Behavioral cladistics of trace fossils: evolution of derived trace-making skills

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Abstract

There is a genetic basis for many fundamental behaviors exhibited by animals (e.g., characteristic feeding patterns, defense instincts and social structures), which have the potential for leaving a trace fossil record. Behavioral cladistics may help us to better understand the evolutionary underpinnings of burrowing patterns and perhaps also the ichnotaxonomic relationships of complex and compound burrow systems. In an ichnologic cladogram, the shared homologous characters that define the branch points in the cladogram represent the expression of increasingly more derived behavior patterns, so a cladogram can depict evolutionary relationships of behavioral components reflected in some common trace fossils. Trace fossil cladograms allow us to conceptualize the acquisition and development of inherited skills for producing various kinds of traces throughout geologic time, and they give us an organized framework for interpreting the evolution of fossil behavior.
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1. Introduction

Behavior evolves. Just as the diagnostic anatomical traits of organism taxa change through time, so do their characteristic behavioral attributes.

Charles R. Darwin (1859) wrote, ''… I can see no difficulty in natural selection preserving and continually accumulating variations of instinct to any extent that was profitable. It is thus, as I believe, that all the most complex and wonderful instincts have originated… No complex instinct can possibly be produced through natural selection, except by the slow and gradual accumulation of numerous, slight, yet profitable, variations.''

Even from the beginning of our understanding of evolution and behavior, it was understood that genetically controlled behaviors (Darwin's 'instincts') can evolve through natural selection. Like any physically expressed trait, behaviors to a large extent are genetically controlled. There may be considerable variation in behavior between individuals, and this can lead to relative competitive advantages that can be acted on by natural selection processes.

Behavioral evolution is tightly linked with, and

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may in fact be a controlling influence on, morphological evolution. Edward O. Wilson (1980, p. 10) wrote, "The multiplier effect, whether purely genetic in basis or reinforced by socialization and other forms of learning, makes behavior the part of the phenotype most likely to change in response to long-term changes in the environment. It follows that when evolution involves both structure and behavior, behavior should change first and then structure. In other words behavior should be the evolutionary pacemaker."

Trace fossils ostensibly are the preserved evidence of organism activity. Thus, the evolution of burrowing behavior patterns by infaunal animals may be studied by examining the development of particular kinds of trace fossils through geologic time. Seilacher (1967, p. 80) asserted, "Scanty though the trace-fossil material now available is, it gives one hope that the early evolution of behavior patterns will become as valid an area of study as the evolution of anatomical structures."

2. Cladistic analysis and trace fossil taxonomy

A commonly inferred goal (some might say the fundamental purpose) of taxonomy is the hope of depicting real evolutionary relationships among particular groups of organisms. The underlying principle is that anatomical similarity implies evolutionary closeness. As a result of this paradigm, precise taxonomy based on the anatomy of body fossils is a necessary precursor to evolutionary interpretations of fossil lineages. The same can be said for trace fossils; precise taxonomy based on the morphology of trace fossils is a necessary precursor to meaningful interpretations of behavioral evolution.

Taxonomic treatment of trace fossils has been a controversial practice since it began in the first half of the 19th century. Although trace fossils are *not* body fossils, they traditionally have been classified and named by means of a morphological approach that conforms strictly to established rules of Linnean taxonomy. This path has paralleled the time-honored approaches to classifying and naming animal and plant body fossils, as

governed by the rules of the International Code of Zoological Nomenclature and International Code of Botanical Nomenclature. The pitfalls of employing taxonomic codes that were designed for body fossils to classify biogenic sedimentary structures are well known to any scientist who deals with trace fossils and need not be reiterated here. (For general overviews of the history of trace fossil taxonomy, including its limitations, see Osgood, 1975; Simpson, 1975; Basan, 1979; Magwood, 1992; Pickerill, 1994; Bromley, 1996.)

In recent decades, in an apparent departure from traditional Linnean approaches, many biologists and paleontologists have sought to cast the conceptual organization of animals and plants within the evolution-based framework of phylogenetic systematics, also known as cladistics. This approach seeks to categorize organism taxa in evolutionarily linked groups, known as clades, based on the successive introduction of homologous characteristics in the groups that are being studied. The relationships among clades of genetically related taxa are depicted in branching fashion in tree-like cladograms. (For general discussions of the basic principles and procedures of cladistic analysis, see Wiley et al., 1991; Pough et al., 1996, pp. 30–38; Prothero, 1998, pp. 43–61.)

