The *other* biodiversity record: Innovations in animal-substrate interactions through geologic time

Luis A. Buatois, *Dept. of Geological Sciences, University of Saskatchewan, 114 Science Place, Saskatoon SK S7N 5E2, Canada, luis. buatois@usask.ca;* and **M. Gabriela Mángano,** *Dept. of Geological Sciences, University of Saskatchewan, 114 Science Place, Saskatoon SK S7N 5E2, Canada, gabriela.mangano@usask.ca*

ABSTRACT

Tracking biodiversity changes based on body fossils through geologic time became one of the main objectives of paleontology in the 1980s. Trace fossils represent an alternative record to evaluate secular changes in diversity. A quantitative ichnologic analysis, based on a comprehensive and global data set, has been undertaken in order to evaluate temporal trends in diversity of bioturbation and bioerosion structures. The results of this study indicate that the three main marine evolutionary radiations (Cambrian Explosion, Great Ordovician Biodiversification Event, and Mesozoic Marine Revolution) detected in the body-fossil record are also expressed in the trace-fossil record. Analysis of ichnodiversity trajectories in marine environments supports Sepkoski's logistic model, which was originally based on analysis of marine body fossils. The trace-fossil record of continental environments suggests variable rates of increases in ichnodiversity, with major radiations in the Ludlow–Early Devonian, Cisuralian, Early Jurassic, Late Cretaceous, and Eocene, and slower increases or plateaus in between these periods. Our study indicates that ichnologic information represents an independent line of evidence that yields valuable insights to evaluate paleobiologic megatrends.

INTRODUCTION

The astounding diversity of animals in modern oceans and continents is the result of macroevolutionary processes operating in deep time. Conservative estimates suggest the modern biosphere hosts close to 13 million species, of which approximately only 4% are marine (Benton, 2001). Despite the impressive growth of fields exploring other sources of data (e.g., molecular), the fossil record is arguably still the main line of evidence to reconstruct the diversity of life through time (Valentine, 1969; Raup, 1972,

1979; Bambach, 1977; Sepkoski, 1978, 1979, 1984, 1997). However, this has been marked by controversies regarding the nature of diversity trajectories and their potential biases (e.g., Sepkoski et al., 1981; Alroy, 2010; Crampton et al., 2003; Holland, 2010; Bush and Bambach, 2015). In these studies, diversity has been invariably assessed based on body fossils.

Trace fossils represent an alternative record to assess secular changes in biodiversity. Trace-fossil data were given less attention and were considered briefly in only one of the more classic studies of biodiversity through time (e.g., the so-called consensus paper by Sepkoski et al., 1981; see also Miller, 2009). Ichnologic information in the consensus paper was based on early attempts of quantifying trace-fossil diversity, which were supported by the very limited data available at the time (Seilacher, 1974, 1977). The decision by Dolf Seilacher to decline co-authorship of the consensus paper reflects his doubts with respect to the support that trace-fossil evidence was actually providing to the diversity curves based on body fossils. In a letter addressed to Sepkoski, dated 23 February 1981, Seilacher stated, "By lumping the two groups you may get a curve that pleases you, but this might be an accident. The curve you have in mind (based on the record of body fossils) is mainly one of shallow marine diversity. Including the flysch (i.e., the deepwater) counts (which by their high diversity influence the results very much), I am afraid will do no justice to the cause, although the result may fit the general picture" (Miller, 2009, p. 379).

No attempts to produce global comprehensive compilations have been done since the pioneer work by Seilacher (see also Crimes, 1974). Subsequent ichnologic compilations focused on specific environments (e.g., Buatois et al., 1998; Orr, 2001; Uchman, 2004; Minter et al., 2016a, 2016b, 2017) or evolutionary radiations (e.g., Mángano

and Droser, 2004; Mángano and Buatois, 2014; Buatois et al., 2016a), rather than on the whole Phanerozoic. In this study we tackle this issue based on a systematic and global compilation of trace-fossil data in the stratigraphic record. We show that quantitative ichnologic analysis indicates that the three main marine evolutionary radiations inferred from body fossils, namely the Cambrian Explosion, Great Ordovician Biodiversification Event, and Mesozoic Marine Revolution, are also expressed in the trace-fossil record. In addition, the trace-fossil record of continental environments suggests variable rates of increases in diversity, with major radiations in the Ludlow–Early Devonian, Cisuralian, Early Jurassic, Late Cretaceous, and Eocene, and slower increases or plateaus in between these periods.

