

## Continental invertebrate and plant trace fossils in space and time: State of the art and prospects

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Continental invertebrate ichnology has experienced a substantial development during the last quarter of century. From being a field marginal to mainstream marine ichnology, represented by a handful of case studies, continental ichnology has grown to occupy a central position within the field of animal-substrate interactions. This evolution is illustrated not only through the accumulation of ichnologic information nurtured by neoichnologic observations and a detailed scrutiny of ancient continental successions, but also through the establishment of new concepts and methodologies.

From an ichnofacies perspective, various recurrent associations were defined (BUATOIS & MANGANO 1995; GENISE et al. 2000, 2010, 2016; HUNT & LUCAS 2007; EKDALE et al. 2007; KRAPOVICKAS et al. 2016), a situation sharply contrasting with the sole recognition of the *Scoyenia* ichnofacies as the only valid one during the seventies and eighties (Table 1; Fig. 1). The ichnofacies model now includes not only freshwater ichnofacies, but also terrestrial ones, most notably those reflecting the complex nature of paleosol trace fossils (GENISE 2017).

Trace fossils are now being increasingly used to establish a chronology of the colonization of the land and to unravel the patterns and processes involved in the occupation of ecospace in continental settings (e.g. BUATOIS & MANGANO 1993; BUATOIS et al. 1998, 2016; KRAPOVICKAS et al. 2016; GENISE et al. 2016; MINTER et al. 2016b,c, 2017). These studies have helped to identify trends of colonization in specific environments, such as deserts (KRAPOVICKAS et al., 2016), yield insights into the evolution of insects (e.g. GENISE et al. 2016), and reconstruct evolutionary events, such as Paleozoic colonization of continental settings (e.g. BUATOIS & MANGANO 1993; MINTER et al. 2016b,c, 2017; FRANCISCHINI et al. 2019) and the Mesozoic Lacustrine Revolution (e.g. BUATOIS et al. 2016).

Another line of research that has been successful in recent years is the study of modern traces as a tool to decipher complex behavior and scrutinize the fossil record (e.g. HASIOTIS et al. 1993; SÁNCHEZ & GENISE 2008, 2015; SARZETTI et al. 2013; 2014; CANTIL et al. 2014, 2015). In particular, experimental neoichnology allows identifying a variety of burrow architectures and their potential producers (e.g. HEMBREE 2009, 2013, 2016; CATENA & HEMBREE 2014). These studies are instrumental to establish more accurate paleobiologic interpretations of continental trace fossils and to better understand the requirements and solutions of different groups to life in land. Neoichnology is providing paleoichnology with a solid ground to establish paleobiologic and paleoecologic inferences, including both qualitative and quantitative data.

Continental ichnology has been benefitted through the use of conceptual and methodological tools derived from the ichnofabric approach. In particular, a framework for the analysis of paleosol ichnofabrics has been proposed and successfully applied to accurately characterize complex paleosol ichnofabrics (GENISE et al. 2004; BEDATOU et al. 2009; BELLOSI et al. 2016; GENISE 2017). The concept of taphonomic pathways provides a way of analyzing the origin of ichnofabrics in freshwater environments, allowing to unravel the generation of composite ichnofabrics (BUATOIS & MANGANO 2004).

The need of integrating invertebrate and vertebrate ichnology has been noted long ago (BUATOIS & MANGANO 1996). Although these two fields still remain quite separate and this may be considered a pending item, a number of recent studies have documented assemblages comprising both invertebrate and vertebrate trace fossils, helping to bridge the gap between these two areas of research (e.g. KRAPOVICKAS et al. 2015; MENEZES et al. 2019). Unifying approaches to the study of invertebrate and

vertebrate trace fossils is desirable (the so-called “one ichnology”), but there has to be room for a plurality of conceptual and methodological tools that take into account the peculiarities of these two fields.

The study of plant bioturbation in paleosols is another pending item that deserves further attention. Many paleosols do not display burrowing and nesting structures and are instead dominated by rhizoliths or other structures recording the activities of plants. MELCHOR et al. (2012) proposed a “potential rhizolith ichnofacies” to embrace these assemblages dominated by plant bioturbation, commonly devoid of discernible animal activity. With the required temporal and spatial recurrence, specific assemblages could define several “potential rhizolith ichnofacies”. Indeed, these assemblages can offer valuable information and, in many cases, they can alternate with other continental Ichnofacies, highlighting significant changes in climate and other paleoenvironmental conditions.

