Decoupled evolution of soft and hard substrate communities during the Cambrian Explosion and Great Ordovician Biodiversification Event

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Contrasts between the Cambrian Explosion (CE) and the Great Ordovician Biodiversification Event (GOBE) have long been recognized. Whereas the vast majority of body plans were established as a result of the CE, taxonomic increases during the GOBE were manifested at lower taxonomic levels. Assessing changes of ichnodiversity and ichnodisparity as a result of these two evolutionary events may shed light on the dynamics of both radiations. The early Cambrian (series 1 and 2) displayed a dramatic increase in ichnodiversity and ichnodisparity in softground communities. In contrast to this evolutionary explosion in bioturbation structures, only a few Cambrian bioerosion structures are known. After the middle to late Cambrian diversity plateau, ichnodiversity in softground communities shows a continuous increase during the Ordovician in both shallow- and deep-marine environments. This Ordovician increase in bioturbation diversity was not paralleled by an equally significant increase in ichnodisparity as it was during the CE. However, hard substrate communities were significantly different during the GOBE, with an increase in ichnodiversity and ichnodisparity. Innovations in macrobioerosion clearly lagged behind animal–substrate interactions in unconsolidated sediment. The underlying causes of this evolutionary decoupling are unclear but may have involved three interrelated factors: (*i*) a Middle to Late Ordovician increase in available hard substrates for bioerosion, (*ii*) increased predation, and (*iii*) higher energetic requirements for bioerosion compared with bioturbation.

bioturbation | bioerosion | trace fossils | evolutionary radiations | rarefaction analysis

The Cambrian Explosion (CE) and the Great Ordovician Biodiversification Event (GOBE) are the two evolutionary radiations that shaped the Paleozoic marine biosphere (1–7). The contrasting natures of the Cambrian and Ordovician radiations have long been recognized. Body fossil information suggests that the vast majority of body plans emerged during of the CE and that taxonomic increases during the GOBE took place at lower taxonomic levels (8). However, there is still debate about whether these two events were independent or whether the GOBE was an extension of the CE (8–10).

Research on the nature of these two events has concentrated on body fossils. Initial research focused on shelly fossils, but later soft-bodied faunas were included due to the spectacular preservation of Burgess Shale-type biotas, originally reported for the Cambrian and lately for the Ordovician (9, 10). In comparison, trace fossil information has not been used to the same degree. Significantly, ichnologic evidence is essential to evaluate how the interactions between organisms and substrate responded to these two major evolutionary events (11, 12). Also, because trace fossils essentially represent a continuous record of soft-bodied organisms, ichnologic information provides an independent line of evidence to that of shelly fossils, therefore helping to calibrate these two evolutionary radiations (12). Assessing changes in animal–substrate interactions in both soft (bioturbation) and hard (bioerosion) substrate communities as a result of the CE and the GOBE may

shed light on the natures of both radiations. Because there is still controversy regarding Sepkoski's nonstandardized curves of Phanerozoic taxonomic diversity (13–15), a rarefaction analysis was performed in an attempt to standardize diversity data. The aims of this paper are to document the contrasting ichnodiversity and ichnodisparity trajectories in soft and hard substrate communities during these two evolutionary events and to discuss the possible underlying causes of this decoupled evolution.

Results

Figs. 1 and 2 summarize ichnodiversity and ichnodisparity changes, respectively, from the Ediacaran through the Ordovician (*SI Appendix*, Tables S1 and S2). According to these data, the early Cambrian (series 1 and 2) displayed a dramatic increase in diversity and disparity of bioturbation structures (12). Whereas a maximum of 10 ichnogenera of bioturbation structures have been recorded in Ediacaran strata (9 in the Vendian and 7 in the Nama subdivisions), 40 ichnogenera are known from Fortunian strata, 59 from stage 2, 71 from stage 3, and 75 from stage 4 (Fig. 1 and *SI Appendix*, Table S1). The rapid increase in behavioral patterns of bioturbation structures is also displayed at the scale of ichnodisparity (Fig. 2 and *SI Appendix*, Table S2). Specifically, there are a maximum of 6 categories of architectural designs (5 in the Vendian and 4 in the Nama subdivisions) in Ediacaran strata in contrast to 20 in Fortunian strata (27 from stage 2, 31 from stage 3, and 32 from stage 4). The maximum increase in both ichnodiversity and ichnodisparity took place during the Fortunian,