3. Behavioral cladistics and trace fossil cladograms

Cladistic analysis seeks to determine evolutionary relationships among taxa, and cladograms are based on homologous characteristics that are shared by the members of the various clades. It has long been understood that there is a genetic basis for many fundamental behaviors in certain groups of animals (e.g., characteristic feeding patterns, defense instincts and social structures). Therefore, the homologous attributes of organisms on which cladograms are based can be behavioral as well as anatomical (e.g., see cladograms in figures in McLennan, 1991, 1996). In fact, numerous past studies have emphasized the importance of behavioral aspects in the classification of animals. In this context, Konrad Z. Lor-

enz (1958, p. 67) observed that "behavior traits are as much a characteristic of a species as bodily structure and form."

Through the observation of mating behaviors in certain birds and fishes, their evolutionary relationships can be elucidated (Mayr, 1958; Amadon, 1959; Van Tets, 1965; McLennan, 1991, 1996, 2001). Niko Tinbergen has made detailed studies of how gulls communicate with one another using specific vocalizations and well-orchestrated displays consisting of various postures and movements. He observed (Tinbergen, 1960, p. 118) that "the comparative study of the differences among species and the comparisons of the present displays and their apparent origins make it possible to approach a description of the evolutionary changes that must have occurred as the ancestral gull family split up into the present 35 or so species of different appearances, habits and distribution." This statement implies that species-specific behaviors have taxonomic as well as evolutionary significance.

In ichnology, trace fossils are treated in analogous fashion to body fossils in taxonomy (e.g., ichnologic taxobases, ichnogenera and ichnospecies) and also in paleoecology (e.g., interpretation of trophic levels). However, it is inherent in the nature of trace fossils, as biogenic sedimentary structures, that no aspect of direct descendency of one ichnospecies from another can be discerned in quite the same way as with body fossils. This is because trace fossils are manifestations of behavioral skills rather than genetically controlled anatomical attributes.

Behavioral cladistics may help us to better understand the evolutionary underpinnings of burrowing patterns and perhaps also the ichnotaxonomy of complex and compound burrow systems. In so doing, it is necessary to differentiate between the 'how' and the 'why' of organism traces. The paleoethologic significance of trace fossils includes both the 'how' (i.e., the method employed to produce the trace) and the 'why' (i.e., the purpose for which the trace is produced). Interpretation of the 'how' (i.e., the specific skills required to produce a certain kind of trace) generally is more objective than the 'why' (i.e., the assignment of a given trace to an ethologic cate-

gory, such as domichnia, fodinichnia, cubichnia, etc.). Therefore, it should be the 'how' aspect of a trace fossil that forms the basis of any behavioral cladistic analysis.

As an example, a carpenter acquires and utilizes certain basic skills for constructing things, and he/she may use the very same constructional skills to build a house (a domichnion), a restaurant (a fodinichnion), a storage shed (a cubichnion) or a boardwalk (a repichnion). In the same way, burrowing animals may employ essentially the same burrowing behaviors to construct burrows for a wide variety of purposes. And it is those behavioral aspects that have evolutionary significance in a cladistic analysis.

Another clarifying example comes from examining the trace fossils *Bergaueria* (a sea anemone resting trace), *Asteriacites* (a starfish resting trace) and *Rusophycus* (a trilobite resting trace). Even though these traces look very different and are unmistakable from one another, they actually represent the same basic behavior. The causative organisms simply excavated a shallow, body-shaped pit in which to rest. On a behavioral cladogram, these traces would occupy the same, quite primitive, position, even though sea anemones, echinoderms and trilobites represent very different levels of morphological complexity. Unlike the carpenter example (using the same tools to make different structures), these traces represent the use of vastly different anatomical tools (but perhaps employing similar methods) to make essentially the same type of structure.

