

Post-Cambrian closure of the deep-water slope-basin taphonomic window

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ABSTRACT

Exceptional faunas (Konservat-Lagerstätten that preserve traces of volatile nonmineralized tissues) are statistically overabundant in the Cambrian Period; almost all examples preserved in continental-slope and shelf-basin environments are of this age. The hypothesis that an increase in the amount and complexity of bioturbation was an important agent in the elimination of this deep-water slope-basin taphonomic window is supported. Post-Cambrian ichnofaunal assemblages contain a higher proportion of pascichnia and agrichnia, ethologies produced by a mobile infauna. They also illustrate the lateral partitioning of organisms into different environmental niches; both opportunistic and equilibrium infaunas occur in low-oxygen environments in which the preservation of nonbiomineralized tissues was favored. Direct consumption of carcasses by bioturbating organisms was less important than changes to sediment properties as a result of bioturbation, notably enhanced microbial degradation of reactive organic matter, increased permeability, and the disruption of geochemical gradients necessary for mineral authigenesis.

Keywords: Burgess Shale, taphonomy, bioturbation, exceptional fauna.

INTRODUCTION

Exceptional faunas, a particular category of Konservat-Lagerstätte in which the decay-prone, nonbiomineralized tissues of organisms are preserved, are overabundant statistically relative to outcrop area in the Cambrian and Jurassic (Allison and Briggs, 1993). Examples in continental-margin (including base of slope) and shelf-basin environments are almost all of Cambrian age (Allison and Briggs, 1991). This restriction has been identified as the deep-water slope-basin taphonomic window (Allison and Briggs, 1991). Most of these Cambrian faunas have been termed "Burgess Shale type" on the basis of either taxonomic (Conway Morris, 1989) or taphonomic (Butterfield, 1990, 1995) similarities; the two criteria are not necessarily synonymous. The taphonomy of many of these Cambrian exceptional faunas has yet to be studied in detail, apart from the Burgess Shale itself (Butterfield, 1990, 1996; Towe, 1996; Orr et al., 1998; Petrovich, 2001). For the purposes of this study, the deep-water slope-basin taphonomic window is defined as the preservation of nonbiomineralized tissues in slope and basin settings during the Cambrian (taphonomic window 1a in Allison and Briggs, 1991, their Fig. 3). It is thus decoupled from both the taxonomic composition and mode of preservation of the faunas within it. Closure of the deep-water slope-basin taphonomic window after the Cambrian has been attributed to more ef-

ficient bioturbation in these environments (Allison and Briggs, 1991). This idea has been challenged on the grounds that it is not supported by the data (Aronson, 1992), or that other factors, most notably the decay-inhibiting effect of clays in preserving Burgess Shale-type faunas (Butterfield, 1995), are more likely agents.

Butterfield (1995) argued that a late Riphean (ca. 850–750 Ma) interval of enhanced organic-walled fossil preservation in shallow-shelf environments represents an earlier period of Burgess Shale-type preservation. Neoproterozoic shallow-marine, possibly lagoonal, shales also yield macrofaunas preserved as carbonaceous compressions, as in the upper part of the Doushantuo Formation, China (Xiao et al., 1998). This mode of preservation may therefore have occurred in shallow-marine environments through most of the Neoproterozoic and continued in deeper-water settings until about the end of the Cambrian (Knoll and Carroll, 1999). The hypothesis that preservation is the result of decay inhibition by clays and is controlled by long-term changes in clay mineralogy and ocean chemistry (Butterfield, 1995) is inconsistent with this temporal distribution because it predicts that exceptional faunas should disappear at about the same time in all environments. The temporal distribution does, however, match the increased ichnofaunal diversity over the late Precambrian to early Phanerozoic interval, which occurred first in shallow-marine, and

subsequently in deeper-water, environments (Crimes, 1992). The observation that Cambrian deeper-water ichnofaunal assemblages have a different ethologic structure than younger assemblages (Orr, 2001) prompts a reconsideration of the impact of bioturbation as an agent in the closure of the deep-water slope-basin taphonomic window.

