# Paleobiology

## Behavioral biology of trace fossils

*Roy E. Plotnick*

# Behavioral biology of trace fossils

*Roy E. Plotnick*

*Abstract.*—The potential of the ichnofossil record for exploring the evolution of behavior has never been fully realized. Some of this is due to the nature of the trace fossil record itself. Equally responsible is the separation of ichnology from the relevant areas of modern behavioral biology. The two disciplines have virtually no concepts, methods, or literature in common. The study of animal behavior and its evolution is thus bereft of the rich data and insights of ichnologists.

One potential pathway forward is for ichnologists to adopt and adapt the movement ecology paradigm proposed several years ago by Ran Nathan and colleagues. This approach views movement as resulting from interactions of the organism's internal state, its movement abilities, and its sensory capabilities with each other and with the external environment. These interactions produce a movement path. The adoption of this paradigm would place trace fossil studies in a far wider common context for the study of movement, while providing the dimension of the evolution of movement behavior in deep time to neontological studies.

A second component of this integration would be for paleontologists to develop a *taphonomy of behavior* that places in a phylogenetic context the range of possible behaviors that organisms can carry out and assesses the potential of each of these behaviors in leaving a diagnostic trace. Parallel to other taphonomic concepts, this approach assesses the preservation potential of particular behaviors; *behavioral fidelity* is the extent to which trace fossils preserve these original behavioral signals.

*Roy E. Plotnick. Department of Earth and Environmental Sciences, University of Illinois at Chicago, 845 West Taylor Street, Chicago, Illinois 60607. E-mail: plotnick@uic.edu*

## Introduction

The study of trace fossils is thriving. There is a well-established journal (*Ichnos*), a fledgling society, and a continuous stream of edited volumes and monographs (Seilacher 2007; Miller 2007a; Buatois and Mangano 2011). Documentation of the trace fossil record has become far more detailed and environmental interpretations based on traces have become increasingly sophisticated. Ichnofossils are critical evidence for the origins of major groups and trophic relationships and for constraining functional interpretations based on preserved skeletal materials. Both observational and experimental analyses of trace formation have become increasingly sophisticated.

Compared to other areas of paleontology, however, the integration of ichnology with evolutionary biology has noticeably lagged. Ichnology and behavioral biology, which one might expect to be closely tied, are largely disconnected from each other (Miller 2007b). Ichnological approaches to behavior and the rich behavioral data potentially available from trace fossil studies are effectively un-known outside of the paleontological community. At the same time, ichnologists rarely use the language or concepts in common usage by behavioral biologists. This disconnect may explain why ichnology has contributed correspondingly little to behavioral biology, even though the evolutionary origins of behaviors is a major topic of interest among behavioral biologists.

The lack of integration of the two disciplines is evident from their respective literature. Ichnologists, in particular invertebrate ichnologists, are predominantly geologically trained paleontologists whose primary interest is the environmental signals provided by traces (Bromley 1996). Virtually all publications on invertebrate trace fossils appear in geologically oriented journals and monographs. The texts *Trace Fossil Analysis* (Seilacher 2007) and *Trace Fossils* (Bromley 1996) contain no references to the behavioral biology literature, although the latter does extensively discuss research on the biology of burrowing organisms. Correspondingly, the existence of trace fossils is scarcely mentioned in the literature of behavioral biology. Standard textbooks do not

mention them at all or only briefly (Drickamer et al. 2001; Bolhuis and Giraldeau 2005; Alcock 2009). Searches using the keywords ''ichnofossil'' and ''trace fossil'' in the journals *Behavioral Ecology* and *Evolution* yielded no hits.

It is the goal of this paper to detail the existing barriers to communication between ichnologists and behavioral biologists and to propose how some of these may be overcome. I will describe how the recently proposed ''movement ecology paradigm'' (Nathan et al. 2008) can be expanded to include ichnofossils. I will also outline a ''taphonomy of behavior,'' which focuses on the range of behaviors that are potentially fossilizable and their phylogenetic context. The integration of ichnology and behavioral biology, along with other relevant areas such as functional morphology, could lead to a ''paleobiology of behavior'' focusing on exploring the evolutionary history of behavior in deep time.

## The Gulf between Ichnology and Behavioral Biology: Barriers to Communication

*Conceptual Differences.*—The two fields differ markedly in language, concepts, and methods, even at the most fundamental levels. Biological concepts of behavior focus on the neurological and/or chemical responses by organisms to an external or internal stimulus and results of these responses. These results may or may not include movement. In contrast, the concept of behavior used among paleontologists is broader and generally does not include concepts of stimulus and response. ''Behavior'' in the paleontological literature has variously referred to aspects of life mode, trophic level, functional morphology, and biotic interactions, as well as topics that fall more clearly into classic ethology (Kitchell 1986; Lockley 1991; Novack-Gottshall 2007; Benton 2010; Boucot and Poinar 2010; Bernardi and Avanzini 2011). Seilacher (1986, p. 62) referred to behavior as ''the rules, or programs, underlying animal activities.'' This algorithmic concept has strongly influenced subsequent behavioral interpretations of traces (see below).

Ethology is the study of animal behavior, with an emphasis on comparative aspects (Lorenz 1981), although this term has largely

fallen out of use in favor of ''behavioral biology'' or ''animal behavior'' (Bolhuis and Giraldeau 2005). Ichnologists use ''ethology'' to refer to the study of behavior inferred from preserved traces (Frey 1973). This concept encompasses an analytical approach based on a detailed examination of the morphology and associated sedimentology of the preserved traces, along with morphological and functional interpretations of putative trace-makers. The result is a scenario with a detailed reconstruction of the movement pattern producing the trace. This method of interpretation is embodied in Seilacher's more than half-century of publication on traces, culminating in his 2007 book.

The conceptual foundation that unites the diversity of disciplines constituting behavioral biology is the ''four problems,'' or sets of problems, originally posed by Tinbergen (1963). The first set deals with internal neurological and chemical processes and the complex interactions of these processes with each other and the external environment. The second set examines ontogenetic changes in behavior, including memory and learning. These two categories encompass proximate explanations or ''hows'' of behavior; e.g., what external stimulus will cause an animal to start feeding, how this stimulus is perceived by the animal, what internal neurobiological or chemical changes occur as a result of the stimulus, how an animal learn that a particular stimulus corresponds to a resource, and so on.

The other categories of research questions focus more on ultimate causes or the ''whys'' of behavior. The third set looks at the roles played by behaviors in survival and reproduction; behaviors are treated as adaptations. For instance, how does the ability to detect a potential resource increase the fitness of a species? The final group places behaviors in their phylogenetic context, and attempts to examine their historical origin; e.g., when did the ability to detect the resource first arise?

Despite their central place in the canon of behavioral biology, Tinbergen's four questions have never been explicitly posed within the trace fossil literature. Nor have behavioral biologists turned to the ichnological record

for insight into them, even in the context of the evolutionary history of behavior. This is especially unfortunate, given that ichnology has a unique perspective on the evolutionary origins of behaviors and on many of their adaptive aspects.

It is true that these problems have been *implicitly* addressed in some trace fossil studies. Drilling by predatory gastropods has become a ''model system'' for the study of predator-prey interactions over geologic time (Kitchell 1986; Dietl and Kelley 2002; Huntley and Kowalewski 2007; Walker 2007). This research has been put into the context of prey selectivity (Kitchell et al. 1981; Kitchell 1986; Roopnarine and Beussink 1999) and optimal foraging theory (Leighton 2002) and thus focuses on the adaptive nature of behaviors, the third of the fundamental questions.

Modern biologists can directly observe the mechanisms of behaviors and their consequences in the field and lab (Schick et al. 2008). In contrast, ichnologists are restricted to just the results of behavior and even then only when the behavior alters the properties of a preexisting substrate (Bertling et al. 2006). This has fundamentally affected how the two disciplines classify behavior. Behavioral biologists tend to divide behaviors by their role in the lives of the organisms, using categories such as communication, foraging, site selection, reproductive behavior, parental care, social behavior, and antipredator behavior (Huntingford 2003; Alcock 2009).