In an ichnologic cladogram, the shared homologous characters (also called synapomorphies) that define the branch points (also called nodes) represent the utilization of increasingly more derived behavior patterns. A cladogram can depict the incorporation of key behavioral skills in the creation of some common trace fossils (Fig. 1). For example, a simple surface trackway, like *Diplichnites*, requires very little behavioral sophistication; all that is required is for the surface of the sediment to be depressed. The method of producing the trace is relatively primitive. In contrast, a very regular, mesh-like, anastomosed agrichnion, like *Paleodictyon*, requires much more complex behavior to produce the trace. Such a complex
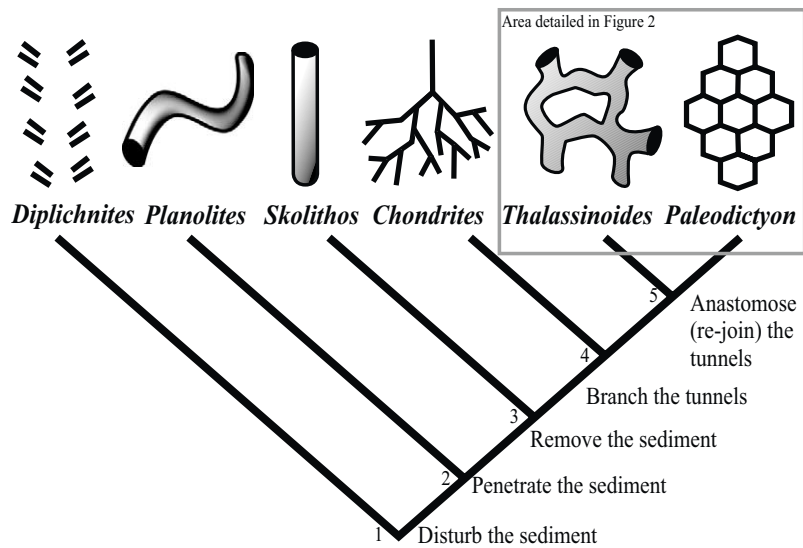
Fig. 1. Cladogram of some common trace fossils (*Diplichnites* to *Paleodictyon*). In this diagram, the nodes (branching points) are defined at the point of development of a shared behavioral trait. The terminal ends of the branches represent the derived trace fossil that possesses all of the traits from the nodes leading up to and including its branching point, but none of the traits from the nodes that are further along the diagram. Node 1 simply indicates disturbing the sediment surface. Node 2 indicates the development of the ability to penetrate the sediment surface. Every derived trace from this node possesses this ability. Node 3 marks the development of the ability to excavate a shaft. At node 4, the ability to branch the tunnel develops. At node 5 the organism is able to rejoin the tunnels to other tunnels, thus creating an anastomosed pattern. This clade of anastomosed burrows is diagrammed in greater detail in Fig. 2.

trace fossil is much more derived in the cladistic sense than is a simple footprint.

It is important to keep in mind that this approach does *not* attempt to organize the trace makers themselves in a cladistic arrangement, but rather to put in a cladistic context the basic skills required for producing more and more complex trace fossils. Thus, it is both possible and appropriate for a simple trace of a very advanced organism (e.g., a hominid footprint) to occupy a primitive position on a trace fossil cladogram, while a complex trace of a very simple organism (e.g., a *Paleodictyon*-like agrichnial burrow network created by something akin to a lowly worm) would occupy a more derived position on the trace fossil cladogram. Thus, even though the animal might have been able to create a more complex trace, the cladogram would only record the behavioral simplicity of what was left behind, not the biological complexity of the trace maker itself.

That being said, there is some possibility that

behavioral cladograms may aid in elucidating evolutionary relationships between certain groups of the trace makers. Within burrow networks constructed by social organisms, for example, the level of burrow complexity reaches great extremes. Detailed analysis and comparison of these kinds of traces through time should expose an evolutionary progression into more and more specialized structures.