CONCEPTS AND METHODS

Trace fossils comprise distinctive structures of biogenic origin, reflecting organism behaviors while interacting with the substrate (Fig. 1). Trace fossils may be preserved in a wide variety of substrates. Bioturbation structures occur in sediment, whereas bio-erosion structures are produced in rigid substrates, such as hardgrounds, clasts, bones, or rocks (Frey and Wheatcroft, 1989). Although the same type of trace-fossil can be produced by phylogenetically unrelated animals, in many instances trace fossils can be attributed to a producer with variable levels of confidence. For example, the branching burrow system *Ophiomorpha* is commonly regarded as produced by decapod crustaceans, typically callianassids (Fig. 1) (Frey et al., 1978). However, such links are not possible to establish in the case of ichnofossils having less distinct morphologic features. The trace-fossil record encompasses marine and continental environments and spans from Ediacaran to Holocene (Buatois and Mángano, 2016).
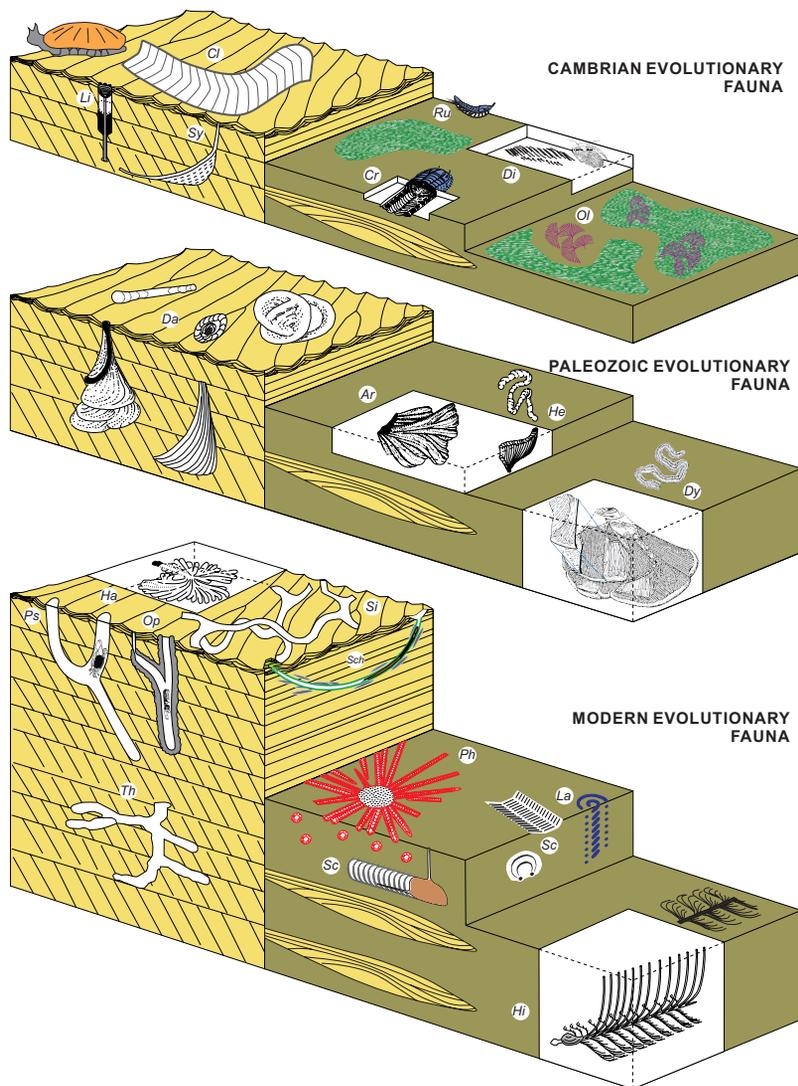
Figure 1. Ichnologic equivalents of Sepkoski's evolutionary faunas. Representative elements of the Cambrian evolutionary fauna include trilobite trace fossils, such as *Rusophycus* (*Ru*), *Cruziana* (*Cr*) and *Dimorphichnus* (*Di*), and the inarticulate brachiopod burrow *Lingulichnus* (*Li*). Trace fossils of worm-like organisms include *Syringomorpha* (*Sy*) and *Oldhamia* (*Ol*), whereas *Climactichnites* (*Cl*) has been attributed to mollusk-like producers. Examples of the Paleozoic evolutionary fauna include ichnotaxa produced by worm-like animals, such as *Daedalus* (*Da*), *Arthrophycus* (*Ar*), *Heimdallia* (*He*), and *Dictyodora* (*Dy*). The Modern evolutionary fauna is dominated by crustacean burrows, such as *Psilonichnus* (*Ps*), *Ophiomorpha* (*Op*), *Thalassinoides* (*Th*), and *Sinusichnus* (*Si*), as well as bivalves, such as *Hillichnus* (*Hi*), and irregular echinoids, such as *Scolicia* (*Sc*). Structures produced by worm-like organisms include *Lapispira* (*La*), *Schaubcylindrichnus* (*Sch*), *Phoebichnus* (*Ph*), and *Haentzschelinia* (*Ha*). For bibliographic sources, see supplementary material in the GSA Data Repository (see text footnote 1).

