

Small-world dynamics drove Phanerozoic divergence of burrowing behaviors

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ABSTRACT

Species of burrowing animals have changed substantially over evolutionary time scales, but, surprisingly, burrows display persisting morphological patterns throughout the Phanerozoic. Deep-sea burrows are geometrically patterned, whereas shallow-marine burrows display simpler morphologies. This divergence between burrow associations is one of the central conundrums of paleontology, but it has never been quantitatively demonstrated, and the organizing principles responsible for this structure remain unknown. We show that the divergence of burrow associations has been shaped by small-world dynamics, which is proposed as a major macroevolutionary force in marine environments. Using network analysis, our study reveals that the association patterns between burrow morphotypes in 45 paleontological sites span ~500 m.y. Strong statistical support is demonstrated for a surprising association pattern, according to which the data set is optimally partitioned into two subgroups of tightly associated burrow types. These groups correspond to shallow- and deep-marine biomes. Our analysis demonstrates that across the Phanerozoic Eon, burrows did not assemble randomly nor regularly, following instead small-world assembly rules remarkably similar to those that shape human social networks. As such, small-world dynamics deeply influenced gene flow and natural variation in heritable behavior across evolutionary time.

INTRODUCTION

Species of burrowing organisms have changed dramatically throughout the Phanerozoic, which comprises the past 541 m.y. of biological evolution on Earth. Nevertheless, burrows and other traces of organism-substrate interactions (e.g., trails, trackways) have maintained similar morphologies throughout the same time span, with each morphology being associated with a specific environmental setting (Frey and Seilacher, 1980). In fact, one of the fundamental hypotheses of paleontology concerns the Phanerozoic divergence between shallow- and deep-sea trace fossil associations. This

hypothesis states that deep-sea associations of trace fossils have retained their distinctiveness from shallow-marine trace fossils throughout most of the Phanerozoic (Seilacher, 1953, 1967, 1978, 2007). In other words, the hypothesis asserts that deep-sea trace fossils are morphologically different from shallow-marine trace fossils (Fig. 1).

The quantum leap in the understanding of life-substrate interactions imparted by this observation (MacEachern et al., 2012) led to the recognition of associations of trace fossils across time and space (i.e., ichnofacies; Seilacher, 1953, 1967). As a consequence of this recognition, trace fossils became a central tool in the reconstruction of ancient ecosystems

(Seilacher, 1953), hydrocarbon exploration (La Croix et al., 2013, 2012; Bednarz and McLroy, 2015), scientific drilling, and characterization of aquifers (Droser and O'Connell, 1992; Cunningham et al., 2009). Ethology is central to this framework because trace fossils are manifestations of behavior, which is controlled by the environment; environmental parameters, in turn, are strongly affected by water depth (Seilacher, 1953; Ekdale, 1988; MacEachern et al., 2012).

Despite its popularity and intuitive recognition, the divergence hypothesis has never been quantitatively tested, and the organizing principles that underpin it remain unknown. This issue is addressed here by analysis of association patterns of Phanerozoic trace fossils. Our study tests the specific predictions of the divergence hypothesis that (1) association patterns of trace fossils are inhomogeneous, i.e., trace fossils are associated neither randomly nor regularly; and (2) any trace-fossil association is related to a specific biome, i.e., shallow or deep marine. Accordingly, the first null hypothesis is that trace fossils are randomly associated; the second is that they are regularly associated; the third is that there is no correlation between groups of associated traces and their environmental setting.

METHODS

The ideal source data for quantitatively testing the divergence hypothesis are the data from which the divergence idea first stemmed (Seilacher,