Likewise, near the Cambrian boundary, during the evolution of many different behavioral styles, trace fossils should preserve a record of this experimentation. There have been multiple studies using trace fossils as biostratigraphic indicators in the Late Precambrian to Early Cambrian (but for a cautionary note, see Seilacher, 1994). The successive variation of such traces through time should represent both the morphological and behavioral evolution of the trace makers. Cladistic analysis of these early traces should provide insights into the behavioral evolution of the organisms burrowing at that time.
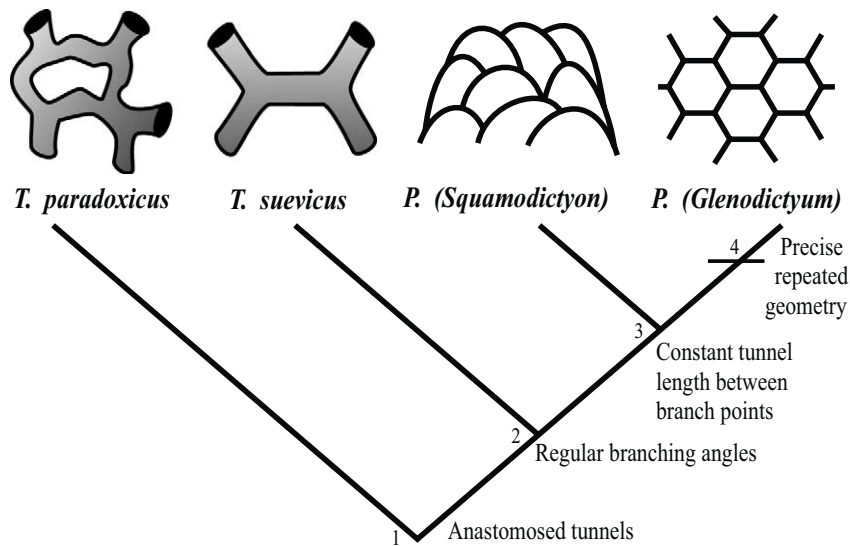
Fig. 2. Cladogram of anastomosed burrows (*Thalassinoides* to *Paleodictyon*). This is a detailed examination of the clade of branching and re-connecting burrows as illustrated from the most derived clade in Fig. 1. In this figure, node 1 represents the ability to reconnect burrows and thus is the same as node 4 from Fig. 1. As depicted in this cladogram, the behaviors that are reflected in *Paleodictyon* (*Squamodictyon*) and *Paleodictyon* (*Glenodictyum*) are more derived than those that are reflected in *Thalassinoides paradoxicus* and *Thalassinoides suevicus*.

4. Clade of anastomosed trace fossils

Anastomosed burrows are trace fossils that contain multiple tunnels that branch frequently and then rejoin to form galleries or mazes. In terms of branching geometry, anastomosed trace fossils may be quite complex and therefore may represent rather sophisticated behavior patterns on the part of the burrowers.

Some such highly branched burrow systems, including the well-known ichnogenera *Thalassinoides* and *Ophiomorpha*, generally are interpreted as fodinichnial tunnels and shafts constructed by infaunal deposit-feeding crustaceans (Frey et al., 1978; Ekdale, 1992). Others, including the enigmatic ichnogenus *Paleodictyon*, typically are interpreted as agrichnial burrows produced by animals that allowed microbes to grow along the burrow walls and then harvested those microbes for food (Seilacher, 1977). Others, including anastomosed galleries produced by infaunal social insects (e.g., ants and termites) and rodents (e.g., prairie dogs and pocket gophers), usually serve more of a dwelling than feeding function (Voorhies, 1975; Hasiotis and Bown, 1992; Genise and Bown,

1994; Hasiotis and Dubiel, 1995). Thus, a behavioral clade of anastomosed trace fossils may include various fodinichnia, agrichnia and domichnia (Fig. 2). (Remember – it is not the *purpose* of the trace, i.e., the Seilacherian ethologic category, that counts in the cladistic analysis; it is only the *behavioral skills* required to produce the trace that count.)