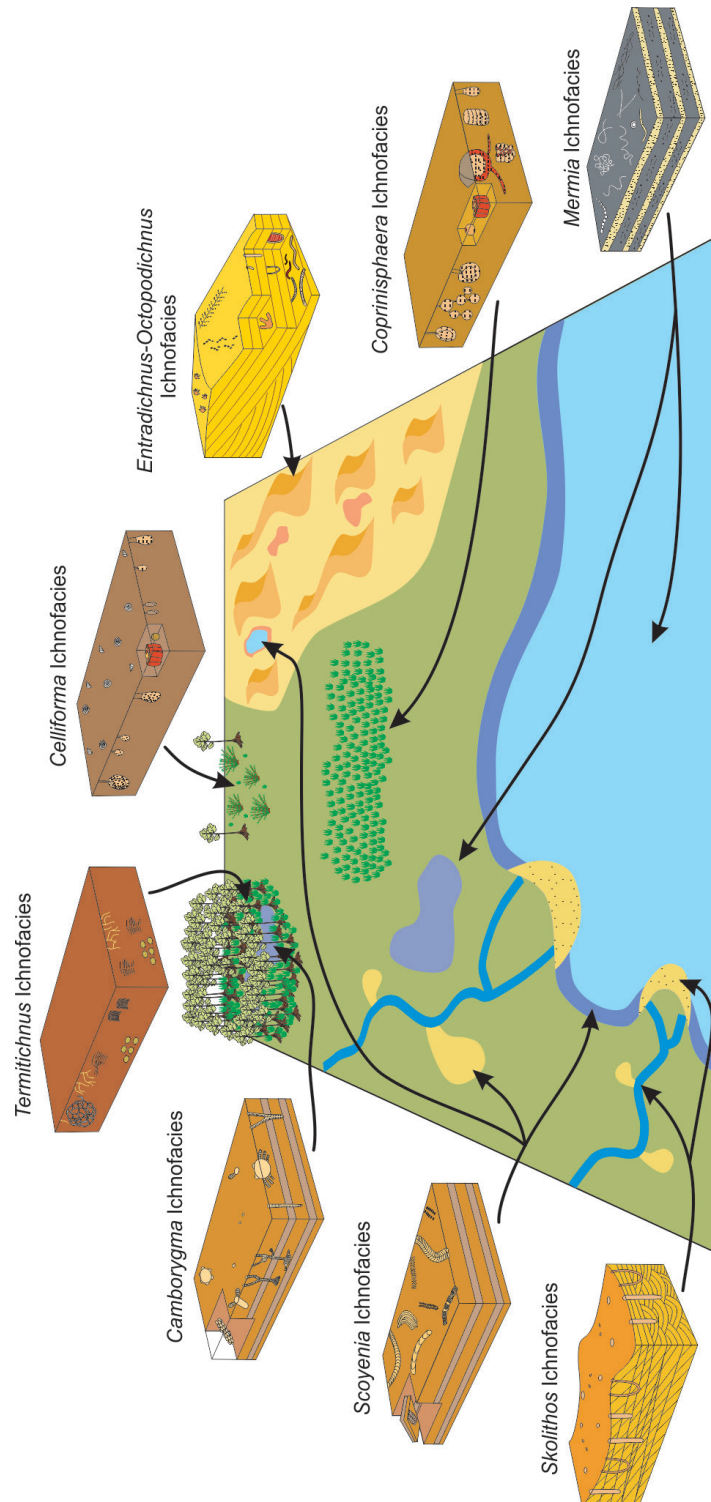


Fig. 1. Environmental distribution of invertebrate continental ichnofacies.

Another need is to attain a better articulation of ichnological and sedimentological datasets within a stratigraphic framework in order to enhance the utility of trace fossils in paleoenvironmental analysis. In this regard, continental ichnology still lags behind marine ichnology. However, studies providing a more refined integration of these lines of evidence are becoming gradually available (e.g. EBERTH et al. 2000; RONCHI 2008).

Last but not least, the field will benefit from increased exploration of continental environments that so far remain poorly studied. This is the case of saline lakes and hot springs, which are typically regarded as stressful and mostly devoid of metazoan life. However, integration of high-resolution sedimentological studies and ichnology reveals the persistence of microbial-animal interactions and a variety of traces recording adaptations and the biological complexity of the inhabitants of these settings (e.g. SCOTT et al. 2007, 2010, 2019; BUATOIS et al. 2017).