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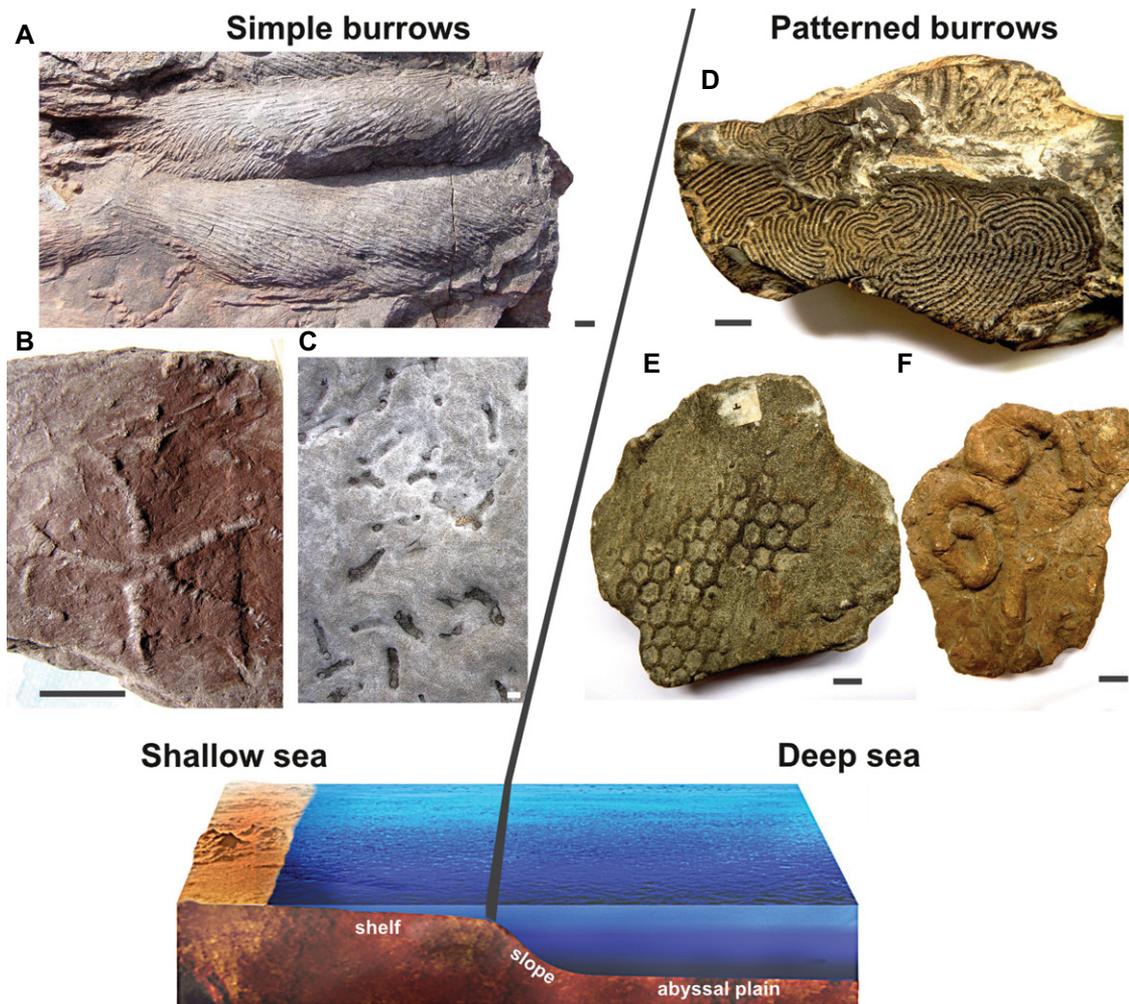


Figure 1. Phanerozoic divergence hypothesis. It predicts that simple burrows (A–C) are found in shallow-sea deposits, and geometrically patterned burrows (D–F) in deep-sea settings. Scale bars are 1 cm wide. (A) *Cruziana* (Ordovician). (B) *Asteriacites* (Triassic). (C) *Diplocraterion* (Jurassic). (D) *Nereites* (Cretaceous). (E) *Paleodictyon* (Cretaceous). (F) *Spirophycus* (Cretaceous). See Table S1 (see footnote 1) for specimen details.