Significance

The majority of body plans were established during the Cambrian Explosion (CE), whereas the significant taxonomic increases during the Great Ordovician Biodiversification Event (GOBE) were manifest at lower taxonomic levels. Data on the diversity and disparity of bioturbation and bioerosion indicate that soft and hard substrate communities experienced decoupled evolution. Ichnofossil data indicate that rapid diversification of bioturbation occurred during the early early Cambrian (Fortunian) rather than during the late early Cambrian as indicated by shelly fossils. The first rapid increase in bioerosion took place during the GOBE approximately 80 My after the CE in bioturbation.
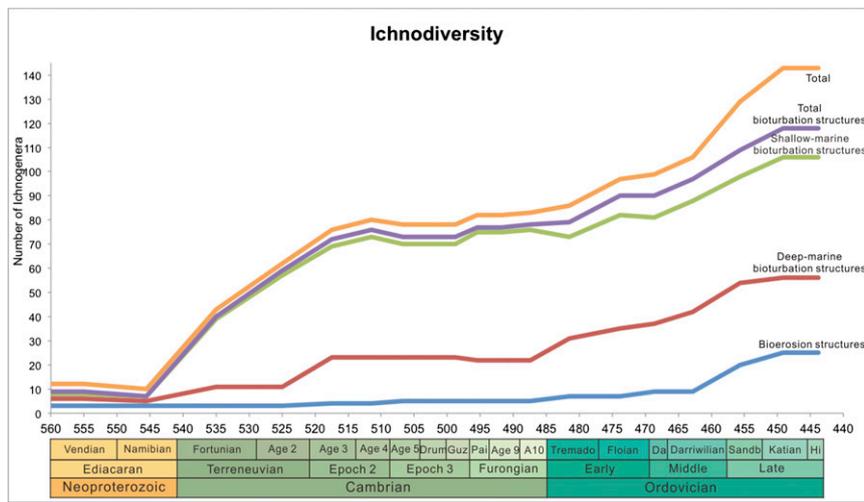
EVOLUTION

Fig. 1. Ichnodiversity changes during the Ediacaran-Ordovician. Ichnogenera were plotted as range-through data (i.e., recording for each ichnogenus its lower and upper appearances and then extrapolating the ichnogenus presence through any intervening gap in the continuity of its record).

which displays a 300% increase in ichnodiversity and 233% in ichnodisparity with respect to Ediacaran data. The subsequent more modest ichnodisparity increase in stage 2 (35% with respect to the Fortunian) reflects in part the appearance of vertical burrows of suspension feeders (i.e., vertical simple burrows, vertical single U- and Y-shaped burrows) and to a lesser extent of detritus feeders (i.e., vertical concentrically filled burrows) (12, 16). Ichnodisparity and ichnodiversity reached a plateau in stages 3 and 4, respectively, which continued during the rest of the Cambrian, suggesting that by the end of the early Cambrian the evolutionary radiation was nearly over (12). This pattern is remarkably consistent with that indicated by the body fossil record (6, 7) and has been confirmed by rarefaction analysis (*SI Appendix, Rarefaction Analysis*).