Whereas the main focus of studies on biodiversity has been on the number of species or higher taxa (Sepkoski, 1997), ichnodiversity (or trace-fossil diversity) studies focus on the different behaviors involved in animal-substrate interactions. Ichnodiversity refers to the number of trace-fossil types (ichnotaxa) present in any given assemblage or geologic period, therefore providing a measurement of behavioral richness (Buatois and Mángano, 2011, 2013). Ichnogeneric compilation was based on literature and personal data (GSA Data Repository Tables DR1 and DR2[1]). The total number of invertebrate ichnogenera identified as valid is 534, encompassing 428 for bioturbation structures and 106 for bioerosion structures (updated from Buatois et al., 2017). We follow the common practice of assessing ichnodiversity at ichnogeneric rank, because there is a general agreement that taxonomy is more firmly established at ichnogenus level than at ichnospecies rank. Only invertebrate trace-fossil data were considered. Individual curves were produced for continental, shallow-marine, and deep-marine bioturbation, and marine and continental bioerosion (Fig. 2). Additional diversity curves were compiled for all marine bioturbation, all marine (bioerosion plus bioturbation), and all continental (bioerosion plus bioturbation) ichnogenera. A rarefaction analysis of the data pertaining to the Cambrian and Ordovician portions of the marine curves showing rapid ichnodiversity increases was undertaken to evaluate the effects of sample size on the curves (Buatois et al., 2016a). Diversity data for the continental Paleozoic were standardized by using the residuals method to evaluate potential sampling biases regarding the abundance of nonmarine clastic rock volume, the number of ichnofossil-bearing formations, and the number of trace-fossil assemblages documented (Minter et al., 2017). Potential biases are discussed in the supplementary material (see footnote 1).