2007; Table S2 in the Supplemental Material¹). This data set includes presence-absence data of environmental proxies and 32 taxa of trace fossils (ichnotaxa) in 45 sites, ranging from Cambrian to Miocene in age. Each assemblage of the data set represents the work of animals that lived in the same biome, but it is not necessarily an ichnocoenose. Using the framework of network analysis (Baucon and Felletti, 2013; Baucon et al., 2014, 2015), the source data table is translated into a network by representing ichnotaxa as nodes and by connecting those taxa that co-occur in at least one paleontological site. The resulting network (Fig. 2), herein named the ichnofossil network, is made of 32 nodes (ichnotaxa), each of which is linked to 19.8 taxa on average (average degree). To test the first and second null hypotheses, we compared the topological properties of the ichnofossil network with those of random and regular null models

that are equivalent; i.e., with the same number of nodes and average degree. We empirically generated 1000 random networks using the Erdős and Rényi (1959) model (Fig. S1A in the Supplemental Material). To test the third hypothesis, subgroups are searched by using only the information encoded in the topology of the ichnofossil network; then the correlation between the detected subgroups and environmental proxies is tested. To detect subgroups, we applied the concept of modularity, which measures the number of links falling within subgroups minus the expected number in a random null model (Newman, 2006; Fortunato, 2010). By optimizing modularity over possible subgroups of the studied network, we determined whether there exist any natural partitions of its nodes (Newman, 2006; Blondel et al., 2008). We then evaluated whether ichnotaxa of each subgroup have a higher probability of being associated with shallow-marine proxies versus deep-marine proxies. The probability of association was quantified using the Jaccard similarity and a χ^2 test (Hammer and Harper, 2006).

We propose a spatial model of ichnotaxa distribution to understand what biogeographic distribution patterns are responsible for the

ichnofossil network topology. The seafloor was simulated by a unidimensional domain across which ichnotaxa are distributed. The spatial range of each taxon can change at discrete points in time according to a defined set of rules: (1) a “specialist rule”, i.e., keeping a narrow spatial range across time; or (2) a “generalist rule”, i.e., keeping a wide range for the entire duration of the simulation. At the end of the simulation, a network was produced based on co-occurrence relationships between taxa, and the network was compared to the ichnofossil network. Detailed methods and definitions are provided in the Supplemental Material.

RESULTS AND DISCUSSION

Ichnofossil Network versus Random and Regular Null Models

In the ichnofossil network, any two nodes are connected by a minimum number of links (distance). For instance, the distance between *Cosmorhappe* and *Spirophycus* is 1 because the corresponding ichnotaxa are found in the same paleontological site(s) (Fig. 2). This implies that these ichnotaxa occupied the same ancient biome because trace fossils cannot be transported; i.e., they represent the *in situ*

¹Supplemental Material. Supplemental text, 7 supplemental figures, 3 supplemental tables, and 4 files of Python code. Please visit <https://doi.org/10.1130/GEOLOGY.S.14120408> to access the supplemental material, and contact editing@geosociety.org with any questions.