It is well known that substrate character may play a role in determining the range of burrow geometries that may be produced. However, in a situation where the composition, texture and consistency of the burrowed substrate are homogeneous, it is logical to conclude that uniform branching angles within an anastomosed burrow system require a more sophisticated burrowing behavior (i.e., a more derived trace-making skill) than non-uniform branching angles. In homogeneous substrates, for example, *Thalassinoides paradoxicus* (with very irregular branching patterns) appears earlier in the fossil record than *Thalassinoides suevicus* (with much more regular branching patterns), so it may be assumed that *T. paradoxicus* is a more primitive trace fossil and that *T. suevicus* is a more derived trace fossil.
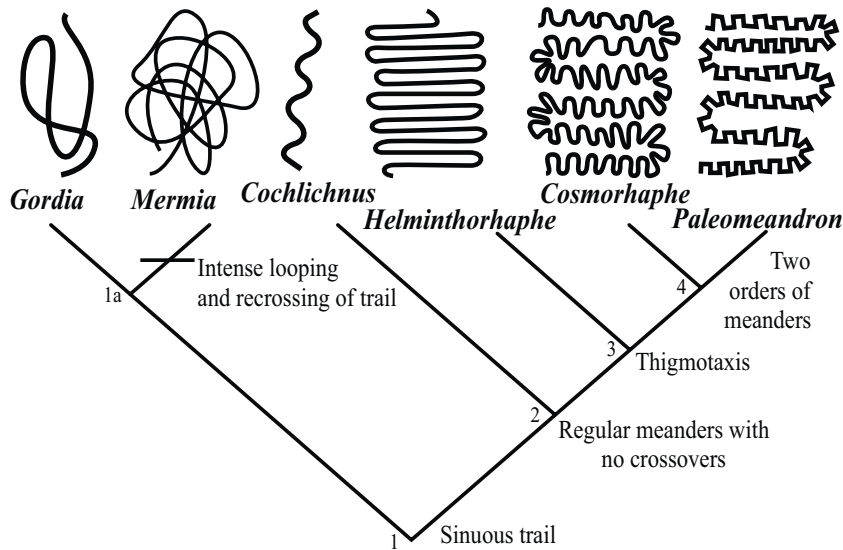
Fig. 3. Cladogram of winding and meandering trails (*Gordia* to *Paleomeandron*). At node 1 in this cladogram, there is the development of a sinuous burrow or trail. Node 1a defines a clade of irregularly sinuous trace fossils, here including the loosely winding *Gordia* and the more intensely looping *Mermia*. At node 2, a regular, back and forth meandering pattern develops, as is illustrated by *Cochlichnus*. At node 3, the back and forth sections become elongated and a constant spacing between successive meanders (thigmotaxis) is maintained. This is carried one step further at node 4, where a layer of regular back and forth meanders is superimposed on the elongate sections of the first meander set. This requires highly defined thigmotaxis and phobotaxis to avoid recrossing previous burrows and to maintain the complex geometry of the burrow system. In *Cosmorhaphe* the secondary meanders are sinusoidal, whereas in *Paleomeandron* the secondary meanders are rectilinear.

There is an implication for the evolution of behavioral complexity in that an organism that can produce a very complex *Paleodictyon* must have had ancestors that were only able to produce a form of less complex *Thalassinoides*-like traces, and before that, earlier ancestors that were only able to produce a form of very simple *Planolites*-like traces.

5. Evolutionary implications

The cladistic approach clearly has implications for interpreting the evolution of burrowing patterns. Much (but not all) evolutionary change is adaptive; this is true for both anatomical and behavioral evolution.

Gould and Lewontin (1979, p. 264) defined adaptation as "the good fit of organisms to their environment", and they noted that adaptations of organisms "can occur at three hierarchical levels with different causes." The first level of adapta-

tion involves uninherited physiological changes that occur during an organism's lifetime to allow it to flourish in specific environmental conditions (e.g., ecophenotypic cardiovascular adjustments in mammals to living at low versus high elevations). The second level involves cultural adaptations that derive from learning (e.g., aspects of postnatal care that do not come naturally among higher primates and in fact must be learned). The third level of adaptation consists of Darwinian selection acting upon genetic variation within natural populations (i.e., survival of the fittest).