EFFECTS OF BIOTURBATION ON MODERN SEDIMENTS

Bioturbation facilitates the transport of particulates and solutes across the sediment-water interface, enhances microbial activity, and stimulates organic matter decomposition. Sediment reworking translocates organic matter and exposes new surfaces for microbial colonization (e.g., Yingst and Rhoads, 1980). Burrowing increases the availability of oxygen as an electron acceptor (Andersen and Kristensen, 1991) by extending the oxic sediment surface; the downward transport of oxygen promotes aerobic decomposition of organic matter within the sediment (Aller and Yingst, 1978). Burrowing can also stimulate anaerobic decomposition: sulfate reduction rates can be three to five times higher in bioturbated sediments compared to similar, nonbioturbated, estuarine sediments (Hines and Jones, 1985). Bioturbation by different trophic groups can affect the properties of sediments in different ways; e.g., permeability can be decreased by sedentary suspension and deposit feeders but increased by mobile deposit feeders (Rhoads, 1974). Lower permeability impedes oxygen supply to microbes.

BIOTURBATION AND THE DEEP-WATER SLOPE-BASIN TAPHONOMIC WINDOW

Consumption by infaunal organisms removes nonbiomineralized tissues from the sedimentary record directly. Bioturbation also inhibits exceptional preservation indirectly by changing the physical, chemical, and biological properties of sediments, notably elevating levels of microbial activity.

The depth of sediment required to protect a carcass from scavengers was less during the Cambrian than subsequently because of the absence of deep burrowers (Allison and Briggs, 1993). Some deep burrowers in Cam-

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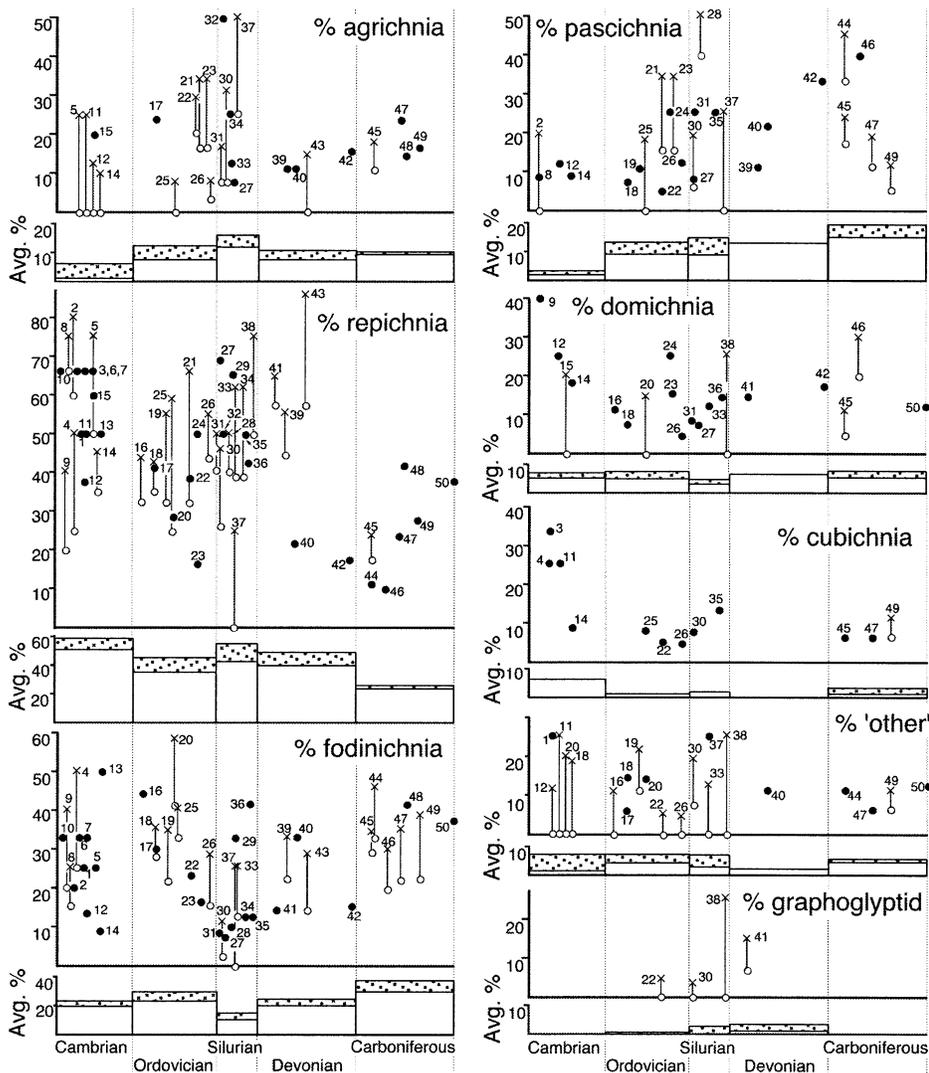