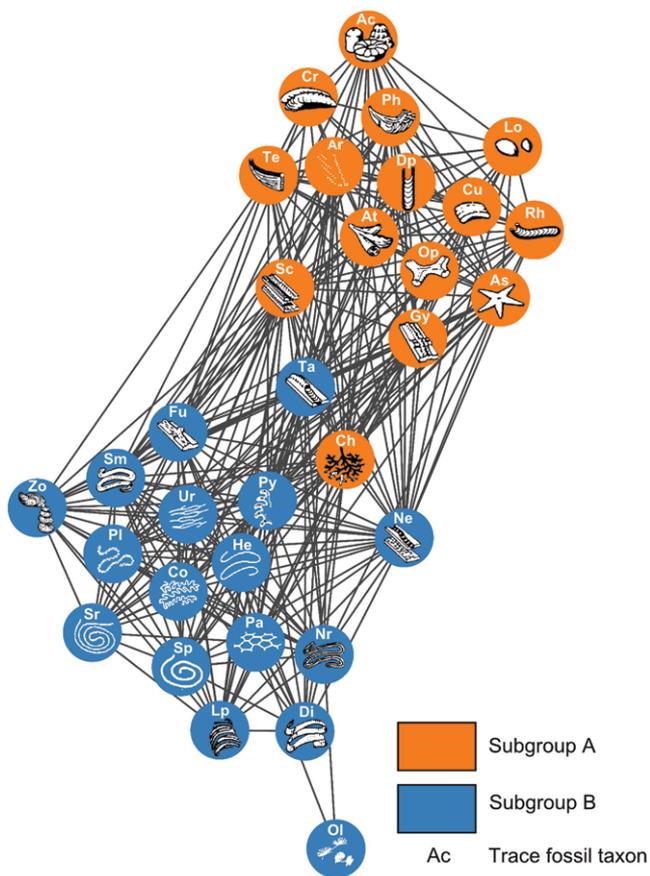


Figure 2. Ichnofossil network. Nodes represent ichnotaxa, and links connect ichnotaxa that co-occur in same paleontological site(s). Node colors indicate modularity-based subgroups. Refer to Table 1 for taxon abbreviations. Trace fossil icons are modified from Seilacher (2007).

record of biogenic activity (Buatois and Mángano, 2011). In the ichnofossil network, average distance is $L_{\text{ichno}} = 1.38$, which is comparable to the average distance of a random network (L_{er} [er—equivalent Erdős-Rényi random network] = 1.36). The ichnofossil network resembles a random network by its short average distance, but, in parallel to the inadequacy of describing social networks as random networks (Newman, 2000), there is a notable challenge using the random network as a model of the ichnofossil network. In a true social network, one's friend's friends are likely to be one's friends, but this does not occur in random networks (Newman, 2000). This property is termed “clustering” and is quantified by the clustering coefficient C (Proulx et al., 2005). The average clustering coefficient of the ichnofossil network ($C_{\text{ichno}} = 0.85$) is higher than the clustering coefficient of equivalent random networks (0.62), equaling the ratio between the average number of links and the total number of nodes (Newman, 2000). A similar result is obtained by averaging the clustering coefficient of the 1000 empirically generated Erdős-Rényi random networks ($C_{\text{er}} = 0.64$; Fig. S1). The higher degree of clustering in the ichnofossil network compared to a random network shows that the ichnofossil network is not random.

A regular network is the opposite of a random network (Newman, 2000); a completely ordered graph in which all nodes have the same

number of links, i.e., they have equal degrees (Caporossi et al., 2003). Consequently, in a regular network, the difference between the maximum and the minimum node degree (degree variability) is $V_{\text{reg}} = 0$. This is not the case of the ichnofossil network, the degree variability of which is $V_{\text{ichno}} = 28$ (Figs. S1B and S2A; see Fig. S2B for additional topological differences from the regular null model).

Node Subgroups

Our results falsify the first and second null hypotheses by showing that random and regular networks do not capture the topology of the ichnofossil network. The ichnofossil network displays characteristics from both (high clustering like regular lattices, and small average distance like random networks). This is typical of small-world networks; i.e., networks presenting a connection topology that is neither completely regular nor completely random (Watts and Strogatz, 1998; Humphries and Gurney, 2008). The network G is said to be a small-world network if it has a similar average distance length to, but greater clustering of nodes than, an equivalent Erdős-Rényi random graph ($L_g \geq L_{\text{er}}$; $C_g \gg C_{\text{er}}$) (Humphries and Gurney, 2008). To test the small-world nature of the ichnofossil network, we calculated the small-worldness index S , which compares clustering and distance of a given network to those of an equivalent random network (Humphries and Gurney, 2008), as does

the small-world measure ω (Telesford et al., 2011), which also considers clustering of an equivalent lattice. A network is deemed a “small world” if $S > 1$ (Humphries and Gurney, 2008), whereas values of ω close to zero denote small-world tendencies (Telesford et al., 2011). Values of these indices ($S_{\text{ichno}} = 1.10$; $\omega_{\text{ichno}} = -0.11$) show that the ichnofossil network falls within the small-world realm.

Small-world networks are commonly characterized by community structure; i.e., they can be partitioned into subgroups of densely connected nodes (Newman, 2006; Fortunato, 2010). Community structure here does not refer to biological communities. Community structure allows the third null hypothesis to be tested: i.e., there is no correlation between ichnoassociations, if present, and their environmental setting. Optimization of modularity reveals two natural subgroups in the ichnofossil network (Table 1; Fig. 2).