This tri-level scheme of adaptive evolution may apply to preservable behavior patterns, which of course can be represented in the geologic record by particular kinds of trace fossils. On the first level, there must be some range of variation of burrowing behavior among different populations of the same species of burrowers that inhabit different substrate conditions. Callianassid shrimp display this level of adaptation depending on whether they are burrowing in firm mud or loose
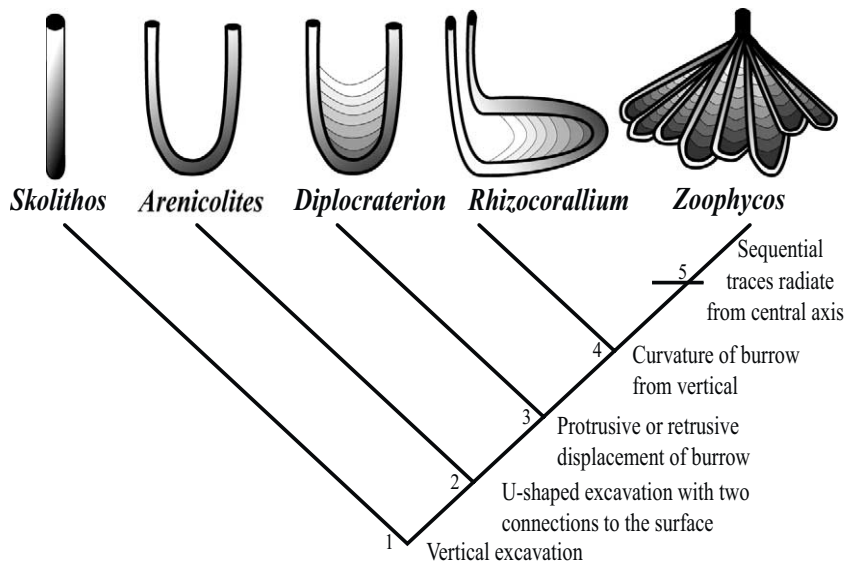
Fig. 4. Cladogram of spreiten burrows (leading to *Zoophycos*). This cladogram represents an evolutionary progression beginning with a simple vertical shaft (*Skolithos*) and culminating with a very complex burrow (*Zoophycos*). Node 1 marks the development of a vertically penetrating burrow. Node 2 shows the development of a U-shaped burrowing behavior. Node 3 illustrates the ability of the organism to reposition the burrow either protrusively or retrusively, creating a spreiten structure that indicates the previous positions of the active burrow. Node 4 marks the development of the ability to deviate the orientation of the active burrow from vertical. Node 5 shows the behavior creating a series of these structures, thereby producing a spreite of spreiten structures coiled around a central axis, as described by Ekdale and Lewis (1991). Thus, the organism that created *Zoophycos* required all of the above behaviors to produce its complete, complex trace.

sand. In cohesive mud the burrows usually are unlined (cf. *Thalassinoides*), while in sand the burrows generally are reinforced with wall pellets (cf. *Ophiomorpha*).

On the second level, trace fossils resulting from learned behaviors must be more common among higher vertebrates (e.g., birds and mammals) than among lower vertebrates (e.g., fish and reptiles) or invertebrates. An example of this may be the construction of tools by hominids. Valentine (1978) remarked that cultural evolution is fundamentally Lamarckian rather than Darwinian in character, because it evolves via the inheritance of knowledge and skills acquired during previous generations.

On the third level, it would seem that natural selection acts directly upon instinctual behaviors, which are fully inheritable. There is a clear evolutionary advantage to producing efficient feeding pathways to maximize the food consumed with the least waste of energy or missed area. The development of complex meander patterns for for-

aging illustrates this evolutionary pressure. Many burrowing organisms have evolved phobotaxis, so that they do not waste energy by recrossing their own pathways, and thigmotaxis, so that they can closely parallel their previous paths in order to minimize unexplored sediment (Seilacher, 1967). Such regular foraging patterns are most likely fully instinctual and are most likely the result of stepwise addition of behavioral instructions to an organism's repertoire.

Natural selection, in the strictest Darwinian sense, is both natural and selective, and therefore it also is adaptive. Thus, assuming that the ambient environmental conditions to which organisms are attempting to adapt remain stable, one should expect to see in the fossil record an evolutionary progression from less adaptive (more generalized?) to more adaptive (more specialized?) behaviors. Seilacher (1974, 1977, 1986) has suggested that just such a trend can be observed, at least in certain morphological categories of trace fossils, such as graphoglyptid burrows.