Figure 1. Temporal changes in ethologic structure of early Phanerozoic deeper-water ichnofaunal assemblages. Plots show minimum (o) and maximum (x) percentages of diversity of each assemblage represented by ethology indicated. Assemblages in which ethology is absent are omitted for clarity. Numbering of assemblages corresponds to that in data set. Histograms indicate average minimum and maximum percentages of that ethology in assemblage for each period.

brian flysch sediments (e.g., *Arenicolites*, *Skolithos*, *Teichichnus*; Pickerill, 1994) may represent doomed pioneers (sensu Föllmi and Grimm, 1990), i.e., organisms introduced with the depositing sediment that do not survive in low-oxygen muddy environments (Allison and Briggs, 1994). Even if other deep burrowers

were autochthonous, they occur in lithologies—and, by implication, environmental niches—other than those that favor the preservation of exceptional faunas. As the majority of these deep traces represent semistationary rather than mobile behavior, they represent neither scavenging nor continuous processing of large

volumes of sediment; their influence on the physical and chemical properties of the sediments is more localized. Although previous models have emphasized an increase over time in the depth to which sediments were bioturbated, changes in the nature and extent of bioturbation are potentially as important. Here we test this hypothesis with the first detailed comparison of the ichnofaunal record of deeper-marine communities between the Cambrian and subsequent periods.

MATERIAL AND METHODS

Data were assembled from the 50 most completely documented trace fossil assemblages of Cambrian–Carboniferous age from slope and basinal settings (Orr, 2001). The ethology of each ichnotaxon occurrence was assessed separately and assigned to one of six categories based on the definitions of Bromley (1996) (Fig. 1; Tables 1 and 2). Graphoglyptid ichnotaxa sensu Seilacher (1977) are predepositional, infaunal, open-burrow networks (typified by *Paleodictyon*). Most can be assigned to agrichnia. Some, however, represent other ethologies: e.g., *Cosmorhapha*, occurs as both a predepositional agrichnion and post-depositional pascichnion. The term “graphoglyptid” is retained for the few examples that could not be reassigned. Ichnotaxa that could not be interpreted are designated “Other.”

The ethology of some examples of ichnotaxa could not be resolved definitively (e.g., at what point is meandering behavior sufficiently systematic to consider the trace fossil a pascichnion rather than a repichnion). Others combine more than one behavior pattern, and different ichnospecies of an ichnogenus may represent different ethologies within a single assemblage. In such cases the data set¹ offers two alternative interpretations of the ethology of the ichnotaxon and therefore yields two sets of values: a minimum abundance including only unequivocal examples of an ethology and a maximum including all possible examples. Further discussion of the criteria used to identify the ethology of each ichnotaxon is provided in the data set, which also includes literature sources and explanatory arguments.

DATA ANALYSIS

The minimum and maximum number of ichnogenera representing each ethology was converted to a percentage of the total ichnogenetic diversity of each assemblage, and these values were plotted at the midpoint of the stratigraphic interval (epoch whenever

TABLE 1. TOTAL NUMBER OF ICHNOTAXA AND MINIMUM AND MAXIMUM FREQUENCY COUNTS OF EACH ETHOLOGY PER PERIOD

	Number of ichnotaxa	A		C		D		F		G		O		P		R		
		min.	max.															
Carboniferous	86	10	11	1	4	4	6	24	32	0	0	4	5	14	13	17	20	21
Devonian	45	3	4	0	0	3	3	9	11	1	2	1	1	5	5	5	19	23
Silurian	105	9	17	3	3	4	5	11	15	0	2	3	8	23	12	19	43	56
Ordovician	130	11	17	3	3	5	6	32	39	0	1	5	9	23	9	13	47	60
Cambrian	76	1	5	4	4	6	7	13	16	0	0	1	6	11	3	4	38	44

Note: Italicized data are total of “Other” per period if ichnotaxa that allow two ethologies are included. Abbreviations: A, agrichnia; C, cubichnia; D, domichnia; F, fodinichnia; G, graphoglyptid; P, pascichnia; R, repichnia.

¹GSA Data Repository item 2003111, ethologic structure of Cambrian–Carboniferous trace fossil assemblages from slope and basinal settings, is available online at www.geosociety.org/pubs/ft2003.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301-9140, USA.