Paleoenvironmental Significance of Subgroups

We visualize the probability of association between subgroups and environmental proxies as configurations of nodes (Fig. 3). Accordingly, each node is an ichnotaxon, while its coordinates represent the probability of association with shallow-marine (x -coordinate) and deep-marine (y -coordinate) proxies. The diagonal segment connecting the upper right to the lower left corner of the plot contains the points of equal probability; hence, it separates the deep-sea from the shallow-sea realm. Results (Fig. 3) show that (1) the shallow-sea realm contains subgroup A ichnotaxa only; (2) all taxa of subgroup B fall into the deep-sea realm; (3) *Chondrites* is the only taxon of subgroup A that is placed in the deep-sea realm. The results disprove the null hypothesis by showing that each group of associated traces pertain to a single biome, shallow or deep marine. This supports the Phanerozoic divergence hypothesis. This result is surprising because this divergence persisted in spite of changing trace makers, e.g., the end-Permian extinction wiped out 96% of marine animal species (Benton and Twitchett, 2003; Twitchett and Barras, 2004).

Chondrites cannot be considered a true outlier because it is a typical environment-crossing ichnogenus (Baucon et al., 2020). The network subgroups A and B show high correspondence with the shallow-sea *Cruziana* ichnofacies and the deep-sea *Nereites* ichnofacies, respectively, which had been only qualitatively outlined in the original studies (Seilacher, 1967, 1978, 2007). These results are confirmed by the χ^2 test (Fig. S3) and hold at least from the Ordovician, given that the source data set does not include any of the characteristic Cambrian shallow-sea graphoglyptids (Crimes and Fedonkin, 1994; Uchman, 2003). Today, the ichnofacies approach is regarded as a key tool in paleoenvironmental

TABLE 1. NODE SUBGROUPS FOUND BY MODULARITY OPTIMIZATION ALGORITHM

Subgroup	Taxon	Abbreviation	First appearance datum	
A	Actinian burrows	Ac	Early Cambrian	
	Arthropod tracks	Ar	?Neoproterozoic, Early Cambrian	
	<i>Asteriacites</i>	As	Cambrian	
	<i>Chondrites</i>	Ch	Neoproterozoic	
	Scolicids	Sc	Early Ordovician	
	<i>Gyrochorte</i>	Gy	Ordovician	
	<i>Cruziana</i>	Cr	Early Cambrian	
	<i>Phycodes</i>	Ph	Early Cambrian	
	<i>Diplocraterion</i>	Dp	Early Cambrian	
	<i>Asterosoma</i>	At	Early Cambrian	
	<i>Rhizocorallium</i>	Rh	Early Cambrian	
	<i>Teichichnus</i>	Te	Early Cambrian	
	<i>Ophiomorpha</i>	Op	Permian	
	<i>Lockeia</i>	Lo	Early Ordovician	
	<i>Curvolithus</i>	Cu	Neoproterozoic	
	B	<i>Nereites</i>	Nr	Early Cambrian
		<i>Dictyodora</i>	Di	Cambrian
		<i>Helminthoidea</i>	He	Cambrian
		<i>Cosmorhapha</i>	Co	Cambrian
		<i>Urohelminthoidea</i>	Ur	Ordovician
<i>Paleomeandron</i>		Pl	Late Cretaceous	
<i>Scolicia</i> (meanders)		Sm	Early Ordovician	
<i>Spirophycus</i>		Sp	Ordovician	
<i>Lophoctenium</i>		Lp	Early Ordovician	
<i>Oldhamia</i>		Ol	Early Cambrian	
<i>Paleodictyon</i>		Pa	Early Cambrian	
<i>Zoophycos</i>		Zo	Cambrian	
<i>Phycosiphon</i>		Py	Ordovician	
<i>Taenidium</i>		Ta	Cambrian	
<i>Fucusopsis</i>		Fu	Ordovician	
<i>Neonereites</i>		Ne	Neoproterozoic	
<i>Spirorhapha</i>		Sr	Silurian	

Note: Stratigraphic ranges are based on the literature (see references in the Supplemental Material [see text footnote 1]).

