

## Abstract

### Latitudinal Controls and Caveats on the Distribution of Trace Fossils and their Resultant Textures in Continental and Marine Depositional Systems

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#### Introduction and Background

Studies on modern biota in continental and marine depositional systems indicate that climate largely controls the diversity and abundance of organisms, as well as their distribution in ecosystems (e.g. Odum 1971, Whittaker 1975, Aber and Melillo 1991, Dworshak 2000, Goldring et al. 2004). Climate, and thus the distribution of biotic systems, varies in a predictable manner with latitude, and this relationship has existed through most of the Phanerozoic (e.g. Benton 1995, Bottjer and Droser 1994, Parrish 1998, Ausich and Bottjer 2001, Goldring et al. 2004). These general trends, however, will vary according to global climatic conditions—icehouse or green house conditions (e.g. Verver et al. 2000, Link 2009)—and are supplanted by the local physicochemical controls and autocyclic processes that operate within sedimentary systems; these particularly influence tracemaking, epi- and endobenthic organisms in the marine realm and epigeal, geophilic, and geobionts in the continental realm (Twitchett and Barras 2004, Hasiotis 2007, Hasiotis and Platt 2012). Latitude, defined by equal points that form East–West parallel lines that ring the Earth (e.g. Snyder 1987), do not change through time, thus, they can be used as a static reference in the description of Earth systems and their biophysicochemical factors under distinct continental and oceanic configurations and global climate conditions (i.e., icehouse, greenhouse, or transitional).

Only a few ichnological studies have explored latitudinal trends in ichnofossil distribution in marine environments. Goldring et al. (2004) provided good evidence that compositional changes in trace-fossil assemblages could be related to climate (i.e., temperature); this work, while significant, was limited in scope and must be built upon. Cadée (2001) discussed latitudinal variation in bioturbation attributed to changes in infaunal composition resulting from a variety of environmental factors. Both of these papers discussed limited earlier efforts at discerning climatic and latitudinal information from the trace-fossil record and draw heavily from biological research, which is more readily available. Quite a few characterizations of tropical ichnology exist (e.g. Jones and Pemberton 1989; Buatois et al. 2008), but these are not contrasted with temperate and polar trace-fossil assemblages. Quiroz et al. (2010) discussed the paleolatitudinal distribution of *Macaronichnus* in cold-water settings, carefully considering the latitudinal significance of trace fossils, if any; papers cited therein contend that it is limited to temperate zones. Schatz et al. (2013) compared some differences between arctic- and temperate-zone fjords; though informative, the effect of physicochemical parameters changing with temperature is not explored. Uchman and Gazdzicki (2006) described trace fossils in Eocene marine deposits on the Antarctic Peninsula, but temperature influence on the assemblage was not discussed. Notably, Eyles et al. (1992) studied the ichnology of a glacially influenced continental shelf and slope, observing that their distributions and composition varied from the marine

norm—characteristic ichnological assemblages were deeper than normal—attributing this to shifts in food distribution, although other factors may be at play. Thus, focused efforts on resolving the influence temperature has on trace-fossil signature are very rare in the literature.

## General Trends

In general, diversity, and thus assumedly ichnodiversity, decreases from the equator to the pole for marine and continental environments. Similarly, organisms are thought to have evolved in equatorial regions as well as in shallow water, and then through time moved poleward and into deeper water (e.g. Niklas et al. 1985, Bottjer and Droser 1994, Ausich and Bottjer 2001).

Body size is also related to latitude. Bergmann's Principle (1848) states that the body sizes of warm-blooded and cold-blooded animals increase towards higher latitudes (Blackburn et al. 1999). Initially thought to apply to land animals, Bergmann's Principle has been verified for marine crustaceans and, to a lesser extent, bivalves. The increase in body size is variably ascribed to higher dissolved oxygen content, slowed metabolism, and longer life spans in lower temperature living conditions (Van Voorhies 1996, Timofeev 2001). As such, trace fossils associated with certain groups of burrowers stand to provide an independent means of assessing temperature simply by their size distribution. Body size tends to increase as water temperature decreases, paralleling the gas solubility of colder water vs. warmer water (e.g. Hallam 1965).

In marine settings, deeper and more penetrative burrowing takes place in the shoreface and becomes shallower into the abyssal zone, as communities shift from suspension-feeding to deposit-feeding to grazing and gardening strategies in the deepest settings (e.g. Seilacher 1967). Abundance in biomass also shifts from shallow coastal settings in low latitude to mid- to outer shelfal settings in high latitudes (Gingras et al. 2008). They have proposed ichnological criteria that distinguish high-latitude conditions. van der Kolk et al. (2014) are investigating possible sedimentary and ichnological signatures of high latitude, storm-dominated marine conditions in comparison to low latitude during a greenhouse global climate. Higher latitude systems appear to have significantly fewer crustacean burrows (i.e. *Ophiomorpha*), whereas *Macronichnus* appears to be much larger diameter than in lower latitude settings.