These categories are rarely used by ichnologists, who instead tend to use the ''ethological classification'' of ichnofossils developed by Seilacher (1953, 1964, 1967), which was the first attempt to produce a trace fossil classification relevant to behavior rather than morphology. This scheme has been frequently reprinted within reviews of ichnology (Ekdale et al. 1984; Bromley 1996; Buatois and Mangano 2011), is covered essentially verbatim in current introductory textbooks of paleontology, and remains in common use (O'Brien et al. 2009).

These ethological categories are unknown to behavioral biologists. They do not appear in any animal behavior texts and a keyword search reveals that they are used only by paleontologists. They do not reflect any categorization of behavior in use by behavioral biologists, nor do they map onto these behavioral categories. Not only can disparate forms carry out similar behaviors and thus leave similar traces (Ekdale et al. 1984; Gingras et al. 2008a), but different activities can also leave similar trace morphologies. Resting traces (cubichnia) can result from a huge range of possible associated behaviors (Martin and Rindsberg 2006). Ambush predators can produce a resting trace when stalking prey, as can prey organisms that are hiding from predators. A satiated predator may also rest after feeding. Repichnia, or crawling traces, refers to tracks and trails made by movements between locations, in an overall general direction, ''wandering from place to place'' (Bromley 1996: p. 192). Locomotion in a single general direction can also arise from a huge number of behavioral causes (Dusenbery 1992; Koy and Plotnick 2007; Nathan et al. 2008), all of which are purposeful.

Concepts from behavioral biology that are used in ichnological research are often outdated. For example, models of tightly meandering patterns (''guided meanders'' or pascichnia) assume that they represent an adaptation for optimally harvesting a feeding area. Seilacher (1967) proposed a modification of a scheme first proposed by Richter (1928), in which an animal obeys a behavioral ''program,'' expressed as a set of ''commands.'' These controls readily lend themselves to computer simulation (Raup and Seilacher 1969; Papentin and Röder 1975; Hammer 1998; cf. Hayes 2003; Plotnick 2007).

The concept that the trace fossil producers followed an optimal rigid program has had a profound influence on subsequent interpretations of trace fossils (Crimes 1977). Crimes and Droser (1992) repeatedly refer to forms such as *Nereites* and *Helminthoida* as being ''very carefully programmed'' or ''closely programmed.'' Seilacher (1986) describes some forms that do not match expected patterns as being the result of the animal making ''mistakes'' or of having problems executing the programs. There is an associated assumption that the more geometrically complex the trace, the more sophisticated is

the underlying program (Seilacher 1967, 1986; Crimes and Droser 1992). This assumption is important in some interpretations of the evolution of trace morphology, and by extension behavior, over time (Seilacher 1986; Ekdale and Lamond 2003).

The modern concept of taxes, in contrast, focuses on orientation and turning of an organism in response to a perceived external stimulus field and does not include directional locomotion itself; a taxis results in turns that change the direction of locomotion (Lorenz 1981). Dusenbery (1992) suggested replacing the term ''taxis'' with that of ''direct guiding,'' in which an organism obtains information about the orientation of a stimulus field and uses this information to determine the direction of a turn. This concept was used in the trace fossil models of Plotnick (2007), which assumed that organisms direct guide and move in response to the direction and intensity of chemical signals emitted by resources.

Behavioral explanation based on the interactions of reflexes and or/taxes are solidly in the context of the ''reflex theory'' that dominated behavioral biology in the first half of the twentieth century. This theory has long since been supplanted by new concepts (Lorenz 1981) and is virtually absent from modern texts. These explanations are strongly rooted in a Cartesian concept of animal behavior; i.e., viewing animals as machines or automata (Mayr 1974; Krebs and Davies 1997). As discussed by Mayr (1974), these are ''closed programs''; nothing can be inserted through experience. In both Seilacher's and Plotnick's models, there is no learning, not even of the most basic kind. Recent research, however, suggests that learning and memory may actually be universal among all organisms with nervous systems (Dukas 2009). Neoichnological studies (Miller and Curran 2001) also support the idea of considerable behavioral plasticity.

*Methodological Differences.*—The study of animal behavior grew out of the long tradition of field observation in natural history. Although still important, it has largely been supplanted by experimental studies in both the field and laboratory at hierarchical levels from molecules to whole organisms. The majority of field studies focus on terrestrial vertebrates, in particular bird and large mammals, as well as on insects; laboratory studies frequently look at a small number of model organisms, such as stickleback fish, mice, rats, and fruit flies. Behavioral research into marine invertebrates or organisms that burrow is rare (Bastardie et al. 2005).

Direct observations of behavior in extinct organisms are, of course, forever unavailable to paleontologists. But empirical observations remain the foundation of neoichnology, the actualistic study of the traces produced by modern organisms (Schäfer 1973). Neoichnological research can also be broadly divided into field and lab studies, with by far most being field based and observational. Many field investigations examine traces in the process of being produced; this involves direct observations of animal movement and the associated trace, leading to clear associations between the movement pattern, the tracemaker, and the trace (Gingras et al. 2008a; Martin and Rindsberg 2007; Kumagai and Farlow 2010). Related to this are field studies in which the behavior is not directly observed, but is inferred after the fact, usually from independent evidence; the association between the traces, its producers, and the traces is also strong (Hasiotis and Mitchell 1993; Hasiotis 2002; Tschinkel 2003; Labandeira 2007).

Laboratory based studies are overall far less common. Most of these are observational investigations that focus on the processes of trace formation and preservation (Milàn and Bromley 2006; Davis et al. 2007; Jackson et al. 2009; Halfen and Hasiotis 2010) or on the rates and processes of bioturbation (Gingras et al. 2008b). Others are attempts to tie trace and tracemaker together (Vannier et al. 2010). Even rarer are lab or field studies involving manipulative treatments of variables potentially controlling behavior and trace formation (Hembree 2009; Koy and Plotnick 2010).

Neoichnologists study a far wider range or organisms, both ecologically and phylogenetically, than most behavioral biologists. Most studies of animal movement focus on terrestrial vertebrates, such as large ungulates or birds, that can be readily tracked. Studies on

invertebrates have most commonly examined insects, notably investigations of bee flight or ant surface foraging. There are some investigations of terrestrial vertebrate burrow formation, looking at animals such naked mole rats and gophers (Reichman and Seabloom 2002). Many of these are tied to the concept of "ecosystem engineering," the modification of the physical environment by organisms and its feedback to organisms (Hastings et al. 2007). The study of movement below the surface, in particular of marine invertebrates, is one area where neoichnology can make a unique contribution to the study of animal behavior.

The last of Tinbergen's problem sets, that of the evolution of behavior, is one that should be a natural place for the interactions of ichnologists and behavioral biologists. As is the case with most other areas of comparative biology, studies of the evolution of behavior have become predominantly phylogenetic or "tree based" (Lauder 1986; Harvey and Nee 1997). Ryan (2005), in a review of methods for studying the evolution of behavior, emphasized the central importance of independent phylogenetic information. The potential use of ichnofossils for studying historical patterns of behavior is absent from this literature.

The use of phylogenetic methods in ichnology is hampered by the central conundrums of ichnology: that except in rare cases, the identity of the tracemaker is unknown and that unrelated organisms can produce morphologically similar traces. When such identifications are made they are typically phylogenetically broad, often to the phylum or class or, at best, family level (Lockley and Gillette 1989; Braddy 2001). The only studies that I am aware of that explicitly place trace fossils in a phylogenetic context are of dinosaur footprints (Olsen and Baird 1986; Carrano and Wilson 2001), in which a particular combination of derived pedal features found in a footprint or trackway can constrain the identity of the producer. This approach is quite distinct from the "behavioral cladistics of trace fossils" proposed by Ekdale and Lamond (2003), which views behavior sensu Seilacher (1967), as the end-product of a hierarchy of rules. If the trace can be produced from a single postulated rule, then this is the inferred primitive condition. If a second rule is added to produce a different trace morphology, this a derived condition and so on. In terms of the tracemakers, the resulting "clades" are massively polyphyletic.