TABLE 2. RESULTS OF CHI-SQUARED ANALYSIS

Ethological categories combined	d of f	Minimum number	Maximum number	Equivocal in other	Rank [§]
None	28	46.02*	51.52 [†]	48.16*	1
C + D	24	43.78 [†]	50.08 [†]	45.85 [†]	1
C + G	24	36.25	41.6*	37.9*	1
C + O	24	41.29*	49.99 [†]	44.58 [†]	1=
D + G	24	38.53*	44.35 [†]	40.28*	1
D + O	24	42.69*	49.44 [†]	44.32 [†]	2
G + O	24	37.55*	43.48 [†]	38.72*	1
C + D + G	20	35.33*	41.16 [†]	36.96*	1
C + D + O	20	39.38 [†]	48.07 [†]	41.15 [†]	2
C + G + O	20	32.08*	40.53 [†]	34.96*	1
D + G + O	20	34.7*	41.37 [†]	35.19*	2
C + D + G + O	16	30.85*	39.08 [†]	31.84*	2

Note: Abbreviations: C, cubichnia; D, domichnia; G, graphoglyptid; O, other; d of f, degrees of freedom in the chi-squared analysis.

*Statistically significant value of χ^2 at $p < .05$.

[†]Statistically significant value of χ^2 at $p < .01$.

[§]1, 1=, and 2 indicate that the sum of the ranked values of $(O - E)^2/E$ for the Cambrian Period (R) is the lowest, joint lowest and second lowest of the five periods.

possible) within which the assemblage occurs (Fig. 1). The average abundance of each ethology in assemblages within each period is expressed as the sum of the percentage in each assemblage divided by the number of assemblages (Fig. 1, histograms). There is a step-like increase in the average abundance of agrichnia and pascichnia between the Cambrian and Ordovician (Fig. 1, histograms). Subsequently, agrichnia show no obvious change in their average abundance with time, whereas pascichnia display a progressive increase (Fig. 1, histograms). Cubichnia are more important in the Cambrian than subsequently. Repichnia show a decrease in importance over time, and fodinichnia show a poorly defined increase. The other ethologies exhibit no systematic change in abundance with time.

Chi-squared analysis of the number of ichnotaxa assigned to each ethology per period (Table 1) indicates that the variation is statistically significant: $X^2_{28} = 46.02$, $p < .05$ (minimum number of ichnotaxa); $X^2_{28} = 51.52$, $p < .01$ (maximum number of ichnotaxa). Two considerations apply to this statistic, but the result remains robust. (1) The minimum data set omits ichnotaxa for which two possible ethologies are offered, whereas the maximum data set counts them twice. However, an analysis based on the actual number of ichnotaxa recorded per period (Table 1), by including ichnotaxa that allow two ethologies in "Other," also yields a statistically significant value: $X^2_{28} = 48.16$, $p < .05$. (2) The chi-squared statistic is expressed as

$$\sum \frac{(O - E)^2}{E},$$

where O is an observed frequency and E is the corresponding frequency expected if there is no association between any of the categories (ethology and period, herein). Thus, for eight ethologies and five periods (Table 1), the chi-

squared statistic is the sum of the 40 individual calculations. The chi-squared statistic requires a sample size large enough to allow all the expected frequencies generated in the analysis to exceed five, but this is not the case here. Some flexibility in interpreting this rule is allowed (Fowler et al., 1998), and the number of expected values less than five can be reduced by aggregating categories. Reanalysis of the data by aggregating the least abundant categories (cubichnia, domichnia, graphoglyptid, and "Other") returns statistically significant values at at least the $p = 0.05$ level in all cases except one (Table 2).

The values of $(O - E)^2/E$ calculated can be ranked in descending magnitude, and the ranks summed for each period. For the minimum and maximum data sets, the Cambrian Period has the lowest sum of ranks for all the combinations of ethologies listed in Table 2. When, as previously described, ichnotaxa for which there are two possible ethologies are included in "Other," the Cambrian Period has the lowest sum of ranks for the majority of combinations (Table 2). Thus, most of the variation in the data reflects the different ethologic structure of Cambrian assemblages.