In continental settings, burrowing organisms are intimately involved in soil formation and show latitudinal trends that parallel the production and depth of weathering products (e.g. Birkeland 1999). This trend, however, does not hold accurate, as nutrient availability is a limiting factor in tropical latitudes, as is vadose accommodation due to high soil moisture levels (e.g. Odum 1971, Aber and Melillo 1991). Bioturbation depth and tiering tends to be shallowest in the tropics, deepest in subtropical regions, decreasing in higher latitudes related to the occurrence of deserts and arid climate, increase in temperate latitudes and ultimately decreases toward the pole regions where high water table, soil moisture, and permafrost preclude penetration (Hasiotis et al. 2007). Bioturbation patterns in soils are shallowest in weakly developed soil as well as in high soil moisture and water table settings; patterns become deeper and more pervasive as soil development increases and soil moisture decreases, and water table depth increase (Hasiotis et al. 2007).

An excellent example of a comparison of high- vs. low-latitude systems comes from research in Antarctica. Miller et al. (2002) and Miller and Labandeira (2002) hypothesized (H) for continental settings that (H1) late Paleozoic and early Mesozoic ichnofossils were more diverse, abundant, and penetrative in high paleolatitude deposits, (H2) deep burrowing may have originated in high paleolatitudes and spread toward lower paleolatitudes, and (H3) colonization of freshwater systems were slowly colonized over hundreds of millions of years. Ongoing research includes data collection from low- and high-latitude continental settings in icehouse and greenhouse global climates to falsify one or more of these hypotheses to determine what trends exist, if any, in terms of latitudinal controls.

## Caveats and Hypothesis Testing

Predictable latitudinal patterns in ichnodiversity, abundance, tiering, and biogenic textures can be strongly controlled by such local physicochemical processes dictated by the environment as depositional energy, sedimentation rate, oxygenation, turbidity, and groundwater profile. These not only vary by latitude but also vary with respect to the associations of juxtaposed depositional environments. In the continental realm, the proximity to ocean bodies, degree of continentality, orographic effects, regional drainage patterns, and wind direction will have an effect on the distribution of moisture and temperature (e.g. Lydolph 1985) such that burrowing organisms and soils will record hydrologic and maturity signals contradictory to the latitude at which they are found. In the marine realm, icehouse vs. greenhouse global climates will play a major role in oceanographic circulation patterns and water mass temperatures. Under icehouse conditions, deep waters are cold, oxygen rich and favor larger bodied sizes in epi- and infauna; this pattern breaks down when overall ocean temperatures are warmer during greenhouse conditions. Bottom water anoxia will inhibit organisms from living in bottom waters, whereas increased seasonal dysoxia will produced reduced by body sizes because of oxygen stress (e.g. Jumars and Wheatcroft 1989, Harper et al. 1991, Urbank 1993). In continental settings, dwarfism in paleosol ichnofossils occurs across the PETM (Paleocene-Eocene Thermal Maximum) due to increased transient warming of 4–7°C and a drying climate (Smith et al. 2009). In high latitudes, high sedimentation rates and freshwater input in marine deltaic systems will produce dwarfed ichnofossil associations that masks the effects of normal salinity and higher dissolved oxygen. A similar pattern is seen in the trace-fossil assemblages and deposits in the Lower Permian Mackellar Formation (Flaig et al. 2013, Jackson et al. 2013).

Testing H1, H2, and H3 in recent Antarctic field research has produced interesting results concerning latitudinal trends in Permian and Triassic continental fluvial-lacustrine deposits. Numerous ichnotaxa appear to be distributed globally by this time. General ichnodiversity and abundance appears to be similar between Triassic high- and low-latitude settings, whether comparing low or high sinuosity river deposits. Tiering depths in channel deposits appear to be deeper in low-latitude settings compared to high latitude. Overbank deposits also record greater ichnodiversity, abundance, and tiering depth in low-latitude settings compared to high-latitude settings (Hasiotis and Flaig 2012). Freshwater colonization recorded by trace fossils appears controlled by physicochemical controls of aquatic depositional systems (Hasiotis 2007). These preliminary results appear to falsify latitudinal trends predicted by H1–H3, however, a greater sample set is necessary to determine the final outcome of these tests and the true nature of any underlying latitudinal trends in continental ichnofossils and depositional systems. This especially significant for understanding those trends in continental and marine systems that deposited sediment and developed soils during icehouse and greenhouse global climate conditions.

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