RESULTS

Behavioral innovations seem to have taken place in pulses rather than at a steady pace (Fig. 2). For marine environments, a 433% increase in ichnodiversity occurred during the Terraneuvian, a 48% increase took place between the Early and Late Ordovician, and a more protracted and modest increase occurred later in the Mesozoic with increases in the Early Jurassic (8%) and Late Cretaceous (20%), totaling an overall increase of 37% (between the Late Triassic and Late Cretaceous) (Table DR3 [see footnote 1]).
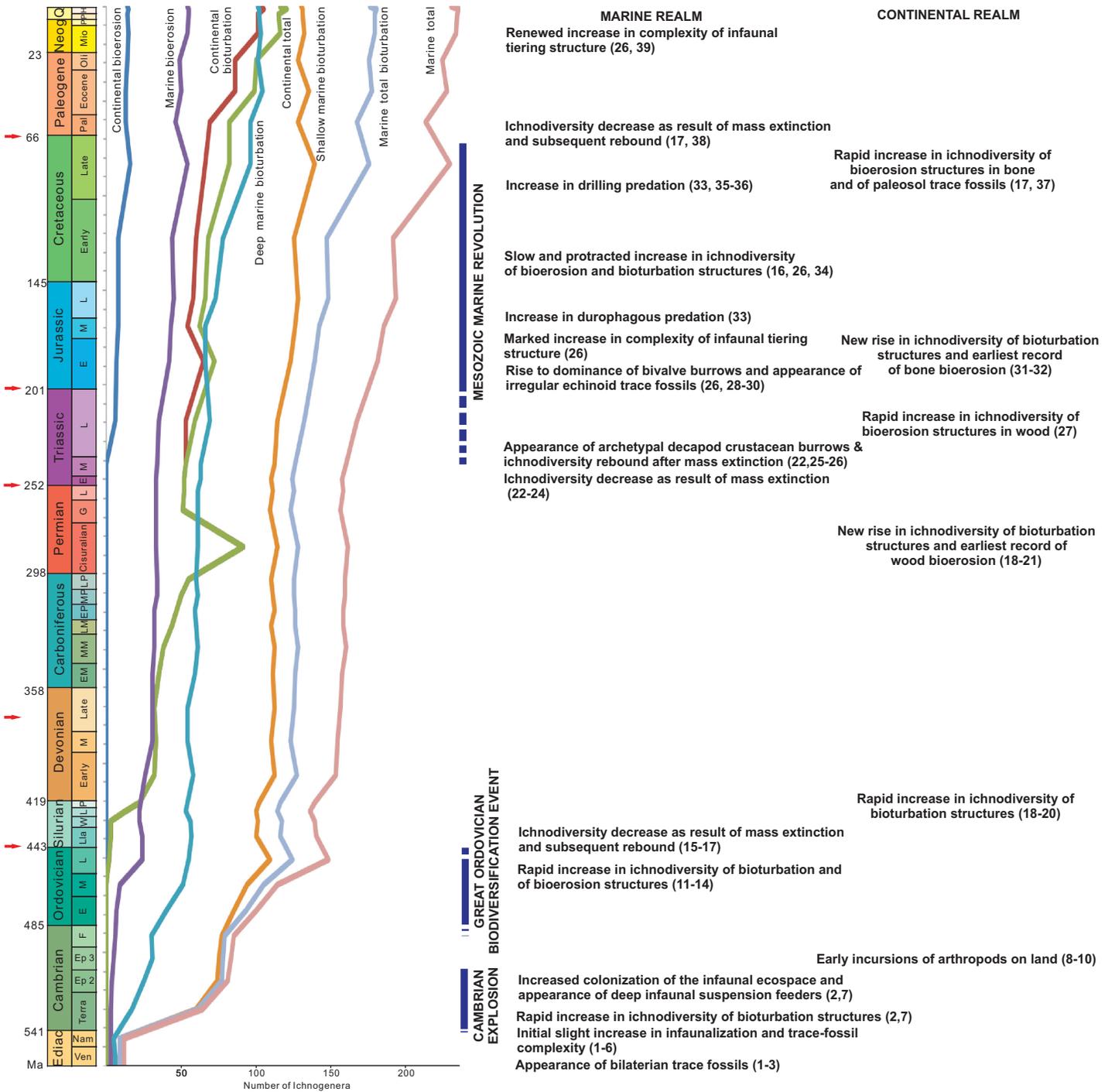

Figure 2. Ichnodiversity changes and milestones in animal-substrate interactions through geologic time as reflected by the trace-fossil record. Arrows indicate mass extinctions. Numbers correspond to bibliographic sources indicated in the supplementary material in the GSA Data Repository (see text footnote 1).

The Terraneuvian increase, attributed to the Cambrian Explosion, is restricted to bioturbation (Mángano and Buatois, 2014; Buatois et al., 2016a). The Cambrian Explosion is characterized by the rise of the Cambrian evolutionary fauna, which was dominated by trilobites, one of the most significant elements not only based on the body-fossil record, but also from an ichnologic perspective (Seilacher, 1985). In addition, inarticulate brachiopods, another important component, are represented by the ichnogenus *Lingulichnus* (Pemberton and Kobluk, 1978). However, the high ichnodiversity that characterizes the Cambrian reflects the activity of soft-bodied clades that are poorly known from the body-fossil record (and, therefore, not listed as members of the Cambrian evolutionary fauna). Several ichnogenera are restricted to the Cambrian (e.g., *Climactichnites, Oldhamia, Syringomorpha*). Trilobite trace fossils, as well as those ichnogenera showing stratigraphic ranges restricted to the Cambrian, may be regarded as the ichnologic equivalent of Sepkoski's Cambrian evolutionary fauna (Figs. 1 and DR1 [see footnote 1]).