Some (but not all) behaviors are easier to acquire through evolution than most (but not all) anatomical attributes. It is intuitive that the more complex and derived a particular behavior is, the more likely it is that the behavior arose only once. Therefore, it is logical to assume that the producers of very complex (highly derived) trace fossils are more likely to be monophyletic. Certain types of burrowing behaviors (e.g., regular meandering patterns of *Cochlichnus* and *Helminthoida*, as shown in Fig. 3) almost certainly arose separately in many different biological lineages of trace-making organisms, whereas other types of more specialized behaviors (e.g., the distinctively coiled spreiten structures of *Zoophycos*, as shown in Fig. 4) may not have been.

Instinctive behaviors differ from learned behaviors, because the former are fully inheritable. However, with respect to the latter, the *capability* of acquiring new behaviors and assimilating them into an organism's daily routine when the opportunity arises also must be inheritable. One can assume that instincts are obligate behaviors that always may be triggered, whereas learned or environmentally mediated behaviors are facultative activities that may or may not be expressed, depending upon the animal's individual experiences. This is a difficult aspect to conceptualize in a cladistic framework, because the distinction between actual (instinctive) and potential (learned) behaviors cannot be depicted in a straightforward way on a cladogram.

In the case of physical (morphologic) evolution, organisms may gain or lose physical attributes only by a purely genetic process. In contrast, in the case of behavioral evolution, organisms may acquire or shed useful behaviors as the opportunity arises from environmental and/or learning processes. One more confounding issue is that each organism should have a maximum possible level of behavioral complexity with which it can produce its trace. Presumably then, an organism should be able to make any of several types of traces that are less complex, but never more complex, than its maximal behavior allows.

An organism that is limited to some level of behavioral complexity must have evolved from a precursor organism that was limited to producing less complex types of traces. In this way, trace fossil cladograms, while not illustrating direct descendency, can indicate the behaviors that the ancestral organisms were limited to. Every complex burrowing organism has ancestors that were limited to creating only simpler burrows.

6. Conclusions

Trace fossil cladograms allow us to conceptualize the acquisition and development of inherited skills for producing various kinds of traces throughout geologic time, and they give us an organized framework for interpreting the evolution of fossil behavior. Increased use of these behavior-based cladograms may help settle long-standing problems in ichnology relating to the classification of trace fossils and the grouping of these structures into an intelligible framework.

References

Amadon, D., 1959. Behavior and classification. Vierteljahrschr. Naturforsch. Ges. Zürich 104, 73–78.

Basan, P.B., 1979. Trace fossil nomenclature: the developing picture. Palaeogeogr. Palaeoclimatol. Palaeoecol. 28, 143–167.

Bromley, R.G., 1996. Trace Fossils: Biology, Taphonomy and Applications. Chapman and Hall, London, 361 pp.

Darwin, C.R., 1859. On the Origin of Species by Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life. John Murray, London.

Ekdale, A.A., 1992. Muckraking and mudslinging: the joys of deposit feeding. In: Maples, C.G., West, R.R. (Eds.), Trace Fossils. Paleontological Society Short Course 5, 145–171.

Ekdale, A.A., Lewis, D.W., 1991. The New Zealand *Zoophy-*

cos revisited: morphology, ethology and paleoecology. Ichnos 1, 183–194.

Frey, R.W., Howard, J.D., Pryor, W.A., 1978. *Ophiomorpha*: its morphologic, taxonomic, and environmental significance. Palaeogeogr. Palaeoclimatol. Palaeoecol. 23, 199–229.

Genise, J.F., Bown, T.M., 1994. New trace fossils of termites (Insecta, Isoptera) from the late Eocene–early Miocene of Egypt, and the reconstruction of ancient isopteran social behavior. Ichnos 3, 155–183.

Gould, S.J., Lewontin, R.C., 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist program. Proc. R. Soc. London B 205, 581–598.

Hasiotis, S.T., Bown, T.M., 1992. Invertebrate trace fossils; the backbone of continental ichnology. In: Maples, C.G., West, R.R. (Eds.), Trace Fossils. Paleontological Society Short Course 5, 64–104.