Common approaches to document the history of behavior as preserved in trace fossils are non-phylogenetic and focus on the "evolution" of the traces themselves, rather than that of the potential trace making organisms. Numerous studies summarize the number of described ichnotaxa through geological time. These papers differ widely in methodology and temporal scope (Crimes 1974, 1992; Seilacher 1974, 1977; Frey and Seilacher 1980; Crimes and Fedonkin 1994; Orr 2001; Uchman 2004; Jensen et al. 2005; Seilacher et al. 2005). A second approach has been to follow trace fossil "lineages" over time and trace changes in their inferred behavioral abilities, in particular within the context of the optimization paradigm (Seilacher 1977, 1986; Frey and Seilacher 1980; cf. Crimes and Fedonkin 1994).

Ichnofossils have also been used to date the first appearances of the producing taxa and thus of their associated behaviors. In some cases these results have suggested considerable extension of known stratigraphic ranges (Carrano and Wilson 2001; Niedzwiedzki et al. 2009). The most controversial topic in this area is identification of Precambrian traces as dating the origin of mobile bilaterians (Bengtson and Rasmussen 2009).

## Behavioral Interpretations of Trace Fossils: One Way Forward

For ichnology to become integrated with behavioral biology a common vocabulary clearly is needed. First and foremost is to use a concept of behavior that would generally exclude trophic relationships and life modes, as well as strictly functional aspects. Instead, behavior should be restricted to refer to cases in which an external physical or biological stimulus and an organism response can be either demonstrated or reasonably inferred. For instance, the burrows described by Hembree (2010) can reasonably be tied to aestivation, and thus a behavioral response to

aridity. This concept is closer to that used in biology in which ecology provides the context for behavior (Krebs and Davies 1997) and allows its adaptive value to be considered. In this context, naticid gastropod predator-prey relationships are biotic interactions and not strictly behavior. What is behavior is evidence for prey and site selectivity.

Second, categories of behavior should likewise be as parallel as possible to those used in behavioral biology. Trace fossils should be discussed as evidence for feeding mechanisms, mating, parental care, etc. The prevailing ethological categories should be abandoned (Miller 2007c). The ethological categories are not behaviors; they are interpretations of the morphology of sedimentary imprints produced by a range of possible behaviors carried out by a disparate range of organisms.

Ichnologists also need to consider the ''four questions'' as a framing context for their discussions of behavior. One potential way of doing this is to adopt some form of the ''movement ecology paradigm'' of Nathan et al. (2008), which was proposed as a unified conceptual framework for the study of motion. This framework has four components (Fig. 1). Three of these are related to the external properties of an individual organism, whereas the fourth is external. For mobile organisms, *navigation capacities* are the cognitive and sensory traits that enable them to obtain and process information about their external environment, which they then use to determine whether and where to move. *Motion capacities* are their biomechanical abilities to move, i.e., their abilities to swim, crawl, fly, etc., separately or in combination; this is the ''how to move?'' portion of the paradigm. *Internal states* are the physiological and/or psychological goals for moving, the ''why move?'' component of the paradigm. Internal states include proximate or ecological motivations, such as searching for food, avoiding a predator, or finding a mate, and reflect ultimate evolutionary goals including survival and reproduction. These goals are time dependent and can co-occur or conflict (Damschen et al. 2008). The three internal factors interact dynamically with each other

and with the external environment. The external environment includes biotic aspects, such as the presence of competitors, potential mates, and predators, and abiotic aspects, such as currents or the presence of obstacles. These external aspects can be both spatially and temporally complex.

The end result of these interactions is movement and the corresponding *movement path*. At its most basic level, the movement path consists of a series of changing coordinates over time that represent a series of steps (coordinates changing between time intervals) and stops (coordinates remains fixed). A series of steps and stops associated with a particular proximate goal or set of goals is a *movement phase*. An organism foraging within a patch (Koy and Plotnick 2007, 2010) is engaging in one movement phase. If the organism then leaves the patch, it has entered another movement phase. The decision to leave the patch is based on some combination of a change in the external environment, such as depletion of a resource or appearance of a predator, the detection of that change, and the internal state of the organism, such as the extent to which it is satiated or feels threatened.

On uniformitarian grounds, the movement ecology paradigm applies equally well to fossil and living organisms and can be used as a conceptual framework for ichnofossils. Its application is dependent on our ability to reconstruct its components in the fossil record. Reconstructing the external factors will rely on detailed paleoenvironmental reconstructions, including both biotic and abiotic aspects. The three internal controls on movement can be inferred with different degrees of certainty in fossil organisms and will always be more general and indirect than can be determined in living organisms.

In the best possible case, navigation capacity can be estimated from the actual preservation of sense organs, such as eyes, ears, and antennae, in fossil forms, e.g., in Lagerstätten such as the Green River Formation or the Burgess shale. Less direct is the inference of soft-tissue sense organs on phylogenetic and anatomical grounds. The presence of eyes in dinosaurs and ichthyosaurs, for example, can be inferred from the preservation of
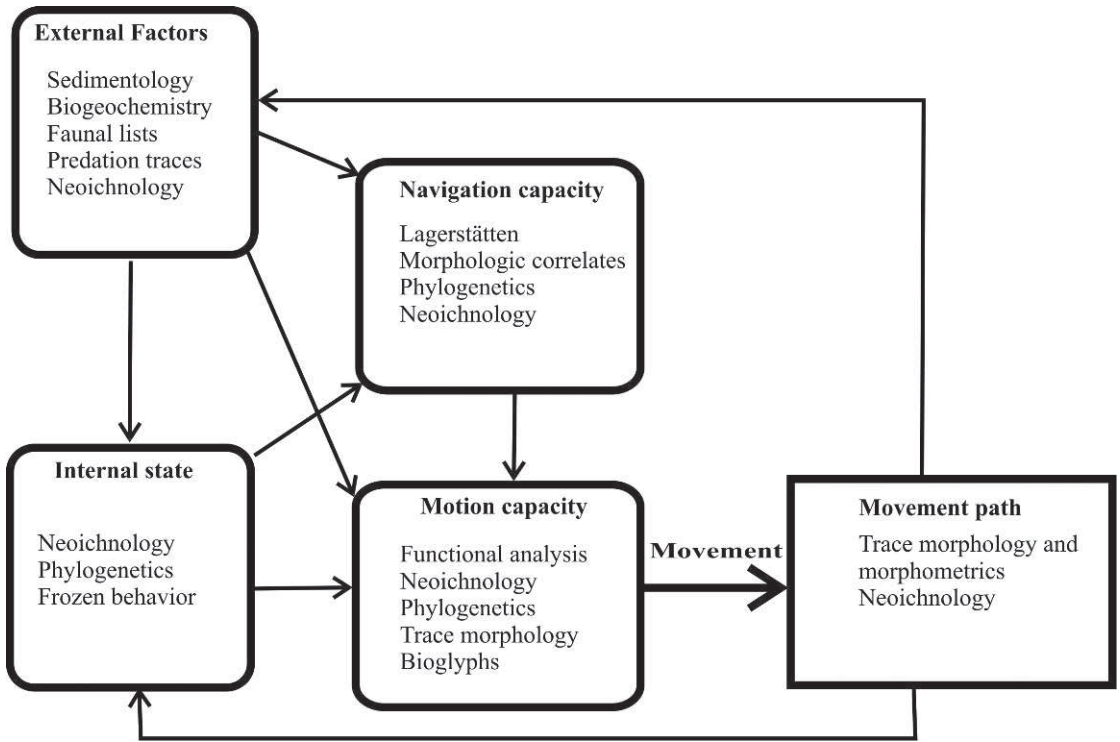
FIGURE 1.   Conceptual framework for motion paleoecology (based on Fig. 2 in Nathan et al. 2009), including potential sources of paleontological evidence. Three components—motion capacity, navigation capacity, and internal state—focus on the individual organism. These components dynamically interact with each other and the external biotic and abiotic environment to produce a movement path. The internal state is the ''why move'' component, which determines if and why the organism is ready to move, such as hunger or the desire to mate. This can be assumed by comparison with modern relatives or analogs and may occasionally be preserved as ''frozen behavior.'' Navigation capacity is ''where to move,'' and reflects the organism's sensory capabilities. Fossil sense organs and sensory abilities can be directly observed or inferred from morphologic correlates or phylogeny. Motion capacity is ''how to move'' and reflects the functional capabilities for movement, determined from morphologic analysis of both potential tracemakers and the trace, as well as comparison with modern forms. The result of the interactions of the three factors with each other and the external environment is the movement path, the potentially preserved burrow, track, trail, etc. Movement itself can also alter the external environment, such as through bioturbation or resource depletion, as well as lead to changes in the internal state.