The Ordovician increase in ichnodiversity is attributed to the Great Ordovician Biodiversification Event and is reflected not only by an increase in diversity of bioturbation, but also by bioerosion structures (Ordovician bioerosion revolution of Wilson and Palmer, 2006) (Fig. 2, Table DR3 [see footnote 1]). This revolution in the ability of organisms to penetrate skeletal material and hardgrounds occurred ~80 m.y. after the Cambrian Explosion in bioturbation (Buatois et al., 2016a). The Great Ordovician Biodiversification Event signals a shift from dominance of elements of the Cambrian evolutionary fauna to those of the Paleozoic and Modern evolutionary faunas (Sepkoski, 1981; Miller and Connolly, 2001). Articulate brachiopods, rugose and tabulate corals, and crinoids are dominant elements of the Paleozoic evolutionary fauna (Sepkoski, 1981). Unsurprisingly given their modes of life, none of these clades are significant from an ichnologic standpoint, obscuring characterization of an equivalent of the Paleozoic evolutionary fauna. However, a few ichnogenera showing restriction or peak abundance during the Paleozoic (e.g., *Arthrophycus, Dictyodora, Daedalus, Heimdallia*) may be regarded as typical of the Paleozoic evolutionary fauna (Figs. 1 and DR1 [see footnote 1]). In addition, the trace-fossil record of the Great Ordovician Biodiversification Event reflects the

dilution of trilobite faunas inferred from the body-fossil record. Contribution of trilobite-produced trace fossils to alpha ichnodiversity at ichnospecies level in the Tremadocian averages 41.5%, whereas only a 30.6% was attained in the Floian–Darriwilian, and just 12.1% for the Sandbian–Hirnantian (Mángano et al., 2016).

The Mesozoic ichnodiversity increase (Fig. 2, Table DR3 [see footnote 1]), concomitant with the rise to dominance of the modern evolutionary fauna (MEF), is attributed to the Mesozoic Marine Revolution. Bivalves, gastropods, echinoids, crustaceans, and marine vertebrates are dominant elements (Sepkoski, 1981). Irregular echinoids, crustaceans, and bivalves are the most important bioturbators in marine settings, in addition to worms (Buatois et al., 2016b), illustrating the ichnologic equivalent of the MEF (Figs. 1 and DR1 [see footnote 1]). Heart urchins (spatangoids), known since the Early Jurassic, are the producers of the ichnogenera *Bichordites, Cardioichnus,* and *Scolicia* (Smith and Crimes, 1983; Plaziat and Mahmoudi, 1988), all typical bioturbators in post-Paleozoic seas. Crustacean burrows include ichnogenera that occurred for the first time during the Mesozoic (e.g., *Ophiomorpha, Psilonichnus, Sinusichnus, Spongeliomorpha*) and a few that are known since the Paleozoic but became more abundant as a result of the Mesozoic Marine Revolution (*Gyrolithes, Thalassinoides*) (Carmona et al., 2004). Other crustacean ichnotaxa occurred for the first time in the Neogene (*Parmaichnus, Lepeichnus*). The most common trace fossils produced by bivalves (*Protovirgularia, Lockeia*), although known since the early Paleozoic, became more abundant since the Mesozoic (Buatois et al., 2016b). *Siphonichnus* is common in the late Paleozoic, reflecting an evolutionary radiation of infaunal bivalves, but it is particularly abundant since the Triassic (Knaust, 2015). *Hillichnus*, attributed to the activities of tellinacean bivalves (Bromley et al., 2003), is a product of the Mesozoic Marine Revolution. Some of the trace fossils produced by worms (e.g., *Haentzschelinia, Lapispira, Patagonichnus, Phoebichnus*) are only known in post-Paleozoic marine strata, but the vast majority (e.g., *Cylindrichnus, Macaronichnus, Schaubcylindrichnus*) have been documented since the Paleozoic. However, some of these ichnogenera became much more common since the Mesozoic (Buatois et al., 2016b). The most significant bioeroders were sponges, gastropods, bivalves, echinoids, and

worms. The sponge bioerosion ichnogenus *Entobia* is known since the Devonian (Tapanila, 2006), but it became abundant in the Mesozoic, when various ichnospecies originated. Significant bioerosion innovations are represented by *Radulichnus* (gastropods and chitons), *Teredolites* (pholadid bivalves), *Gnathichnus* (regular echinoids), and *Maeandropolydora* (spionid polychaetes) (Taylor and Wilson, 2003; Radley, 2010; Villegas-Martín et al., 2012).