Contrasting with this evolutionary explosion in bioturbation structures, Cambrian bioerosion structures are only represented by four categories of architectural design: circular holes, cylindrical vertical to oblique borings, fracture-shaped borings, and globular to spherical borings. *Oichnus, Trypanites,* and *Mandibulichnus* are known from Cambrian strata (17–20), the former being already present in Ediacaran strata (21). Two microbioerosion ichnogenera

(*Granulohyalichnus* and *Tubulohyalichnus*) have their first occurrence in the Archean (22, 23). Although these ichnogenera have not been recorded in Ediacaran-Ordovician strata, they do occur in younger rocks (23) and, therefore, have been added to the list. *Granulohyalichnus* has been placed in the category of globular to spherical borings. However, microborings included in *Tubulohyalichnus* display a wide variety of morphologies, most likely representing more than one ichnogenus. Its type ichnospecies, *T. simplus,* is included within the architectural category of cylindrical vertical to oblique borings, whereas the remaining ichnospecies are awaiting taxonomic review.

In contrast with CE data, a different pattern emerges from the analysis of GOBE global ichnodiversity and ichnodisparity data. After the middle to late Cambrian plateau, diversity of bioturbation structures shows a continuous increase during the Ordovician in both shallow- and deep-marine environments. The Ordovician increase in diversity is expressed in both raw and rarified data (*SI Appendix, Rarefaction Analysis*). However, rarefaction analysis demonstrates that the middle to late Cambrian diversity plateau for deep-marine environments is simply an artifact resulting from lack
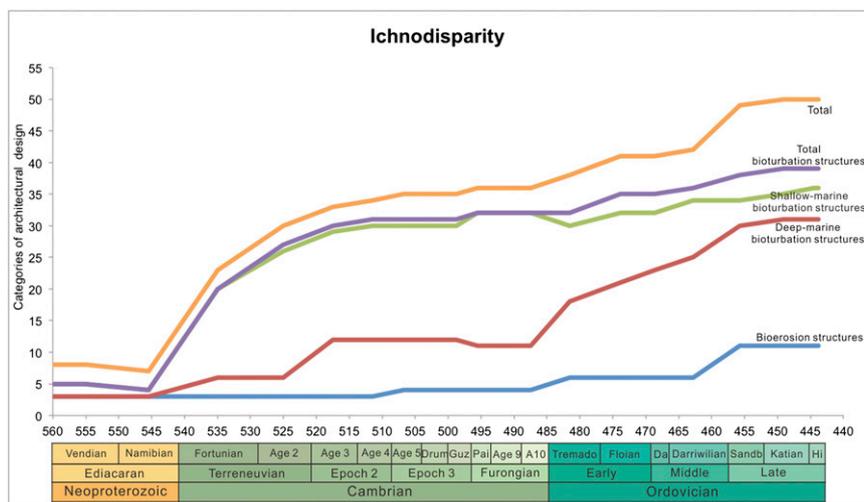

Fig. 2. Ichnodisparity changes during the Ediacaran-Ordovician. Categories of architectural design were plotted as range-through data (i.e., recording for each category its lower and upper appearances and then extrapolating the presence of each category through any intervening gap in the continuity of its record).

of data. The data compilations indicate that diversity of Ordovician bioturbation structures showed a 46% increase from the Tremadocian (72 ichnogenera) to the Hirnantian (105 ichnogenera) in shallow-marine environments and a 77% increase (31 ichnogenera in the Tremadocian to 55 ichnogenera in the Hirnantian) in deep-marine environments (Fig. 1 and *SI Appendix*, Table S1). In contrast to the trends during the CE, this Ordovician increase in diversity of bioturbation structures is not paralleled by an equally significant increase in ichnodisparity (21% with respect to Cambrian levels). If both shallow- and deep-marine ichnodisparity are plotted separately, then it is clear that the increase in ichnodisparity for the most part took place in deep-marine settings and that ichnodisparity in shallow-marine settings was similar during both the Cambrian and Ordovician. Because a significant number of the architectural categories that characterize Ordovician deep-sea settings first occurred in shallow-marine settings during the Cambrian and later migrated to the deep sea, the taxonomic innovations taking place in the deep sea were probably limited, therefore resulting in a minor increase in global ichnodisparity. Incidentally, data analysis provides robust support for the "onshore-offshore model," which invokes onshore origination of evolutionary innovations and their subsequent expansion to deeper water (24, 25).

