record of burrowing decapod crustaceans: evaluating evolutionary radiations and behavioural convergence. In: Webby BD, Mángano MG, Buatois LA (eds) Trace fossils in evolutionary palaeoecology. Fossils & Strata 51:141–153

Crimes TP, Anderson MM (1985) Trace fossils from Late Precambrian-Early Cambrian strata of southeastern Newfoundland (Canada): temporal and environmental implications. J Paleontol 59:310–343

DiMichele WA, Aronson RB (1992) The Pennsylvanian-Permian vegetational transition: a terrestrial analogue to the onshore-offshore hypothesis. Evolution 46:807–824

Droser ML, Bottjer DJ (1989) Ordovician increase in extend and depth of bioturbation: implications for understanding Early Paleozoic ecospace utilization. Geology 17:850–852

Droser ML, Jensen S, Gehling JG (2004) Development of early Palaeozoic ichnofabrics: evidence from shallow marine siliciclastics. In: McIlroy D (ed) The application of ichnology to palaeoenvironmental and stratigraphic analysis, vol 228. Geol Soc Spec Publ, London

Ekdale AA (1985) Paleoecology of the marine endobenthos. Palaeogeogr Palaeoclimatol Palaeoecol 50:63–81

Erwin DH (1992) A preliminary classification of evolutionary radiations. Hist Biol 6:133–147

Erwin DH (2007) Disparity: morphological pattern and developmental context. Palaeontology 50:57–73

Foote M (1993) Contributions of individual taxa to overall morphological disparity. Paleobiology 19:403–419

Foote M (1997) Evolution of morphological diversity. Annu Rev Ecol Syst 28:129–152

Fraiser ML, Bottjer DJ (2009) Opportunistic behaviour of invertebrate marine tracemakers during the Early Triassic aftermath of the end-Permian mass extinction. Aust J Earth Sci 56:841–857

Frey RW (1975) The realm of ichnology, its strengths and limitations. In: Frey RW (ed) The study of trace fossils: a synthesis of principles, problems, and procedures in ichnology. Springer, New York

Frey RW, Seilacher A (1980) Uniformity in marine invertebrate ichnology. Lethaia 13:183–207

Furnes H, Banerjee NR, Muehlenbachs K, Staudigel H, de Wit M (2004) Early life recorded in Archean pillow lavas. Science 304:578–581

Furnes H, Banerjee NR, Staudigel H, Muehlenbachs K, de Wit M, McLoughlin N, Van Kranendonk M (2007) Bioalteration textures in recent to mesoarchean pillow lavas: a petrographic signature of subsurface life in oceanic igneous rocks. Precambrian Res 158:156–176

Gehling JG (1999) Microbial mats in terminal Proterozoic siliciclastics: Ediacaran death masks. Palaios 14:40–57

Genise JF (2000) The ichnofamily Celliformidae for *Celliforma* and allied ichnogenera. Ichnos 7:267–282

Genise JF (2004) Ichnotaxonomy and ichnostratigraphy of chambered trace fossils in palaeosols attributed to coleopterans, ants and termites. In: McIlroy D (ed) The application of ichnology to palaeoenvironmental and stratigraphic analysis, vol 228. Geol Soc Spec Publ, London

Gibert JM de (2003) Criterios icnológicos para reconocer comportamientos homólogos y homoplásticos en el registro fósil. In: Buatois LA, Mángano MG (eds) Icnología: hacia una convergencia entre geología y biología. Argent Assoc Paleontol Spec Publ 9:9–15

Gould SJ (1980) The promise of paleobiology as a nomothetic, evolutionary discipline. Paleobiology 6:96–118

Hansen TA, Kelley PH, Haasl DM (2004) Paleoecological pattern in molluscan extinctions and recoveries: comparison of the Cretaceous–Paleogene and Eocene–Oligocene extinctions in North America. Palaeogeogr Palaeoclimatol Palaeoecol 214:233–242

Häntzschel W (1975) Trace fossils and problematica. In: Teichert C (ed) Treatise on Invertebrate Paleontology, Part W, Miscellanea, Supplement 1. Geological Society of America and University of Kansas Press, Lawrence

Harries PJ, Knorr PO (2009) What does the "Lilliput effect" mean? Palaeogeogr Palaeoclimatol Palaeoecol 284:4–10

Herringshaw LG, Davies NS (2008) Bioturbation levels during the end-Ordovician extinction event: a case study of shallow marine strata from the Welsh Basin. Aquat Biol 2:279–287

Hitchcock E (1858) Ichnology of New England: a report on the sandstone of the Connecticut Valley, especially its fossil footmarks. W. White, Boston

Hitchcock E (1865) Supplement to the ichnology of New England. Commonwealth of Massachusetts, Boston

Hofmann R, Buatois LA, MacNaughton RB, Mángano MG (2015) Loss of the sedimentary mixed layer as a result of the end-Permian extinction. Palaeogeogr Palaeoclimatol Palaeoecol 428:1–11