osteological correlates (Witmer 1995; Motani 2005). Where there are no hard-tissue correlates, the presence of sensory organs can be inferred phylogenetically using parsimony; for example, because modern *Nautilus* and other living cephalopods possess eyes and osphradia, we can assume that the fossil cephalopods likely did also.

Motion capacity can also be indirectly determined. This will mainly be a matter of careful functional analysis of locomotory abilities, often accompanied by actualistic observations of movement. Functional studies of vertebrate and arthropod gaits are already well integrated with ichnology (Farlow et al. 2000; Minter and Braddy 2006; Sellers et al.

2009). Mechanisms for burrowing and boring are also a form of motion capacity and are well studied in many modern groups (Savazzi 1994).

Internal states, of course, will be unknown. Nevertheless, it can be assumed that extinct organisms responded to the same proximal and ultimate goals as living organisms. One available line of evidence for these is ''frozen behavior,'' such as cases where a tracemaker is found within its burrow or at the end of a trail (Boucot and Poinar 2010; Hasiotis 2002). The presence of an adult *Oviraptor* in apparent life position above a clutch of eggs in a nest strongly suggests the existence of parental care in these dinosaurs (Norrell et al. 1995). These

cases can also act as tests of trace-tracemaker associations predicted by other means.

What paleontologists have in abundance are preserved movement paths. The movement ecology paradigm can readily be adopted to discuss the movements of extinct organisms and the nature of their preserved trails, tracks, and borrows. Each movement phase corresponds to some combination of internal and external controls that is reflected in a distinct movement pattern. Distinct behaviors, in this context, consist of movement phases, both steps and stops, and the transitions between them. Careful morphologic study of the preserved trace reveals the relative, if not the absolute timing of movements (Seilacher 2007). For example, a trilobite that produces a resting trace (*Rusophycus*) and then transitions into a directed locomotion trace (*Cruziana*) has engaged in three distinct behaviors.

Hagadorn et al. (2000) illustrated examples of the Cambrian form *Taphrhelminthopsis* that have both meandering and looping movement phases. Alternating walking (*Stiaria*) and jumping (*Tonganoxichus*) by Permian apterygote insects was documented by Minter and Braddy (2006), with the jumping possibly a response to predator threat. Similarly, Lockley (1991) indicated that behavioral changes in dinosaurs are indicated by shifts in step and stride patterns. Note that the movement phase concept focuses on the actions that are taken, which can be represented by traces, and not the proximate purposes of the actions, which are generally unknown.

A key activity in the study of organism behavior is the mathematical description of movement paths and attempts to compare these paths with models of underlying behaviors, such as correlated random walks and fractal Lévy flights (Turchin 1998; Benhamou 2004; Nathan et al. 2008; Koy and Plotnick 2010; de Jager et al. 2011). Paths are usually recorded as series of coordinate localities at discrete time intervals and described using parameters such step length, total or mean displacement, velocity, turning angles, and headings.

Some of these methods and models can be applied to the analysis of ancient paths, but there are limitations, in particular for surface movement paths. The first of these is that most are only short samples of the extended path; it is relatively rare to be able to map a large path (see Hagadorn et al. 2000). A more important limitation is the lack of absolute temporal data. In most cases, it is necessary to assume that velocity within a path was constant. The inferred steps are thus equal length, rather than equal time divisions of the path. This was the approach used by Kitchell (1979), Hofmann (1990), and Hagadorn et al. (2000). The choice of discretization interval can directly affect the values of descriptive metrics (Benhamou 2004). In rare cases, as in the case of tetrapod tracks, it is theoretically possible to estimate changes of relative speed and perhaps use these as a proxy for time. One available metric is the tortuosity of the track (Benhamou 2004); the more tortuous a path, the greater is its deviation from straight line motion. The underlying assumption is that a straight line represents an animal efficiently moving toward a goal.

The movement ecology paradigm can also be readily applied to trace types other than locomotion traces, such as burrows. In this case, the navigation capacity incorporates the ability to detect the physical, chemical, and biological properties of the surrounding sediments and adjacent water column, which constitute the external environment. These external factors will often be well known. The motion capacity includes the various methods by which an organism burrows (Savazzi 1994). Internal states, while they have to be assumed, obviously incorporate factors that are relevant to a burrowing organism. The resulting movement path is the burrow itself. One major advantage is that the movement path is relatively far more complete than it is in the case of surface movement trails. There also are existing metrics, such as that used by Hembree and Hasiotis (2006).

*Taphonomy and Systematics of Behavior.*—Behaviors are as much part of an organism's phenotype as are its tissues; they, too, die with the organism. It is reasonable, therefore, to discuss a taphonomy of behavior that can be treated in the same way as other taphonomic processes (Fig. 2). Taphonomy is used in the sense here of Behrensmeyer and
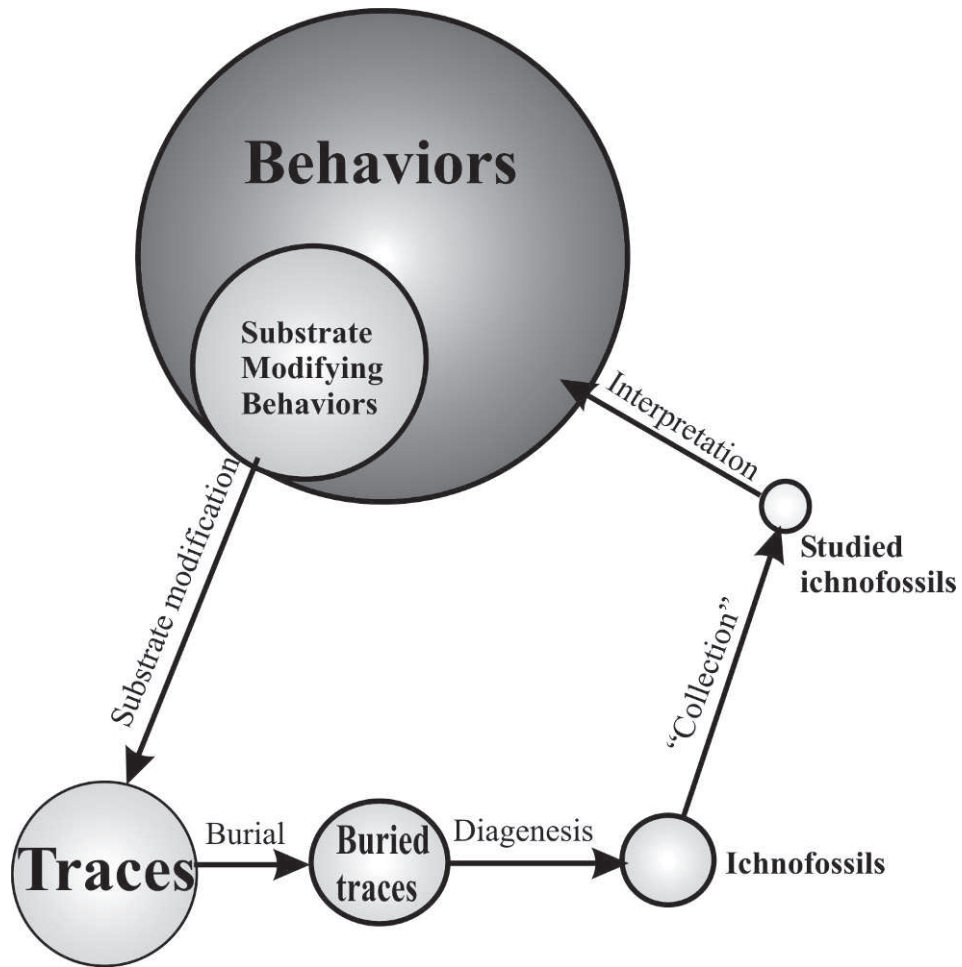
FIGURE 2. Taphonomy of behavior, showing the pathway from the biological signal of behavior to its ichnological interpretation (based on Fig. 1 in Behrensmeyer et al. 2000). Sizes of the ellipses indicate relative information retained at each step. Individual organisms or groups of organisms are capable of a wide spectrum of behavior. Only a fraction of these have the potential for modifying a substrate. Traces are produced when one of these behaviors actually modifies a substrate. Only a fraction of these traces are buried (e.g., below the active layer) and many of these are modified diagenetically to produce ichnofossils. These are then studied, often in situ, to reconstruct the original behavior.