In contrast with bioturbation, the historical pattern for bioerosion structures is significantly different, with an increase not only in ichnodiversity but also in ichnodisparity during the Ordovician. Two ichnogenera (*Gastrochaenolites* and *Podichnus*) were added during the Early Ordovician and two more (*Caedichnus* and *Tremichnus*) during the Middle Ordovician. Raw data indicate that the abrupt increase in diversity of bioerosion structures, however, took place during the Late Ordovician with the addition of 16 new ichnogenera to reach a total of 25 ichnogenera by the end of the Ordovician (178% increase). This large change is also displayed by ichnodisparity data (Fig. 2 and *SI Appendix*, Table S2), with 6 categories of architectural design being present during the Early and Middle Ordovician vs. 14 during the Late Ordovician (133% increase). Therefore, the systematic analysis of raw ichnodiversity data clearly supports the notion of an Ordovician bioerosion revolution (26). Rarefaction analysis based on actual counting of specimens of bioerosion structures (*SI Appendix, Rarefaction Analysis*) also supports this marked increase in diversity.

Discussion

Notably, the ichnodiversity curve (Fig. 1) is strikingly similar to that of Phanerozoic diversity curves of marine animal genera (27). Both trace fossil and shelly fossil genera show an explosive diversification during the early Cambrian and more continuous diversification during the Ordovician. As with the curves showing marine animal diversity during the early Paleozoic (1), bioturbation diversity supports a two-phase kinetic model of logistic diversification, corresponding to the CE and the GOBE. Each phase is characterized by an initial lag stage, followed by a growth stage, and culminating in an equilibrium stage. This pattern suggests common trends in shelly and soft-bodied organisms, therefore reinforcing the notion of overarching evolutionary radiations rather than taphonomic or sampling artifacts.

Two main departures with respect to curves based on body fossils are noted. First, ichnologic evidence indicates that rapid diversification took place during the early early Cambrian (12) rather than during the late early Cambrian as indicated by shelly fossils. Accordingly, the early early Cambrian (Fortunian) may be regarded as part of a phylogenetic fuse, pushing the earliest fossil record of most of the main body plans back in time close to the Ediacaran-Cambrian boundary (12). Second, whereas marine animal genera show minor diversity fluctuations during the middle to late Cambrian, raw data show that trace fossil diversity reached a plateau at the beginning of the GOBE. However, rarefied diversity data show that this pre-GOBE plateau may be an artifact related with sampling size and that fluctuations in the diversity of bioturbation structures that may have occurred during the middle Cambrian to Furongian.

In addition, the data reveal that the contrasting natures of the CE and the GOBE are expressed not only by body fossils but also by trace fossils. Analysis of the body fossil record indicates that the overwhelming majority of body plans emerged during the CE and that taxonomic increases during the GOBE occurred at lower taxonomic levels (8). The fossil record of bioturbation mimics this pattern. Whereas the CE data show a rapid increase of both diversity and disparity of bioturbation structures, the GOBE data display a remarkable increase in diversity of bioturbation structures, which is not paralleled by an equally significant increase in ichnodisparity. In fact, Ordovician shallow-marine ecosystems show disparity levels of bioturbation structures that are very similar to those in the Cambrian. This pattern is similar to that noted with body fossils, revealing a rapid disparity increase that exceeds initial diversification, therefore implying early large steps in disparity and smaller ones subsequently (28–30).