**Keywords: bioturbation, continental ichnology, ichnofacies, evolutionary paleoecology**

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<b>Ichnofacies</b>	<b>Characteristics</b>	<b>Representative ichnogenera</b>	<b>Implications</b>
<i>Scoyenia</i>	Abundance of horizontal meniscate backfilled traces; abundance of locomotion traces, including both trackways and bilobate trails; presence of vertical domiciles; a mixture of invertebrate (mostly arthropod), vertebrate and plant traces; low to moderate ichnodiversity, and localized high abundance.	<i>Scoyenia</i> , <i>Beaconites</i> , <i>Taenidium</i> , <i>Umfolozia</i> , <i>Merostomichnites</i> , <i>Diplichnites</i> , <i>Hexapodichnus</i> , <i>Permichnium</i> , <i>Acripes</i> , <i>Cruziana</i> , <i>Rusophycus</i> , <i>Planolites</i> , <i>Palaeophycus</i> , <i>Cochlichnus</i> , <i>Skolithos</i> , <i>Cylindricum</i> and <i>Fuersichnus</i> .	Sediments periodically exposed to air or periodically inundated, and intermediate between aquatic freshwater and terrestrial environments. Low-energy. Silty-sandy, soft to firm substrates. Fluvial overbank settings, such ponds, levees, and crevasse splays. Lake-margin areas in both open and closed lacustrine basins, and in both ephemeral and perennial lakes. Wet interdunes.
<i>Mermia</i>	Dominance of horizontal to subhorizontal grazing and feeding traces produced by mobile deposit feeders; subordinate occurrence of locomotion traces; relatively high to moderate ichnodiversity; high abundance, and low degree of specialization of grazing and feeding patterns.	<i>Mermia</i> , <i>Gordia</i> , <i>Helminthopsis</i> , and <i>Helminthoidichnites</i> , <i>Cochlichnus</i> , <i>Treplichnus</i> , <i>Circulichnis</i> , <i>Undichna</i> and <i>Diplopodichnus</i> .	Permanent subaqueous freshwater environments. Low-energy. Silty-sandy, soft substrates. Well-oxygenated settings. Abundant food supply. Open perennial lacustrine basins, typically hydrologically open. Floodplain water bodies under subaqueous conditions. Fjord settings under freshwater conditions due to glacial melting.
<i>Coprinisphaera</i>	Dominance of trace fossils of bees, wasps, ants, and beetles; subordinate presence of termite ichnofossils; dominance of nesting traces or calichnia; tiering structures that result from variable depths of emplacement of hymenopterous, termite, and dung-beetle nests; moderate to relatively high ichnodiversity, and high abundance.	<i>Coprinisphaera</i> , <i>Pallichnus</i> , <i>Eatonichnus</i> , <i>Monesichnus</i> , <i>Fontanai</i> , <i>Teisseirei</i> , <i>Celliforma</i> , <i>Uruguay</i> , <i>Ellipsoideichnus</i> , <i>Palmiraichnus</i> , <i>Rosellichnus</i> , <i>Chubutolithes</i> , <i>Attaichnus</i> , and <i>Parowanichnus</i> .	Paleosols associated with herbaceous plant communities, mostly savannas, grasslands, prairies, and steppes. Climatically ranging from dry and cold to humid and warm conditions. Various depositional systems subject to subaerial exposure and soil development, such as alluvial plains, overbank, and eolian environments.
<i>Termitichnus</i>	Dominance of trace fossils of termites; low ichnodiversity, and high abundance.	<i>Termitichnus</i> , <i>Vondrichnus</i> , <i>Fleaglellinus</i> , <i>Krausichnus</i> and <i>Masrichnus</i> .	Paleosols formed in closed forests with plant growth under warm and humid conditions. Abandoned channels and overbank areas.

<i>Celliforma</i>	Dominance of halictid bee nests; association with hackberry endocarps, and freshwater and terrestrial snail shells; dominance of callichnia; presence of pupichnia; moderate ichnodiversity, and high abundance.	<i>Celliforma</i> , <i>Rosselichnus</i> , <i>Pallichnus</i> , <i>Rebuffoichnus</i> , <i>Palmiraichnus</i> , <i>Teisseirei</i> and <i>Taenidium</i> .	Carbonate-rich paleosols associated with scrubs and woodlands. Palustrine environments and calcretes.
<i>Camborygma</i>	Dominance of burrows produced by crayfishes and earthworms; common cross-cuttings relationships; low ichnodiversity; and high abundance.	<i>Camborygma</i> , <i>Loloichnus</i> , <i>Dagnichnus</i> , <i>Cellichnus meniscatus</i> , and <i>Edaphichnium</i> .	Paleosols formed in forests, scrubs, and open herbaceous communities, particularly in marshes, bogs, swamps or wetlands. High and fluctuating water table, mostly under warm climates. Various depositional systems subject to subaerial exposure and soil development, such as abandoned channels, floodplains, levees, crevasse splays, and loessic, ponds.
<i>Octopodichnus-Entradichnus</i>	Low-to more rarely moderate ichnodiversity; dominance of simple sub-superficial dwelling traces produced mostly by members of Coleoptera, Orthoptera and Arachnida, with horizontal and/or vertical orientation; superficial locomotion traces produced by arthropods, especially arachnids; and subordinate feeding simple and meniscate traces.	<i>Octopodichnus</i> , <i>Paleohelcura</i> , <i>Entradichnus</i> , <i>Digitichnus</i> , <i>Planolites</i> , <i>Palaeophycus</i> , <i>Taenidium</i> , <i>Arenicolites</i> and <i>Skolithos</i> .	Mobile and temporary stabilized sandy substrates, subject to frequent erosion and deposition, and to strong seasonality. Environments with reduced humidity and low nutrient availability. Sand dune, dry interdune, and sand sheet deposits of wet eolian systems typically associated with arid deserts and/or in arid intervals of hyper-arid deserts.

Table 1. Summary of continental invertebrate ichnofacies (after Minter et al., 2016a). A continental equivalent of the typically marine *Skolithos* Ichnofacies may be present as well (Fig. 1).