Ichnodiversity in continental environments (Fig. 2, Table DR3 [see footnote 1]) is more difficult to evaluate due to the patchiness of the trace-fossil record (Minter et al., 2016a, 2016b, 2017). A 967% ichnodiversity increase characterizes the Silurian–Devonian transition, followed by a plateau until the Early Mississippian (Table DR3), although the latter most likely reflects the scarcity of Upper Devonian continental strata (Minter et al., 2016b). New rises in ichnodiversity took place during the Cisuralian (65%) and the Early Jurassic (22%) (Table DR3). Subsequent to this peak, ichnodiversity experienced a gradual and continuous increase. The earliest uncontroversial evidence of continental bioerosion is from the late Permian (Labandeira et al., 2017), but it is by the Late Triassic when rapid diversification took place (Tapanila and Roberts, 2012). The earliest record of bone bioerosion is from the Early Jurassic (Xing et al., 2015). An increase in ichnodiversity of continental bioerosion occurred in the Late Cretaceous (100%) followed by a plateau that continues until the Holocene (Fig. 2, Table DR3). Overall, the ichnodiversity increases that took place in continental environments by the end of the Mesozoic may reflect the appearance of sophisticated insect nesting structures in soils (Genise, 2016).

DISCUSSION: SIGNIFICANCE, CAVEATS, AND PROSPECTS

The concepts of Cambrian Explosion, Great Ordovician Biodiversification Event, and Mesozoic Marine Revolution are all based on body fossils. The fact that these evolutionary radiations are also reflected by the trace-fossil record provides independent support to the notion that these were truly macroevolutionary events, rather than taphonomic artifacts (Buatois and Mángano, 2016). Although some hard-bodied invertebrates (e.g., bivalves) produce trace fossils, most biogenic structures are made by soft-bodied organisms (sometimes collectively and informally referred to as worms, but in fact

encompassing a wide variety of clades) or poorly skeletonized invertebrates (e.g., thalassinidean crustaceans). The trace-fossil record provides information on animals that are typically underrepresented in the body-fossil record. Assessing the record of small and soft-bodied organisms making the majority of the biomass ("tackling the 99%" in Sperling's 2013 analogy) is of fundamental importance to reconstructing the history of life. Also, our results are consistent with the observation that each evolutionary fauna shows more ecologic complexity than the previous one, revealing an increased use of the ecospace (Bambach et al., 2007; Bush et al., 2007).

Diversification curves may adopt three different patterns, as illustrated by the straight (representing additive increase), exponential (implying doubling of diversity within fixed units of time if speciation and extinction rates remain constant), and logistic (comprising initial slow diversification followed by a rapid rise and a plateau) models (Benton, 2001). In turn, logistic models represent equilibrium models because they imply that global equilibria in diversity is attained, whereas exponential models are non-equilibrium models implying that a ceiling to diversity has not been reached or that there is no such ceiling (Benton, 2001). Diversification of marine invertebrates is apparently best described by a logistic model (Sepkoski, 1978, 1984), but diversification of continental biotas may have followed an exponential model (Benton, 1985, 2001; Labandeira and Sepkoski, 1993). However, in recent years it has been argued that fluctuating equilibrium diversities through time may produce a pattern of intervals of relative stability alternating with times of radiations, which is apparently similar to a coupled logistic model, but resulting from a different underlying evolutionary dynamics (Alroy, 2010; Foote, 2010; Bush et al., 2016).

According to the logistic model, marine evolutionary radiations display the pattern of early slow growth, subsequent rapid growth, and final slowing of growth reaching a plateau (Sepkoski, 1978, 1984). This is particularly illustrated by the Cambrian Explosion and the Great Ordovician Biodiversification Event, which displayed very rapid growths of diversity in their initial stages until reaching a plateau (Sepkoski, 1978, 1979). In contrast, diversity rose more slowly during the initial phase of the Mesozoic Marine Revolution and apparently has not

reached a plateau yet (Sepkoski, 1981, 1984). The three-phase kinetic model developed by Sepkoski (1984) provided an analytical view of marine diversification with different global equilibria for each of the three evolutionary radiations (but see Kowalewski et al., 2006; Kiessling et al., 2008; Alroy et al., 2008; Alroy, 2010, 2014). Studies based on standardized curves indicated that late Cenozoic diversity is only slightly higher than the Paleozoic maximum (e.g., Alroy et al., 2008; Alroy, 2010, 2014). However, recent work shows a pattern that is more consistent with the original Sepkoski's curves, indicating Cenozoic diversity levels that doubled Paleozoic values (Bush and Bambach, 2015).