This study points to contrasting ichnodiversity and ichnodisparity trajectories in soft and hard substrate communities during the CE and GOBE. Innovations in bioerosion clearly lagged behind animal–substrate interactions in unconsolidated sediment. Data compilations show that the rapid increase in bioerosion took place ~80 My after the Cambrian explosion in bioturbation. The underlying causes of this decoupling between bioerosion and bioturbation are unclear, but three interrelated factors may have been involved. First, it is possible there was a Middle to Late Ordovician increase in available hard substrates for bioerosion, which would have increased ecospace for boring animals. Although carbonate hardgrounds may have been locally common during the Early Ordovician (31), they increased in global abundance later during the Ordovician (32, 33). However, the recent discovery of Cambrian series 3 nonbioeroded hardgrounds suggests that substrates were available for potential macroborers in at least some settings (34). In any case, the absence of bioerosion in these hardgrounds may be taken as further evidence of the macroevolutionary lag displayed by hard substrate communities. Shelly substrates appear to have become more common from the Middle to Late Ordovician (35, 36), but detailed stage-by-stage data are lacking. Second, whereas the trend toward infaunalization in unconsolidated substrates started well before a marked increase in predation pressures (37), the penetration of infaunal organisms into hard substrates during the GOBE may have been driven by increased predation. The endolithic realm may have served as a refugium from predation, likely even safer than the infaunal habitat (38). At the same time, some bioerosion structures themselves (e.g., *Oichnus*) were produced by predators, therefore resulting in feedback loops promoting further penetration in hard substrates. Third, in most cases, the energy involved in penetrating hard substrates is greater than that involved in disturbing unconsolidated sediment. Modern ecologic work on this topic is sparse, although it is reasonable to infer that the mechanical grinding of a cemented substrate is a much more energetic process than burrowing in unconsolidated sediment. An energy-based explanation is consistent with the fact that bioerosion in continental environments also experienced a significant macroevolutionary lag with respect to bioturbation in similar settings (39).

Finally, the present study shows that increases in ichnodiversity are invariably linked to evolutionary radiations but are not necessarily sufficient conditions for an increase in ichnodisparity. The CE and GOBE data suggest that the key factor in ichnodisparity construction is the exploitation of empty or underused ecospace (39). In the present case, this conclusion is supported by the fact that the CE and GOBE instances of remarkable ichnodisparity increases were clearly linked to colonization of new ecospace, namely the overall increase in disparity of bioturbation

EVOLUTION

structures during the Fortunian and the overall increase in disparity of bioerosion structures during the Late Ordovician.

Materials, Methods, and Concepts

The concepts of ichnodiversity and ichnodisparity (40) are central to the data analysis of this paper. In particular, global ichnodiversity (i.e., number of ichnogenera per time slice or trace fossil richness) is used as a proxy for behavioral changes and evolutionary innovations during the CE and GOBE. In addition, the concept of ichnodisparity (i.e., number of trace fossil architectural designs) is used to record basic morphological plans in biogenic structures (*SI Appendix*, Table S3). It is implied that ichnodisparity reveals major innovations in body plan, locomotory system, and behavioral program (12).

Ichnodiversity trajectories were reconstructed using a compilation of ichnogenera from the Ediacaran to the Ordovician. A previous trace fossil database encompassing the Ediacaran to lower Cambrian (12) was taken as a starting point. This compilation is based on systematic and critical examination of the literature, collection material, and field data. This database is here expanded by the addition of middle Cambrian to Late Ordovician ichnofaunas. Bioerosion and bioturbation ichnotaxa were considered separately (*SI Appendix*, Tables S4–S6). The same procedure was followed for ichnodisparity by plotting architectural designs (*SI Appendix*, Tables S7–S9). Data were plotted using 5-My bins. Nineteen time slices: 2 informal Ediacaran subdivisions, Vendian and

Nama (41), and the 10 and 7 official stages for the Cambrian and Ordovician, respectively, were considered. Ichnogeneric and categories of architectural design occurrences were compiled on a case-by-case basis, thereby summarizing actual occurrences. Ichnogenera and categories of architectural designs were plotted as "range-through" data (i.e., recording the lower and upper appearances for each ichnogenus/architectural design and then extrapolating the design presence through any intervening gap in the continuity of its record) to avoid the noise introduced by uneven sampling and availability of studies. To evaluate the effects of sample size on the diversity curves, a rarefaction analysis of these data were undertaken (*SI Appendix*, Figs. S1–S5). Because of the need for a consistent ichnotaxonomic approach, each original taxonomic determination was revised, and synonymies were checked. The ichnodiversity curves were compiled at the ichnogenus level because the genus taxonomy is more firmly established than the species taxonomy.

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