Kidwell (1985) with the focus on how biological information is preserved in the fossil record. The original biological information is the suite of behaviors that an organism or group of organisms (i.e., a community) carry out. A subset of these behaviors may interact with a substrate. The interactions with the substrate produce traces, which represent a still smaller and modified subset of that original signal. The traces are then subject to sedimentological and diagenetic processes which may destroy or further modify it and the information it preserves. The resulting ichnofossils are then collected

and examined and its residual behavioral signal is interpreted. This process is a form of assessing ascertainment bias, i.e., the extent to which trace fossils are a sample of the range of behaviors and the degree to which this sample is biased.

*Behavioral fidelity* is the extent to which trace fossils preserve original behavioral signals, from either a single species or a group of species. This is parallel to other concepts of taphonomic fidelity (Behrensmeyer et al. 2000). Savrda (2007) recognized *ichnologic fidelity*, where high ichnologic fidelity implies that most produced traces are preserved in

the fossil record. The concept of behavioral fidelity is somewhat broader, as it also includes behaviors that are not trace-producing. Kitchell (1986) similarly demarcated those aspects of the naticid predator-prey interaction that are potentially retrievable from the fossil record.

Assessing behavioral fidelity will necessarily differ between taxa with and without extant representatives. For organisms with modern representatives, direct knowledge of the behaviors exhibited by the group, as well as its morphology, is available. The evaluation of behavioral fidelity begins with the identification of a target organism or organisms, such as fiddler crabs (*Uca*). Within this target group, the suite of behaviors should be identified and described in a manner consistent with the vocabulary used by behavioral biologists, such as predator avoidance or mating. The next steps are to establish which of these behaviors involve interactions with substrates and thus can leave a potentially preservable trace, and whether the preservable trace might contain features that are diagnostic of the producing taxon, the behavior, or both. In the case of *Uca*, sexual display by claw waving is a mating behavior that will not leave a trace; in contrast, the morphologically distinctive breeding burrows built by some of these crabs (Christy 1982) is an aspect of mating behavior that can be preserved. The final step is to assess the preservation potential of the trace once it forms and how it may be modified by subsequent processes.

For organisms without modern representatives, the suite of possible behaviors will have to be predicted from their phylogenetic context, as well as from functional analysis. This is not a phylogeny of the traces themselves, but rather the phylogeny of potential tracemakers. The aim is to identify those regions of the phylogeny potentially associated with a range of behaviors and resultant trace morphologies. This approach is an extension of that used by Carrano and Wilson (2001) and an adaptation of methods used previously to infer soft-tissue morphology and function, in particular the ''extant phylogenetic bracket'' of Witmer (1995; see also Bryant and Russell 1992). It is also related to

efforts to identify patterns of character evolution, such as the nature of ancestral states (Finarelli and Flynn 2006; Goldberg and Igic 2008). As a simple example, modern archosaurs (birds and crocodilians) have parental care, usually accompanied by the building of nests. Given that birds are the dinosaur in-group and crocodilians are an out-group, phylogenetic bracketing predicts the existence of parental care and nesting in dinosaurs. Both are now well established in dinosaurs (Isles 2009).

The first step in this approach will be finding an independently derived phylogeny of both extant and extinct potential tracemakers. Given the lack of possible specificity of the trace producer, the taxonomic level will probably not be more precise than that of the family, perhaps even order or class. This phylogeny will then be a framework on which to map additional data sets. The first of these are life habits and behavior, as documented for extant organisms from actualistic studies. The particular focus here would be to identify those subsets of overall behavior that could reasonably be predicted to be possessed by the extinct form and have the potential of being captured as traces. For example, Christy (1987) summarized available information on mating behavior in brachyuran crabs. Of his eight categories of behavior, several are directly associated with the use of burrows, which can be morphologically distinctive. Such behavioral information should provide expanded context for studies of putative crab burrows in the fossil record (Frey et al. 1984; Curran and Martin 2003). Other well-known cases would be nesting behavior by ants or predation by naticid gastropods.

The second data set consists of the morphology and function of characters that can potentially interact with substrates. Examples include the forms and movements of tetrapod feet (Carrano and Wilson 2001), distal appendages of arthropods (Braddy 2001; Poschmann and Braddy 2010), parapodia of annelids, or jaw parts of insects (Labandeira 2007). The primary information for this is neoichnological, based on laboratory or field observations. For extinct forms, this could be based on functional reconstructions that are derived

from biomechanics (Plotnick and Baumiller 2000), although this will be less reliable than that directly observed in living forms. Combined with the morphological data, these functional interpretations constrain the nature of the substrate modifications that an organism is capable of, including detailed morphologic features of the potential trace such as bioglyphs (engravings in burrow or boring walls [Ekdale and De Gibert 2010]).

Additional pieces of neoichnological, sedimentological, and paleontological information enter at this point. The primary one is whether the substrate modification can be preserved, i.e., the ichnologic fidelity of Savrda (2007). In sum, this methodology predicts the occurrence in the fossil record of particular trace morphologies on the basis of our knowledge of the following:

• the phylogenetic relationships of potential tracemakers, both living and extinct;
• the range of behaviors carried out by these organisms;
• the subset of behaviors that are capable of modifying a substrate;
• the morphology and function of the substrate-modifying parts of these organisms, as they reflect these behaviors; and
• the extent to which these modified substrates can be preserved.

Much of this method is already implicit in the work of some paleontologists or can be readily applied to available analyses and data. Ultimately, the aim is to limit behavioral interpretations of traces to what is actually testable given the available data. It allows the making of probabilistic predictions of the preservation potential of behaviors, akin to taphonomic studies that focus on relative preservation of body parts.

Of course, this method is fraught with potential issues. Phylogenies of potential tracemakers are often revised. The number of organisms with fully documented behaviors is small. Even for those organisms, very few have been examined using neoichnology to see what types of traces they are capable of producing. Certain behaviors may be unique to extinct organisms or are rampantly polyphyletic. Finally, behaviors should show a strong "stem-ward slip," similar to that identified by Samsom et al. (2010) for chordate characters subject to decomposition. In other words, the chances of assigning a particular trace to a lower-level taxonomic group or to a detailed behavior are very small. We may never be able to say anything more definitive for most ichnofossils than "trilobite locomotion trail" or "theropod nest."

*Neoichnology and Models.*—Implementing this methodology will require expanded attention to neoichnology, both empirical and experimental. Of particular importance is an expansion of the range of organisms studied. Important steps have already been taken in this direction through the work on terrestrial arthropods by Hembree (2009) and Halfen and Hasiotis (2010). Still, only a fraction of potential tracemakers have been examined in either field or laboratory settings. Field and laboratory studies also need to become better integrated, to determine the extent that experimentally produced traces match those found in nature. Experimental work should also focus more on manipulation of behavioral variables (Koy and Plotnick 2010). Experimental protocols need to be developed in cooperation with behavioral biologists, so that ichnologists don't "reinvent the wheel" in terms of concepts and methods.