PALEOECOLOGY OF EARLY PHANEROZOIC DEEPER-WATER COMMUNITIES

More extensive colonization of deeper-water environments after the Cambrian has been attributed to higher levels of organic detritus or oxygen concentrations (Crimes, 1992, p. 179). More likely it was a consequence of an onshore to offshore displacement of ichnotaxa from shelf settings (Bottjer et al., 2000), as a result of competition for ecospace and/or resources (Orr, 2001). The colonization of deeper-water environments was characterized by the first widespread occurrence of agrichnia and pascichnia and the establishment of the typical *Nereites* ichnofacies (Sei-

lacher, 1967). This change marks an increase in the amount of continuous locomotion by infaunal organisms, including the processing of large volumes of sediment in a systematic manner (pascichnia) and the creation of open-burrow networks connected to the overlying water column (agrichnia).

Lateral partitioning of ichnofauna into a series of different environmental niches clearly occurred by the Early Silurian and probably appeared earlier (the same ethologies, represented by many of the same ichnotaxa, also occur in Ordovician sequences). In Llandovery strata of the Welsh basin, equilibrium assemblages dominated by pascichnia occur in a variety of finer-grained lithofacies; apart from a requirement for oxygenated sediment (they maintain no connection to the water column), they were independent of lithology and depositional setting (Orr, 1995). The equilibrium community in fine-grained, oxygen-limited lithofacies was dominated by agrichnia, mainly various ichnospecies of *Paleodictyon*; these turbiditic sediments were bioturbated first by an opportunistic infauna immediately following deposition. *Paleodictyon* networks maintained connections to the overlying water column and are preferentially oriented (Crimes and Crossley, 1980); like many modern marine open-burrow systems, they may have exploited bottom currents for ventilation (Oke, 1990).

IMPACT OF BIOTURBATION ON PRESERVATION OF EXCEPTIONAL FAUNAS

Anoxia is ineffective as a long-term conservation medium for more labile nonbiomineralized tissues (Allison, 1988). Anaerobically driven authigenic mineral formation is essential; the steep, decay-generated chemical gradients required must be maintained while mineralization occurs (Sagemann et al., 1999).

The sequence in which different invertebrates decay (Briggs and Kear, 1993, 1994) under a range of conditions is similar; successively more recalcitrant tissues remain with time. The rate of decomposition may be increased where the oxygen content of the pore waters is elevated or replenished (aerobic decay). Thus, the delay of authigenic mineralization affects the fidelity of preservation. Bioturbation disrupts the establishment of anaerobic or dysaerobic conditions and the maintenance of chemical gradients in the vicinity of decaying organisms (Sagemann et al., 1999).

The preservation of many Cambrian exceptional faunas in deeper-water settings, including the Burgess Shale, was a consequence of transportation by events and deposition in poorly oxygenated muddy environments (Al-

lison and Briggs, 1993, 1994; Fletcher and Collins, 1998). Such fossiliferous sequences may contain low-diversity ichnofaunas dominated by semistationary ethologies, but paschichnia and agrichnia are absent (Robison, 1991; Allison and Brett, 1995). Autochthonous shelly benthos associated with bioturbation in the Burgess Shale represent opportunistic colonization during episodes of benthic oxygenation. The soft-bodied fossils, in contrast, were preserved under low-oxygen conditions (Allison and Brett, 1995). Equilibrium communities of mobile infauna did not become prevalent in such low-oxygen environments until after the Cambrian (Fig. 1; Table 1: although the precise O₂ requirement of the producers of agrichnia is unknown, the trace fossils are diagnostic of low-oxygen levels in the sediment). Likewise, event beds newly deposited in low-oxygen environments were not colonized opportunistically until after the Cambrian (Orr, 1995).

The organically preserved parts of many Burgess Shale fossils, including sclerites of *Wiwaxia* and setae of *Canadia* (Butterfield, 1990), represent the most recalcitrant non-biomineralized tissues. More labile tissues, however, including possible muscles, are only preserved through replication in authigenic clay minerals (Orr et al., 1998) or, in the case of the midguts of certain arthropods, calcium phosphate (Butterfield, 2002). The fidelity of preservation therefore depends on both the rate of decay and the timing of mineral authigenesis. Post-Cambrian changes in the extent and type of bioturbation in deeper-water low-oxygen environments enhanced microbial activity and accelerated rates of decay, inhibiting the establishment of the chemical gradients essential for the formation of authigenic minerals. Any increase in sediment permeability would have elevated microbial activity and reduced the concentration of ions (necessary for mineral authigenesis) in the sediment column. Post-Cambrian closure of the deep-water slope-basin taphonomic window was therefore not just a product of the onset of deep bioturbation; it was in large part due to temporal changes in the ecology of the actual environments where exceptional preservation occurred.

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