Holub V, Kozur H (1981) Arthropodenfährten aus dem Rotliegenden der CSSR. Geol Paläont Mitt Innsbruck 11:95–148

Jablonski D, Bottjer DJ (1990) The ecology of evolutionary innovation: the fossil record. In: Nitecki MH (ed) Evolutionary innovations. University of Chicago Press, Chicago

Jablonski D, Raup DM (1995) Selectivity of end-Cretaceous marine bivalve extinctions. Science 268:389–391

Jablonski D, Sepkoski JJ Jr, Bottjer DJ, Sheehan PM (1983) Onshore-offshore patterns in the evolution of Phanerozoic shelf communities. Science 222:1123–1125

Jensen S, Mens K (1999) A Lower Cambrian shallow-water occurrence of the branching "deep-water" type trace fossil *Dendrorhaphe* from the Lontova Formation, Eastern Latvia. Paläontol Z 73:187–193

Jensen S, Droser ML, Gehling JG (2005) Trace fossil preservation and the early evolution of animals. Palaeogeogr Palaeoclimatol Palaeoecol 220:19–29

Jensen S, Droser ML, Gehling JG (2006) A critical look at the Ediacaran trace fossil record. In: Kaufman J, Xiao, S (eds) Neoproterozoic Geobiology and Paleobiology. Topics in Geobiology 27:115–157

Knaust D (2012) Trace fossil systematics. In: Knaust D, Bromley, RG (eds) Trace fossils as indicators of sedimentary environments. Developments in Sedimentology 64:79–101

Knaust D (2013) The ichnogenus *Rhizocorallium*: classification, trace makers, palaeoenvironments and evolution. Earth Sci Rev 126:1–47

Magwood JPA (1992) Ichnotaxonomy: a burrow by any other name? In: Maples CG, West RR (eds) Trace Fossils. Short Courses in Paleontology 5:15–33

Mángano MG, Buatois LA (2014) Decoupling of body-plan diversification and ecological structuring during the Ediacaran–Cambrian transition: evolutionary and geobiological feedbacks. Proc R Soc B 281:20140038

Mángano MG, Buatois LA (2015) The trace fossil record of tidal flats through the Phanerozoic: Evolutionary innovations and faunal turnover. In: Mcllroy D (ed) Ichnology: papers from Ichnia III. Geol Assoc Canada Misc Publ 9:157–177

Mángano MG, Buatois LA, Maples CG, Lanier WP (1997) *Tonganoxichnus*, a new insect trace fossil from the Upper Carboniferous of eastern Kansas, USA. Lethaia 30:113–125

Mángano MG, Buatois LA, West RR, Maples CG (2002) Ichnology of an equatorial tidal flat: the Stull Shale Member at Waverly, eastern Kansas. Bull Kans Geol Surv 245:1–130

Mángano MG, Buatois LA, Hofmann R, Elicki O, Shinaq R (2013) Exploring the aftermath of the Cambrian explosion: the evolutionary significance of marginal to shallow marine ichnofaunas of Jordan. Palaeogeogr Palaeoclimatol Palaeoecol 374:1–15

McCann T (1990) Distribution of Ordovician-Silurian ichnofossil assemblages in Wales: implications for Phanerozoic ichnofaunas. Lethaia 23:243–255

McLoughlin N, Furnes H, Banerjee NR, Muehlenbachs K, Staudigel H (2009) Ichnotaxonomy of microbial trace fossils in volcanic glass. J Geol Soc London 166:159–169

Miller MF, Labandeira CC (2002) Slow crawl across the salinity divide: delayed colonization of freshwater ecosystems by invertebrates. Geol Soc Am Today 12:4–10

Noffke N (2010) Geobiology: microbial mats in sandy deposits from the Archaean Era to Today. Springer, Berlin

Peters SE, Foote M (2001) Biodiversity in the Phanerozoic: a reinterpretation. Paleobiology 27:583–601

Rainforth EC (2005) Ichnotaxonomy of the fossil footprints of the Connecticut Valley (Early Jurassic, Newark Supergroup, Connecticut and Massachusetts). Columbia University, New York

Raup DM (1976) Species diversity in the Phanerozoic: an interpretation. Paleobiology 2:289–297

Raup DM (1979) Size of the Permo-Triassic bottleneck and its evolutionary implications. Science 206:217–218

Seilacher A (1977) Pattern analysis of *Paleodictyon* and related trace fossils. In: Crimes TP, Harper JC (eds) Trace fossils 2. Geol J Spec Issue 9:289–334. Seel House Press, Liverpool

Seilacher A (1986) Evolution of behavior as expressed in marine trace fossils. In: Kitchell JA, Nitecki MH (eds) Evolution of animal behavior: paleontological and field approaches. Oxford University Press, New York

Sepkoski JJ Jr (1978) A kinetic model of Phanerozoic taxonomic diversity I. Analysis of marine orders. Paleobiology 4:223–251

Sepkoski JJ Jr (1979) A kinetic model of Phanerozoic taxonomic diversity II. Early Phanerozoic families and multiple equilibria. Paleobiology 5:222–251