Hasiotis, S.T., Dubiel, R.F., 1995. Termite (Insecta; Isoptera) nest ichnofossils from the Upper Triassic Chinle Formation, Petrified Forest National Park, Arizona. Ichnos 4, 119–130.

Lorenz, K.Z., 1958. The evolution of behavior. Sci. Am. 199, 67–78.

Magwood, J.P.A., 1992. Ichnotaxonomy: a burrow by any other name…? In: Maples, C.G., West, R.R. (Eds.), Trace Fossils. Paleontological Society Short Course 5, 15–33.

Mayr, E., 1958. Behavior and systematics. In: Roe, A., Simpson, G.G. (Eds.), Behavior and Evolution. Yale University Press, New Haven, CT, pp. 341–362.

McLennan, D.A., 1991. Integrating phylogeny and experimental ethology: from pattern to process. Evolution 45, 1773–1789.

McLennan, D.A., 1996. Integrating phylogenetic and experimental analyses: the evolution of male and female nuptial coloration in the stickleback fishes (Gasterosteidae). Syst. Biol. 45, 261–277.

McLennan, D.A., 2001. The phylogeny of the gasterosteidae: combining behavioral and morphological data sets. Cladistics 17, 11–27.

Osgood, R.G. Jr., 1975. The history of invertebrate ichnology. In: Frey, R.W. (Ed.), The Study of Trace Fossils; A Synthesis of Principles, Problems, and Procedures in Ichnology. Springer-Verlag, New York, pp. 3–12.

Pickerill, R.K., 1994. Nomenclature and taxonomy of invertebrate trace fossils. In: Donovan, S.K. (Ed.), The Palaeobiology of Trace Fossils. Johns Hopkins University Press, Baltimore, MD, pp. 3–42.

Pough, F.H., Heiser, J.B., McFarland, W.N., 1996. Vertebrate Life, 4th edn. Prentice Hall, Upper Saddle River, NJ, 798 pp.

Prothero, D.R., 1998. Bringing Fossils to Life: An Introduction to Paleobiology. WCB/McGraw-Hill, Boston, MA, 457 pp.

Seilacher, A., 1967. Fossil behavior. Sci. Am. 217, 72–80.

Seilacher, A., 1974. Flysch trace fossils; Evolution of behavioural diversity in the deep-sea. N. Jahrb. Geol. Paläontol. Monatshefte 4, 233–245.

Seilacher, A., 1977. Pattern analysis of *Paleodictyon* and related trace fossils. In: Crimes, T.P., Harper, J.C. (Eds.), Trace Fossils II. Seel House Press, Liverpool, pp.

Seilacher, A., 1986. Evolution of behavior as expressed in marine trace fossils. In: Nitecki, M.H., Kitchell, J.A. (Eds.), Evolution of Animal Behavior; Paleontological and Field Approaches. Oxford University Press, New York, pp. 62–87.

Seilacher, A., 1994. How valid is *Cruziana* stratigraphy? Geol. Rundsch. 83, 752–758.

Simpson, S., 1975. Classification of trace fossils. In: Frey, R.W. (Ed.), The Study of Trace Fossils. Springer Verlag, New York, pp. 39–54.

Tinbergen, N., 1960. The evolution of behavior in gulls. Sci. Am. 203, 118–130.

Valentine, J.W., 1978. The evolution of multicellular plants and animals. Sci. Am. 230, 80–89.

Van Tets, G.F., 1965. A comparative study of some social communication patterns in the Pelecaniformes. Ornithol. Monogr. 2, 1–88.

Voorhies, M.R., 1975. Vertebrate burrows. In: Frey, R.W. (Ed.), The Study of Trace Fossils; A Synthesis of Principles, Problems, and Procedures in Ichnology. Springer Verlag, New York, pp. 325–350.

Wiley, E.O., Siegel-Causey, D., Brooks, D.R., Funk, V.A., 1991. The compleat cladist: a primer of phylogenetic procedures. Univ. Kansas Mus. Nat. Hist. Publ. 19, 158 pp.

Wilson, E.O., 1980. Sociobiology: The Abridged Edition. The Belknap Press of Harvard University Press, Cambridge, MA, 366 pp.