

# The Story of O: The Dominance of Organisms as a Soil-Forming Factor From an Integrated Geologic Perspective and Modern Field and Experimental Studies

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## Abstract

Geological and neoichnological evidence demonstrates the dominance of organisms through their life histories and behaviors as a major soil-forming factor since the Late Ordovician (~460 million years of Earth history). Continental deposits since that time preserve an abundance of paleosols that contain a great variety of trace fossils (i.e., krotovina) of microbes, plants, and animals. Trace fossils produced by animals preserve the burrows, nests, tracks, and trails that are intimately associated with a range of sedimentary and pedogenic structures indicative of immature to mature soil development in fluvial, alluvial, lacustrine, and eolian depositional systems. Neoichnological studies of organisms—field and experimental research on their tracemaking activity—in terrestrial environments confirm their tremendous influence on sediment mixing, soil formation, and soil turnover. Burrowing animals displace sediments by diffusive (mm-scale particle movement) and advective (cm- to m-scale particle movement) methods via a combination of carrying, pulling, pushing, raking, breaking or cutting, and forcing that result in traces. These traces have distinct three-dimensional shapes and volumes that are repeated in space and time, resulting in soil formation. Many of these traces have changed little through 100's of millions of years of evolution based on comparisons between modern and ancient animal traces.

## Key Words

Ichnofossils, ichnology, nests, paleosols, bioturbation, biomanale

## Introduction

Organisms, particularly animals, have been and currently are one of the most important of all the soil-forming factors (Figure 1) for most the Phanerozoic, at least since the Late Ordovician (~460 million years ago) (e.g., Wallwork, 1970; Hole, 1981; Hasiotis, 2003, 2007). Research of modern soils and soil biota shows that animals are extremely effective at mixing sediment and soils within the subsurface, acting to help build and destroy pedogenic structures and voids, and playing a major role in nutrient cycling via the work of detritivores and saprovores (e.g., Darwin, 1881; Wallwork, 1970; Hole, 1981; Halfen and Hasiotis, this volume). Recent research on continental deposits shows that trace fossils—the study of tracks, trails, burrows, nests, rooting patterns, borings, and biolaminates—abound in immature to very mature paleosols that can be attributed to a variety of microbial communities, plants, and animals, based on the comparisons of three-dimensional (3D) morphology to modern burrows (krotovina) and their tracemakers (e.g., Hasiotis, 2003, 2007, and references therein).

The purpose of this paper is to summarize the significance of animal bioturbation as a major soil-forming factor and ecosystem maintenance through the mixing of sediment and formation of soils, soil turnover, regulation and modulation of ecosystems as ecosystem engineers, and a major contributor to the evolution of terrestrial ecosystems since the Ordovician. The relationship between the effects of modern animals and that of their work preserved in the geologic record is demonstrated through the perspective of neoichnological and geological research. Neoichnology—the study of traces produced by modern organisms—provides the basis for understanding traces that result from a variety of behaviours from different organisms, so that those 3D structures produced can be related to: (1) particular behavior(s); (2) the physicochemical conditions—the effects of climate, topography, parent material—under which they were produced; (3) the time it took to produce the structure and how long it was used; and (4) the groundwater profile and greater hydrologic system of the landscape in which they occur (e.g., Hasiotis, 2007). Neoichnological field and laboratory research provides the detailed information that allow trace fossils in the geological record to be used as proxies for: 1) biodiversity of soil biotic communities not recorded by body fossils in that strata or geologic time interval; 2) soil moisture and water table level and its seasonal fluctuations; 3) early stages in soil formation (Entisols, Inceptisols) for which there are few abiotic pedogenic features; and 4) climatic setting relating to the amount of precipitation or through by analogy of occurrence in modern settings and its average temperature and precipitation.