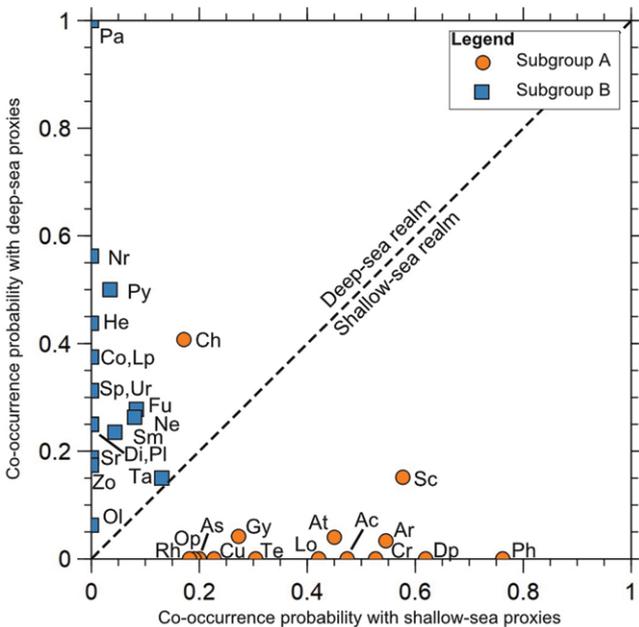


Figure 3. Node layout showing co-occurrence probability between ichnotaxa and environmental proxies, as quantified by the Jaccard index. Nodes correspond to taxa (see Table 1 for labels); links are not depicted for graphical clarity (refer to Fig. 2 for links).

analysis, although some researchers have argued that it may lead to overgeneralized, low-resolution interpretations (Goldring, 1993; MacEachern et al., 2007).

Biogeographic Distribution Patterns of Burrowing Behaviors

The simple generalist and specialist rules of our proposed model result in complex patterns of trace fossil association that are comparable to those observed in the real-world ichnofossil network (see the Supplemental Material, and Fig. S4 and Code S4 therein). All major topo-

logical measures of the ichnofossil network (average path length, clustering coefficient, density, and degree; number of communities) are within one standard deviation from the mean of 1000 model-generated networks (Fig. S7). The model displays the tendency to generate networks (1) with the average distance increasing slower than the logarithm of the network size (Fig. S5A); (2) with the average degree increasing linearly with the number of nodes (Fig. S5B); and (3) with high clustering (>0.8) and small distance (<1.5) (Fig. S6). These are typical features of small worlds (Humphries and Gurney, 2008; Junker

and Schreiber, 2008). These results demonstrate how the divergent, small-world structure of Phanerozoic trace-fossil associations derives from simple spatial patterns, i.e., most ichnotaxa maintaining a narrow range (specialists) and few ichnotaxa with a wide and/or unstable range (generalists).

CONCLUSIONS

By integrating network analysis and global paleontological data, we quantitatively demonstrate that deep-sea trace fossils have been morphologically cohesive and distinguishable from shallow-marine ones for most of the Phanerozoic.

The divergence reported here has applied implications for scientific research and for the energy industry, which relies on paleoenvironmental analysis for identifying resource-bearing deposits. This work settles a fundamental paleontological hypothesis (Phanerozoic divergence) and method (ichnofacies approach), proposed nearly 50 years ago (Seilacher, 1967, 1978, 2007).

Our model shows that two universal ecological guilds—specialists and generalists—controlled the spatial distribution of burrowing behaviors across the Phanerozoic. It finds a parallel in the development of social networks, with most individuals associating with (making friends with) individuals who are geographically close (environment-specific taxa) and few moving around (environment-crossing taxa) (Newman, 2000).

Burrow shape reflects the behavior of its producer. By demonstrating the persisting divergence of burrow shape over evolutionary time scales, this work suggests that small-world dynamics deeply influenced extended phenotypes and ecosystem engineering, thus controlling gene flow and natural variation in heritable behavior across the Phanerozoic. This indicates that small-world dynamics has been a major, but hitherto neglected, macro-evolutionary force in marine environments for the Phanerozoic.

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