Paired with new work in neoichnology should be continued development of new and more realistic models. Again, these models should be developed in consultation with behavioral biologists so they capture the most relevant aspects of behavior and are framed correctly. As succinctly summarized by Krebs and Davies (1997), optimality models of behavior have three basic components: these are assumptions about what is being maximized, what choices are available, and what constraints exist. Ichnological models of behavior, which usually assume optimality, need to identify these components explicitly. Models also need to incorporate learning, both long- and short-term. As discussed earlier, current research suggests that some capacity for learning and memory may exist in the majority of animals with a central nervous system. There is a demonstrable need to get away from the pure taxis-reflex conceptual model of behavior.

One promising avenue is the use of various evolutionary robotic, artificial life, and artificial intelligence models. These models often incorporate learning, detection of stimuli at a distance, and navigation (Floreano and Keller 2010). This work also dovetails with studies based on the anatomy of real organisms, such as dinosaurs (Sellers et al. 2009).

## Final Comments

One area in which paleontological information has yet to be integrated within the larger body of evolutionary biology is the study of behavior. Almost universally, behavioral biologists appear to be unaware of the widespread occurrence, rich documentation, and long history of study of the fossilized record of behavior represented by trace fossils. At the same time, paleontologists have generally failed at bringing this information to the attention of biologists and at utilizing the conceptual frameworks of evolutionary behavioral biology. Even among paleobiologists, the behavioral record contained in trace fossils is rarely discussed. Despite the intense interest in biodiversity history, it has been more than 30 years since the publication of synoptic studies of the overall history of trace diversity (Crimes 1974; Seilacher 1977). A *Web of Science* topic search in *Paleobiology* reveals that only three papers use ''ichnofossil'' or ''trace fossil,'' and perhaps ten more use ''trace'' when not referring to trace elements.

The aim of this paper has been to describe a possible path towards a paleobiology of behavior based on the trace fossil record. For this to happen, ichnologists should initiate research interactions with the large community of behavioral biologists. This will require that ichnologists learn the theoretical and empirical framework of behavioral biology, so that both communities' observations and interpretations use the same language and concepts and reflect current understanding in the two fields. At the same time, behavioral biologists need to become aware of the vast untapped data and concepts that ichnology can provide their field. This is only way in which ichnology can provide them the ''deep time'' component of the evolution of behavior. Finally, paleobiologists need to pay more attention to the fossil record of behavior and find means to incorporate it into their databases, analyses, and evolutionary models.

## Acknowledgments

## Literature Cited

Alcock, J. 2009. Animal behavior: an evolutionary approach. Sinauer, Sunderland, Mass.

Bastardie, F., Y. Capowiez, P. Renault, and D. Cluzeau. 2005. A radio-labelled study of earthworm behaviour in artificial soil cores in term of ecological types. Biology and Fertility of Soils 41:320–327.

Behrensmeyer, A. K., and S. M. Kidwell. 1985. Taphonomy's contributions to paleobiology. Paleobiology 11:105–119.

Behrensmeyer, A. K., S. M. Kidwell, and R. A. Gastaldo. 2000. Taphonomy and paleobiology. Paleobiology 26:103–147.

Benhamou, S. 2004. How to reliably estimate the tortuosity of an animal's path: straightness, sinuosity, or fractal dimension? Journal of Theoretical Biology 229:209–220.

Bengtson, S., and B. Rasmussen. 2009. Paleontology: new and ancient trace makers. Science 323:346–347.

Benton, M. J. 2010. Studying function and behavior in the fossil record. PLoS Biology 8:e1000321.

Bernardi, M., and M. Avanzini. 2011. Locomotor behavior in early reptiles: insights from an unusual *Erpetopus* trackway. Journal of Paleontology 85:925–929.

Bertling, M., S. Braddy, R. Bromley, G. Demathieu, J. Genise, R. Mikulas, J. Nielsen, K. Nielsen, A. Rindsberg, M. Schlirf, and A. Uchman. 2006. Names for trace fossils: a uniform approach. Lethaia 39:265–286.

Bolhuis, J. J., and L. A. Giraldeau, eds. 2005. The behavior of animals. Blackwell, Malden, Mass.

Boucot, A. J. 1990. Evolutionary paleobiology of behavior and coevolution. Elsevier, Amsterdam.

Boucot, A. J., and G. O. Poinar Jr. 2010. Fossil behavior compendium. CRC Press, Boca Raton, Fla.

Braddy, S. J. 2001. Trackways: arthropod locomotion. Pp. 389–393 *in* D. E. G. Briggs and P. R. Crowther, eds. Palaeobiology II. Blackwell, Oxford.

Bromley, R. G. 1996. Trace fossils: biology, taphonomy, and applications. Chapman and Hall, London.

Buatois, L. A., and G. M. Mangano. 2011. Ichnology. Cambridge University Press, Cambridge.

Bryant, H. N., and A. P. Russell. 1992. The role of phylogenetic analysis in the inference of unpreserved attributes of extinct taxa. Philosophical Transactions of the Royal Society of London B 337:405–418.

Carrano, M. T., and J. A. Wilson. 2001. Taxon distributions and the tetrapod track record. Paleobiology 27:564–582.

Christy, J. H. 1982. Burrow structure and use in the sand fiddler crab, *Uca pugilator* (Bosc). Animal Behaviour 30(AUG):687–694.

———. 1987. Competitive mating, mate choice and mating associations of brachyuran crabs. Bulletin of Marine Science 41:177–191.

Crimes, T. P. 1974. Colonization of the early ocean floor. Nature 248:328–330.

———. 1977. Modular construction of deep-water trace fossils from the Cretaceous of Spain. Journal of Paleontology 51:591–605.

———. 1992. The record of trace fossils across the Proterozoic-Cambrian boundary. Pp. 177–204 in J. H. Lipps and P. W. Signor, eds. Origin and early evolution of the Metazoa. Plenum, New York.

Crimes, T. P., and M. L. Droser. 1992. Trace fossils and bioturbation: the other fossil record. Annual Review of Ecology and Systematics 23:339–360.

Crimes, T. P., and M. A. Fedonkin. 1994. Evolution and dispersal of deep-sea traces. Palaios 9:74–83.

Curran, H. A., and A. J. Martin. 2003. Complex decapod burrows and ecological relationships in modern and Pleistocene intertidal carbonate environments, San Salvador Island, Bahamas. Palaeogeography, Palaeoclimatology, Palaeoecology 192:229–245.

Damschen, E. I., L. A. Brudvig, N. M. Haddad, D. J. Levey, J. L. Orrock, and J. J. Tewksbury. 2008. The movement ecology and dynamics of plant communities in fragmented landscapes. Proceedings of the National Academy of Sciences USA 105:19078–19083.

Davis, R. B., N. J. Minter, and S. J. Braddy. 2007. The neoichnology of terrestrial arthropods. Palaeogeography, Palaeoclimatology, Palaeoecology 255:284–307.

de Jager, M., F. J. Weissing, P. M. J. Herman, B. A. Nolet, and J. van de Koppel. 2011. Lévy Walks evolve through interaction between movement and environmental complexity. Science 332:1551–1553.

Dietl, G. P., and P. H. Kelley. 2002. The fossil record of predator-prey arms races: coevolution and escalation hypotheses. In M. Kowalewski and P. H. Kelley, eds. The fossil record of predation. Paleontological Society Special Paper 8:353–374.

Drickamer, L. C., S. H. Vessey and E. Jakob. 2001. Animal behavior: concepts, processes, and methods. Wadsworth, Belmont, Calif.