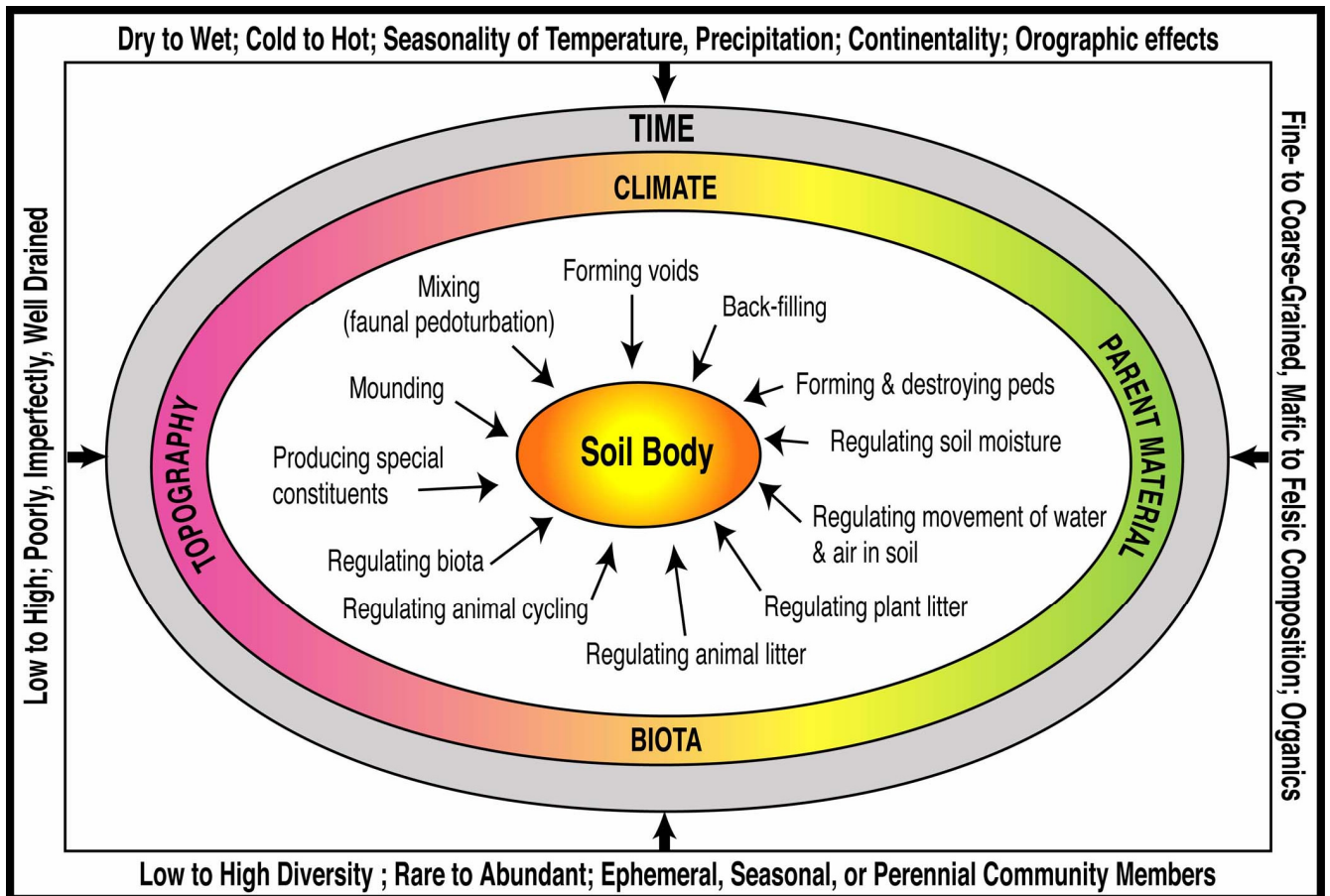


Figure 1. The effects of the five major soil-forming factors on the soil body (modified from Hole, 1981; Hasiotis, 2007). Note that at any one time, the biota, climate, topography, and parent material will vary. Time is also the only variable that proceeds at a relatively constant rate and is predictable when reconstructing deep time Earth history.

### Linking the Work of Animals to Soil Formation

The presence of animals categorized as geophiles and geobionts in soils (Figure 2) has been defined based on the amount of time and portion of their life cycle spent within subsurface: transient, temporary, periodic, permanent, and accidental—listed in order from the least amount of time and effect on the subsurface to the most time and effect (Wallwork, 1970; Hole, 1981; Hasiotis, 2007). The impact of animals on sediments and soils is through the work of adults and juveniles (=nymph [incomplete metamorphosis], larva [complete metamorphosis], or juvenile) of invertebrates and vertebrates. In general, the more time spent within the subsurface, the greater degree and depth of bioturbation and mixing and, therefore, the greater effect on soil formation. Bioturbation, which produces burrows and nests, produces macrochannels and macropores that will impact the rate and degree of such soil processes as translocation, transformation, and the additions and losses of constituents to soils (Hole, 1981; Hasiotis, 2003, 2007). Bioturbation, in combination with the abiotic effects of shrink-swell clays, cryoturbation, haloturbation, and gravitational draining and movement of material, is considered pedoturbation. The role of bioturbation is significant to pedoturbation in that the work of animals produces the channels and voids in which abiotic pedoturbation can take place, as well as allowing for greater exchange between the soil atmosphere and Earth's atmosphere, greater infiltration of precipitation and overland flow, and greater incorporation of organic matter into the subsurface (Wallwork, 1970; Hole, 1981; Hasiotis, 2007).