The curves for marine invertebrate trace fossils show a similar trajectory to that of body fossils (Sepkoski, 1997), providing empiric independent support to the three-phase kinetic (logistic) model (Sepkoski, 1984) and indicating similar diversity trajectories for animal diversity and their behaviors. The explosive Terraneuvian diversification in bioturbation was preceded by a slow increase during the terminal Ediacaran and followed by a plateau during the middle to late Cambrian, underscoring the logistic nature of the Cambrian Explosion. This diversification preceded the Cambrian Explosion as indicated by body fossils, which took place later in the early Cambrian (Mángano and Buatois, 2014). A similar case of logistic pattern of diversification can be made for the Great Ordovician Biodiversification Event with a rapid rise taking place through the Ordovician and a plateau lasting for roughly the remaining of the Paleozoic. In turn, the rapid rise in ichnodiversity of the Late Cretaceous was preceded by a more protracted increase that started during the recovery after the end-Permian mass extinction and was followed by a plateau until the present. This represents a departure from the diversity trajectory of post-Paleozoic faunas, which does not show any evidence of a plateau (Sepkoski, 1981, 1984).

Variable rates of increases in ichnodiversity are detected for continental bioturbation, with major radiations in the Ludlow–Early Devonian, Cisuralian, Early Jurassic, Late Cretaceous, Eocene, and Miocene (Fig. 2, Table DR3 [see footnote 1]). No plateau indicative of an equilibrium stage is apparent, suggesting that the invasion of the land is still an ongoing process (Miller and Labandeira, 2002). This is consistent with the non-equilibrium nature of models currently envisaged for diversification in continental

environments based on body fossils (Benton, 2001). On the contrary, a plateau seems to have been reached by the end of the Mesozoic in the case of continental bioerosion. However, our knowledge of continental bioerosion lags considerably behind that of bioturbation, so available patterns should be taken with extreme caution.

Forty years of ichnologic research since the compilation by Dolf Seilacher prompt us to question if his reluctance to get involved in the consensus papers is still justified by the now available evidence. Our study shows that after the initial burst in ichnodiversity that took place during the Cambrian Explosion, subsequent diversification was most clearly manifested in the deep sea (83% increase between the end of the Cambrian and the end of the Ordovician and 58% between the Middle Jurassic and the Eocene) (Table DR3 [see footnote 1]). However, the increase was not restricted to the deep sea, but also took place in shallow water (42% increase between the end of the Cambrian and the end of the Ordovician and 26% through the whole Mesozoic) (Table DR3). Further ichnodiversity increases are apparent for bioerosion, which cannot be attributed to innovations in the deep sea (Fig. 2).

However, Seilacher's original compilations, showing constant ichnodiversity levels in shallow water and increased diversification in the deep sea, were not of global ichnodiversity, but of maximum alpha ichnodiversity. Therefore, these curves reflect richness at a community level rather than globally. Ongoing work is attempting to produce a database compiling alpha ichnodiversity for specific environments through the Phanerozoic in order to evaluate changes in within- and inter-habitat ichnodiversity. Previous work on deep-sea trace fossils by Uchman (2004) suggested a more nuanced scenario to that originally indicated by Seilacher (1974, 1977). Although an overall increase in maximum alpha ichnodiversity is apparent, this trend has been punctuated by several fluctuations, including significantly low levels from the Carboniferous to the Middle Jurassic (Uchman, 2004). Comparative analysis of brackish-water marginal-marine environments indicates that, even in these stressful settings, alpha ichnodiversity has increased through the Phanerozoic (Buatois et al., 2005).

The explosive development of analytical paleobiology demonstrates the need for standardizing trace-fossil data in the same fashion that has been done with body-fossil

data. Ongoing ichnologic work is showing the usefulness of this approach, which has produced robust trace-fossil data to compare the Cambrian Explosion and the Great Ordovician Biodiversification Event (Buatois et al., 2016a), and to reconstruct the Paleozoic invasion of the continents (Minter et al., 2017). In conclusion, ichnologic information has a lot to offer to the reconstruction of the history of life, representing an independent line of evidence that yields valuable insights to evaluate paleobiologic megatrends.

ACKNOWLEDGMENTS

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