Sepkoski JJ Jr (1984) A kinetic model of Phanerozoic taxonomic diversity III. Post-Paleozoic families and mass extinctions. Paleobiology 10:246–267

Sepkoski JJ Jr (1991) A model of onshore–offshore change in faunal diversity. Paleobiology 17:58–77

Sepkoski JJ Jr (1997) Biodiversity: past, present, and future. J Paleontol 71:533–539

Sepkoski D (2012) Rereading the fossil record: the growth of paleobiology as an evolutionary discipline. University of Chicago Press, Chicago

Sepkoski JJ Jr, Sheehan PM (1983) Diversification, faunal change, and community replacement during the Ordovician radiations. In: Tevesz MJS, McCall PL (eds) Biotic Interactions in Recent and Fossil Benthic Communities, Plenum, New York

Sepkoski JJ Jr, Miller AI (1985) Evolutionary faunas and the distribution of Paleozoic benthic communities in space and time. In: Valentine JW (ed) Phanerozoic diversity patterns: profiles in macroevolution. Princeton University Press, Princeton

Simões M, Breitkreuz L, Alvarado M, Baca S, Cooper JC, Heins L, Herzog K, Lieberman BS (2016) The evolving theory of evolutionary radiations. Trends Ecol Evol 31:27–34

Smith AB, Jeffrey CH (1998) Selectivity of extinction among sea urchins at the end of the Cretaceous period. Nature 392:69–71

Stanley DCA, Pickerill RK (1993) Shallow marine *Paleodictyon* from the Upper Ordovician Georgian Bay Formation of southern Ontario. Atlantic Geol 29:115–119

Tapanila L, Roberts EM (2012) The earliest evidence of holometabolan insect pupation in conifer wood. PLoS One 7(2):e31668

Tchoumatchenco P, Uchman A (2001) The oldest deep-sea *Ophiomorpha* and *Scolicia* and associated trace fossils from the Upper Jurassic-Lower Cretaceous deep-water turbidite deposits of SW Bulgaria. Palaeogeogr Palaeoclimatol Palaeoecol 169:85–99

Twitchett RJ (2006) The palaeoclimatology, palaeoecology and palaeoenvironmental analysis of mass extinction events. Palaeogeogr Palaeoclimatol Palaeoecol 232:190–213

Twitchett RJ (2007) The Lilliput effect in the aftermath of the end-Permian extinction event. Palaeogeogr Palaeoclimatol Palaeoecol 252:132–144

Uchman A (1995) Taxonomy and paleoecology of flysch trace fossils: the Marnoso-arenacea Formation and associated facies (Miocene, Northern Apennines, Italy). Beringeria 15:1–115

Uchman A (1998) Taxonomy and ethology of flysch trace fossils: revision of the Marian Ksiazkiewicz collection and studies of complementary material. Ann Soc Geol Poloniae 68:105–218

Uchman A (2003) Trends in diversity, frequency and complexity of graphoglyptid trace fossils: evolutionary and palaeoenvironmental aspects. Palaeogeogr Palaeoclimatol Palaeoecol 192:123–142

Uchman A (2004) Phanerozoic history of deep-sea trace fossils. In: McIlroy D (ed) The application of ichnology to palaeoenvironmental and stratigraphic analysis, vol 228. Geol Soc Spec Pub, London

Urbanek A (1993) Biotic crises in the history of Upper Silurian graptoloids: a palaeobiological model. Hist Biol 7:29–50

Villegas-Martín J, de Gibert JM, Rojas-Consuegra R, Belaústegui Z (2012) Jurassic *Teredolites* from Cuba: new trace fossil evidence of early wood-boring behavior in bivalves. J S Am Earth Sci 38:123–128

von Kušta J (1880) Bohrgänge von insecten in einen verkieselten Araucarite von Bránov bei Pürglitz. Sitzunsberg Böhmisch Gesel Wiss Math Naturwiss Cl 1880:202–203

Walter H (1983) Zur taxonomie, ökologie und biostratigraphie der ichnia limnisch-terrestrischer arthropoden des mitteleuropaischen Jungpaläozoikums. Freiberg Forschungsh C 382: 146–193

Wiest LA, Buynevich IV, Grandstaff DE, Terry DO, Maza ZA (2015) Trace fossil evidence suggests widespread dwarfism in response to the end-Cretaceous mass extinction: Braggs, Alabama and Brazos River, Texas. Palaeogeogr Palaeoclimatol Palaeoecol 417:105–111

Wilson MA, Palmer TJ (2006) Patterns and processes in the Ordovician bioerosion revolution. Ichnos 13:109–112

Wooton RJ (1988) The historical ecology of aquatic insects: an overview. Palaeogeogr Palaeoclimatol Palaeoecol 62:477–492

Xing L, Parkinson AH, Ran H, Pirrone CA, Roberts EM, Zhang J, Burns ME, Wang T, Choiniere J (2015) The earliest fossil evidence of bone boring by terrestrial invertebrates, examples from China and South Africa. Hist Biol. doi:10.1080/08912963.2015.1111884