Overall, the rate and depth of work conducted by animals is much greater than that of plants via root penetration and tree throw. Although plants contribute the vast majority of organic matter and that their organic acids assist in the breakdown of lithic constituents, their roots displace very little material in comparison to the material displaced upward and downward by animals (e.g., Hole, 1981; Hasiotis, 2003, 2007; Halfen and Hasiotis, this volume; and references therein). The burrows and nests of animals can penetrate to ~100 m below the surface, and modify over 1 km<sup>3</sup> to as much as ~10 km<sup>3</sup> for an individual nest of some social insects (Hasiotis, 2003, 2007). Animals displace sediments by diffusive (mm-scale particle

movement) and advective (cm- to m-scale particle movement) methods via a combination of carrying, pulling, pushing, raking, breaking or cutting, and forcing that result in traces (Hasiotis, 2003, 2007; Halfen and Hasiotis, this volume; and references cited within these works). The depth of penetration and amount of mixing will also depend on the amount of soil moisture in the vadose zone and the position of the phreatic zone (e.g., Wallwork, 1970; Hasiotis, 2007). Through  $10^1$  to  $10^6$  years this work on a landscape will result in vegetable moulds, biomantles, and features that define soil orders (e.g., Darwin, 1881; Hole, 1981; Johnson, 1981; Hasiotis, 2007).