Dukas, R. 2009. Learning mechanisms, ecology, and evolution. Pp. 7–26 in R. Dukas and J. M. Ratcliffe, eds. Cognitive ecology II. University of Chicago Press, Chicago.

Dusenbery, D. B. 1992. Sensory ecology: how organisms acquire and respond to information. W. H. Freeman, New York.

Ekdale, A. A., and J. M. De Gibert. 2010. Paleoethologic significance of bioglyphs: fingerprints of the subterraneans. Palaios 25:540–545.

Ekdale, A. A., and R. E. Lamond. 2003. Behavioral cladistics of trace fossils: evolution of derived trace-making skills. Palaeogeography, Palaeoclimatology, Palaeoecology 192:335–343.

Ekdale, A. A., R. G. Bromley, and S. G. Pemberton. 1984. Ichnology: trace fossils in sedimentology and stratigraphy. Society of Economic Paleontologists and Mineralogists, Tulsa, Okla.

Farlow, J. O., S. M. Gatesy, T. R. J. Holtz, J. R. Hutchinson, and J. M. Robinson. 2000. Theropod locomotion. American Zoologist 40:640–663.

Finarelli, J. A., and J. J. Flynn. 2006. Ancestral state reconstruction of body size in the Caniformia (Carnivora, Mammalia): the effects of incorporating data from the fossil record. Systematic Biology 55:301–313.

Floreano, D., and L. Keller. 2010. Evolution of adaptive behaviour in robots by means of Darwinian selection. PLoS Biology 8(1):e1000292.

Frey, R. W. 1973. Concepts in the study of biogenic sedimentary structures. Journal of Sedimentary Research 43:6–19.

Frey, R. W., and A. Seilacher. 1980. Uniformity in marine invertebrate ichnology. Lethaia 13:183–207.

Frey, R. W., H. A. Curran, and S. G. Pemberton. 1984. Tracemaking activities of crabs and their environmental significance: the ichnogenus Psilonichnus. Journal of Paleontology 58:333–350.

Gingras, M. K., S. E. Dashtgard, J. A. MacEachern, and S. G. Pemberton. 2008a. Biology of shallow marine ichnology: a modern perspective. Aquatic Biology 2:255–268.

Gingras, M. K., S. G. Pemberton, S. Dashtgard, and L. Dafoe. 2008b. How fast do marine invertebrates burrow? Palaeogeography, Palaeoclimatology, Palaeoecology 270:280–286.

Goldberg, E. E., and B. Igic. 2008. On phylogenetic tests of irreversible evolution. Evolution 62:2727–2741.

Hagadorn, J. W., S. A. Schellenberg, and D. J. Bottjer. 2000. Paleoecology of a large Early Cambrian bioturbator. Lethaia 33:142–156.

Halfen, A. F., and S. T. Hasiotis. 2010. Neoichnological study of the traces and burrowing behaviors of the western harvester ant Pogonomyrmex occidentalis (Insecta: Hymenoptera: Formicidae): paleopedogenic and paleoecological implications. Palaios 25:703–720.

Hammer, Ø. 1998. Computer simulation of the evolution of foraging strategies: application to the ichnological record. Palaeontologia Electronica 1(2):21.

Harvey, P. H., and S. Nee. 1997. The phylogenetic foundations of behavioural ecology. Pp. 333–349 in J. R. Krebs and N. B. Davies, eds. Behavioural ecology: an evolutionary approach. Blackwell, Malden, Mass.

Hasiotis, S. T. 2002. Continental trace fossils. SEPM Short Course Notes 51:1–132.

Hasiotis, S. T., and C. E. Mitchell. 1993. A comparison of crayfish burrow morphologies: Triassic and Holocene fossil, paleo-, and neo-ichnological evidence, and the identification of their burrowing signatures. Ichnos 2:291–314.

Hastings, A., J. E. Byers, J. A. Crooks, K. Cuddington, C. G. Jones, J. G. Lambrinos, T. S. Talley, and W. G. Wilson. 2007. Ecosystem engineering in space and time. Ecology Letters 10:153–164.

Hayes, B. 2003. In search of the optimal scumsucking bottom-feeder. American Scientist 91:392–397.

Hembree, D. I. 2009. Neoichnology of burrowing millipedes: linking modern burrow morphology, organism behavior, and sediment properties to interpret continental ichnofossils. Palaios 24:425–439.

———. 2010. Aestivation in the fossil record: evidence from ichnology. Pp. 245–262 in C. A. Navas and J. E. Carvalho, eds. Aestivation: molecular and physiological aspects. Springer, Berlin.

Hembree, D. I., and S. T. Hasiotis. 2006. The identification and interpretation of reptile ichnofossils in paleosols through modern studies. Journal of Sedimentary Research 76:575–588.

Hofmann, H. J. 1990. Computer simulation of trace fossils with random patterns, and the use of goniograms. Ichnos 1:15–22.

Huntingford, F. A. 2003. A history of Animal Behaviour by a partial, ignorant and prejudiced ethologist. Animal Behaviour 66:409–415.

Huntley, J. W., and M. Kowalewski. 2007. Strong coupling of predation intensity and diversity in the Phanerozoic fossil record. Proceedings National Academy of Sciences USA 104:15006–15010.

Isles, T. E. 2009. The socio-sexual behaviour of extant archosaurs: implications for understanding dinosaur behaviour. Historical Biology 21:139–214.

Jackson, S. J., M. A. Whyte, and M. Romano. 2009. Laboratory-controlled simulations of dinosaur footprints in sand: a key to understanding vertebrate track formation and preservation. Palaios 24:222–238.

Jensen, S. R., M. L. Droser, and J. G. Gehling. 2005. Trace fossil preservation and the early evolution of animals. Palaeogeography, Palaeoclimatology, Palaeoecology 220:19–29.

Kitchell, J. A. 1979. Deep-sea foraging pathways: an analysis of randomness and resource exploitation. Paleobiology 5:107–125.

———. 1986. The evolution of predator-prey behavior: naticid gastropods and their molluscan prey. Pp. 88–112 in M. H. Nitecki and J. A. Kitchell, eds. Evolution of animal behavior. Oxford University Press, New York.

Kitchell, J. A., C. H. Boggs, J. F. Kitchell, and J. A. Rice. 1981. Prey selection by naticid gastropods: experimental tests and application to the fossil record. Paleobiology 7:533–552.

Koy, K., and R. E. Plotnick. 2007. Theoretical and experimental ichnology of mobile foraging. Pp. 427–440 in Miller 2007a.

———. 2010. Ichnofossil morphology as a response to resource distribution: insights from modern invertebrate foraging. Palaeogeography, Palaeoclimatology, Palaeoecology 292:272–281.

Krebs, J. R., and N. B. Davies. 1997. The evolution of behavioural ecology. Pp. 3–12 in J. R. Krebs and N. B. Davies, eds. Behavioural ecology: an evolutionary approach. Blackwell, Malden, Mass.

Kumagai, C. J., and J. O. Farlow. 2010. Observations on the traces of the American crocodile (Crocodylus acutus) from northwestern Costa Rica. New Mexico Museum of Natural History and Science Bulletin 51:41–49.

Labandeira, C. C. 2007. Assessing the fossil record of plant-insect associations: ichnodata versus body-fossil data. Pp. 9–26 in R. G. Bromley, L. A. Buatois, G. Mangano, J. F. Genise, and R. N. Melchor, eds. Sediment-organism interactions: a multifaceted ichnology. SEPM (Society for Sedimentary Geology), Tulsa, Okla.

Lauder, G. V. 1986. Homology, analogy, and the evolution of behavior. Pp. 9–40 in M. H. Nitecki and J. A. Kitchell, eds. Evolution of animal behavior. Oxford University Press, New York.

Leighton, L. R. 2002. Inferring predation intensity in the marine fossil record. Paleobiology 28:328–342.

Lockley, M. 1991. Tracking dinosaurs. Cambridge University Press, Cambridge.

Lockley, M. G., and D. D. Gillette. 1989. Dinosaur tracks and traces: an overview. Pp. 3–10 in D. D. Gillette, and M. G. Lockley, eds. Dinosaur tracks and traces. Cambridge University Press, Cambridge.