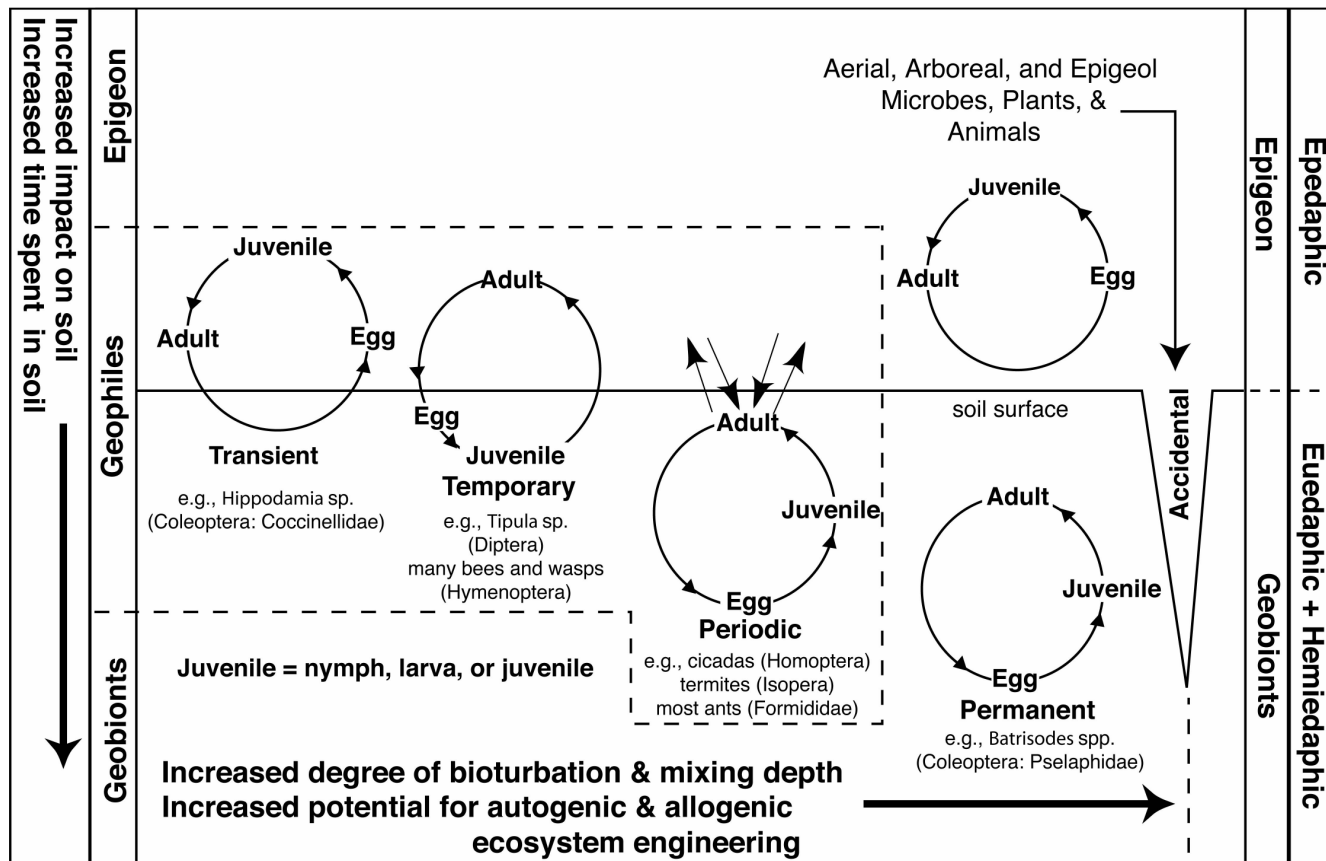


Figure 2. The presence of animals in soil and their impact on bioturbation, pedogenesis, and potential to act as ecosystem engineers (modified from Wallwork, 1970; Hole, 1981; Hasiotis, 2007).

### Linking Trace Fossils to the Work of Animals in Paleosols in the Geological Record

Animals that inhabit modern terrestrial settings and play a role in soil formation are the result over 460 Ma of years of evolution. Many of stem groups of these organisms have their evolutionary roots in the mid- to late Paleozoic and early Mesozoic (Triassic) (Hasiotis, 2003, 2007; and references therein). Trace fossils of these animals, therefore, represent their activity and work in the same way that krotovina. Trace fossils, studied via their architectural and surficial morphologies and the material that fills them, record information about the tracemaker and the physicochemical conditions of its surroundings. Interpretation of the tracemaker is often inferred from the trace fossil and its relationship to the strata. Most importantly, these interpretations are also made via comparison to similar structures found in modern depositional systems and environments that are analogous to the geologic deposits. Such actualistic studies of the effects of termites, ants, dung beetles, wasps, crayfish, spiders, earthworms, and mammals on soil formation (e.g., Darwin, 1881; Wallwork, 1970; Johnson, 1981; Halfen and Hasiotis, this volume) have been used to interpret similar structures and their significance in the rock record, including earlier extensions of their fossil records (Hasiotis, 2003, 2007). For example, crayfish burrows have been identified in Triassic and possibly Permian rocks, and can be used to interpret the paleo-water table level. Meniscate backfilled burrows attributed to beetle larvae and cicada nymphs, by comparison to neoichnological experiments have been identified in Permian and Triassic paleosols (Counts and Hasiotis, 2009). The advantage to studying animal behavior and its effects on pedogenesis in paleosols is that diagenesis has enhanced the redoximorphic characteristics of biogenic and biogenically mediated pedogenic features.

## Ecosystem Engineers and Geoengineers

Jones *et al.* (1994) defined ecosystem engineers as those organisms that create, modify, and maintain habitats by directly or indirectly modulating the availability of resources to other species. Two types of ecosystem engineers are defined: autogenic engineers that change the habitat via their own physical structures, and allogenic engineers that change the environment by shifting living or nonliving material from one physical situation to another. A variety of macro- and mesoscopic soil animals can be classified as both autogenic and allogenic ecosystem engineers because they bioturbate and redistribute soil material, create and destroy pedogenic structures and macrochannels-pores, and ventilate and irrigate soils. The result of this work is the creation of dynamic landscapes composed of soil mosaics, increase oxygenation of sediments, stimulate microflora and decomposition rates, and change and regulate the biophysicochemical properties of the sediment (e.g., Wallwork, 1970; Johnson, 1980). Animal trace fossils and their intimate association with the paleosols also preserve how their activity shaped the ancient landscapes in which they lived, and how above- and belowground ecosystems and soils evolved through time. Such soil animals as termites, ants, crayfish, burrowing mammals, and earthworms, therefore, should be considered geoengineers as they have well-documented trace fossil records in paleosols as far back as the Triassic and Jurassic, and in some cases as early as the late Paleozoic.

## Conclusions

Terrestrial ecosystems, soil-forming factors, and the animals that bioturbate, turnover soil, and engineer the landscape are the result of nearly 4 Ga of evolution. The evidence that links the modern studies of soil formation and ecosystem nutrient cycling to the geological record of paleosols and the evolution of terrestrial ecosystems is preserved as microbial, plant, and animal trace fossils. Trace fossils in paleosols preserve the results of extensive bioturbation of sediments that lead to paleosols in which the animals continue to bioturbate. Results of neoichnological and soil biologic studies demonstrate that the structures and mixing produced by animals can be attributed to similar structures and fabrics preserved in paleosols. Future research should focus on work of modern animals and it produces pedogenic features, and its linkage to terrestrial trace fossils in continental deposits. Geologic studies should focus on the linkage between trace fossils and paleosols, and how those they can be used to interpret the biophysicochemical conditions under which those paleosols formed.

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