Lorenz, K. 1981. The foundations of ethology. Springer, New York.

Martin, A. J., and A. K. Rindsberg. 2006. Cubichnia revisited; when ''resting'' is more than just ''resting.'' Geological Society of America Abstracts with Programs 38:476.

———. 2007. Arthropod tracemakers of Nereites? Neoichnological observations of juvenile limulids and their paleoichnological applications. Pp. 478–491 in Miller 2007a.

Mayr, E. 1974. Behavior programs and evolutionary strategies. American Scientist 62:650–659.

Milàn, J., and R. G. Bromley. 2006. True tracks, undertracks and eroded tracks, experimental work with tetrapod tracks in laboratory and field. Palaeogeography, Palaeoclimatology, Palaeoecology 231:253–264.

Miller, M. F., and H. A. Curran. 2001. Behavioral plasticity of modern and Cenozoic burrowing thalassinidean shrimp. Palaeogeography, Palaeoclimatology, Palaeoecology 166:219–236.

Miller, W., III, ed. 2007a. Trace fossils. Elsevier, Amsterdam.

———. 2007b. Introduction: a user's guide. Pp. xiii–xv in Miller 2007a.

———. 2007c. Complex trace fossils. Pp. 458–465 in Miller 2007a.

Minter, N. J., and S. J. Braddy. 2006. Walking and jumping with Palaeozoic apterygote insects. Palaeontology 49:827–835.

Motani, R. 2005. Evolution of fish-shaped reptiles (Reptilia: Ichthyopterygia) in their physical environments and constraints. Annual Review of Earth and Planetary Sciences 33:395–420.

Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences USA 105:19052–19059.

Niedzwiedzki, G., P. Szrek, K. Narkiewicz, M. Narkiewicz, and P. E. Ahlberg. 2009. Tetrapod trackways from the early Middle Devonian period of Poland. Nature 463:43–48.

Norell, M. A., J. M. Clark, L. M. Chiappe, and D. Dashzeveg. 1995. A nesting dinosaur. Nature 378:774–776.

Novack-Gottshall, P. M. 2007. Using a theoretical ecospace to quantify the ecological diversity of Paleozoic and modern marine biotas. Paleobiology 33:273–294.

O'Brien, L. J., S. J. Braddy, and J. D. Radley. 2009. A new arthropod resting trace and associated suite of trace fossils from the Lower Jurassic of Warwickshire, England. Palaeontology 52:1098–1112.

Olsen, P. E., and D. Baird. 1986. The ichnogenus Atreipus and its significance for Triassic biostratigraphy. Pp. 61–87 in K. Padian, ed. The beginning of the age of dinosaurs: faunal change across the Triassic-Jurassic boundary. Cambridge University Press, New York.

Orr, P. J. 2001. Colonization of the deep-marine environment during the early Phanerozoic: the ichnofaunal record. Geological Journal 36:265–278.

Papentin, F., and H. Röder. 1975. Feeding patterns: the evolution of a problem and a problem of evolution. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1975:184–191.

Plotnick, R. E. 2007. Chemoreception, odor landscapes, and foraging in ancient marine landscapes. Palaeontologia Electronica 10.

Plotnick, R., and T. Baumiller. 2000. Invention by evolution: functional analysis in paleobiology. In D. H. Erwin and S. L. Wing, eds. Deep time: Paleobiology's perspective. Paleobiology 26(Suppl. to No. 4):305–323.

Poschmann, M., and S. Braddy. 2010. Eurypterid trackways from Early Devonian tidal facies of Alken an der Mosel (Rheinisches Schiefergebirge, Germany). Palaeobiodiversity and Palaeoenvironments 90:111–124.

Raup, D. M., and A. Seilacher. 1969. Fossil foraging behavior: computer simulation. Science 166:994–995.

Reichman, O. J., and E. W. Seabloom. 2002. The role of pocket gophers as subterranean ecosystem engineers. Trends in Ecology and Evolution 17:44–49.

Richter, R. 1928. Psychische Reaktionen fossiler Tiere,. Helminthoiden und Nereiten als Fragen der Fährtenkunde an die Tierpsychologie. Palaeobiologica 1:225–244

Roopnarine, P., and A. Beussink. 1999. Extinction and naticid predation of the bivalve Chione Von Mühlfeld in the late Neogene of Florida. Palaeontologia Electronica 2.

Ryan, M. J. 2005. Evolution of behavior. Pp. 294–314 in J. J. Bolhuis and L. A. Giraldeau, eds. The behavior of animals. Blackwell, Malden, Mass.

Sansom, R. S., S. E. Gabbott, and M. A. Purnell. 2010. Nonrandom decay of chordate characters causes bias in fossil interpretation. Nature 463:797–800.

Savazzi, E. 1994. Functional morphology of boring and burrowing invertebrates. Pp. 43–82 in S. K. Donovan, ed. The paleobiology of trace fossils. Johns Hopkins University Press, Baltimore.

Savrda, C. E. 2007. Taphonomy of trace fossils. Pp. 92–109 in Miller 2007a.

Schäfer, W. 1972. Ecology and palaeoecology of marine environments. University of Chicago Press, Chicago.

Schick, R. S., S. R. Loarie, F. Colchero, B. D. Best, A. Boustany, D. A. Conde, P. N. Halpin, L. N. Joppa, C. M. McClellan, and J.

S. Clark. 2008. Understanding movement data and movement processes: current and emerging directions. Ecology Letters 11:1338–1350.

Seilacher, A. 1953. Studien zur Palichnologie. I. Uber die Methoden der Palichnologie. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 96:421–452.

———. 1964. Sedimentological classification and nomenclature of trace fossils. Sedimentology 3:253–256.

———. 1967. Fossil behavior. Scientific American 217:72–80.

———. 1974. Flysch trace fossils: evolution of behavioural diversity in the deep-sea. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1974:233–245.

———. 1977. Evolution of trace fossil communities. Pp. 359–376 *in* A. Hallam, ed. Patterns of evolution. Elsevier, Amsterdam.

———. 1986. Evolution of behavior as expressed in marine trace fossils. Pp. 62–87 *in* M. H. Nitecki and J. A. Kitchell, eds. Evolution of animal behavior. Oxford University Press, New York.

———. 2007. Trace fossil analysis. Springer, Berlin.

Seilacher, A., L. A. Buatois, and M. G. Mangano. 2005. Trace fossils in the Ediacaran-Cambrian transition: behavioral diversification, ecological turnover and environmental shift. Palaeogeography, Palaeoclimatology, Palaeoecology 227:323–356.

Sellers, W. I., P. L. Manning, T. Lyson, K. Stevens, and L. Margetts. 2009. Virtual palaeontology: gait reconstruction of extinct vertebrates using high performance computing. Palaeontologia Electronica 12(3).

Tinbergen, N. 1963. On aims and methods of ethology. Zeitschrift für Tierpsychologie 20:410–433.

Tschinkel, W. R. 2003. Subterranean ant nests: trace fossils past and future? Palaeogeography, Palaeoclimatology, Palaeoecology 192:321–333.

Turchin, P. 1998. Quantitative analysis of movement. Sinauer, Sunderland, Mass.

Uchman, A. 2004. Phanerozoic history of deep-sea trace fossils. Pp. 125–140 *in* D. McIroy, ed. The application of ichnology to paleoenvironmental and stratigraphic analyses. Geological Society, London.

Vannier, J., I. Calandra, C. Gaillard, and A. Zylinska. 2010. Priapulid worms: pioneer horizontal burrowers at the Precambrian-Cambrian boundary. Geology 38: 711–4.

Walker, S. E. 2007. Traces of gastropod predation on molluscan prey in tropical reef environments. Pp. 324–344 *in* Miller 2007a.

Witmer, L. M. 1995. The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. Pp. 19–33 *in* J. J. Thomason, ed. Functional morphology in vertebrate paleontology.