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# Paleobiology of complex trace fossils

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## Abstract

Complex trace fossils include structurally elaborate biogenic structures such as the large, spiral forms of *Zoophycos* and the intricately organized graphoglyptids; compound structures consisting of connected parts that would receive different ichnotaxonomic labels if preserved in isolation; and recurrent spatial associations of different trace fossils that probably represent strong ecologic interaction. These complicated animal artefacts should not be viewed so much as preservational rarities or taxonomic puzzles, but rather as neglected sources of information on the ethologic, ecologic and evolutionary characteristics of trace producers. Trying to fit these structures into the traditional behavioral classification scheme of Seilacher is bound to fail. Many complex trace fossils appear to have been occupied for long intervals and to record re-engineering or active control of proximal habitats by the trace-producing organisms. Attempting to understand their actual biologic significance will require new descriptive and interpretive approaches. One possible descriptive approach involves making comprehensive inventories of structural elements that record particular kinds of adaptive behavior or interaction (behavioral tokens). Portraying the spatial and temporal order of tokens could be done using a kind of systems diagram (paleoethologic 'blueprint') that summarizes construction, operation and maintenance of complex biogenic structures. New approaches to interpretation involve viewing the structures as evidence of physiologic projection of the trace producers, or as the extended phenotypes of these organisms. A reorganized approach to the study of complex biogenic structures emphasizing biologic properties would not only lead to some very old puzzles finally being solved, but also would revitalize ichnology and forge new and productive connections to ecology and evolutionary biology.

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## 1. Introduction

Most of what ichnologists do is related to either diagnosing and identifying biogenic structures (including coining names, recognizing undescribed forms, proposing synonymies, and compiling descriptions or redescriptions of local assemblages)

or to identifying patterns of spatial or temporal distribution of relevance to sedimentary geology (supporting interpretation of oxygen levels, physical properties of substrata, paleobathymetry, nature of food supplies and productivity, and characteristics of disturbance regimes). These endeavors not only have been crucial in the conceptual development of ichnology, but are the ways we continue to justify our existence: we actually have scientific names for most of those mysterious

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organism-produced structures in sedimentary rocks, and we can provide high-resolution environmental interpretations based on repeated occurrences of such structures. The application to geology is always seen as our ‘bread and butter’.

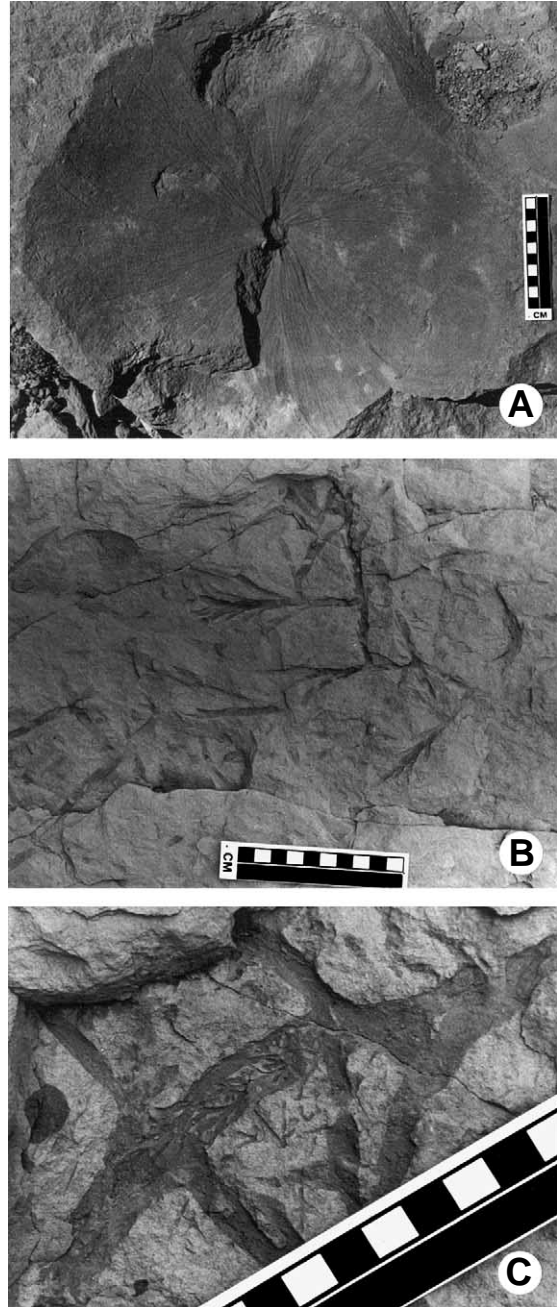
By comparison, much less attention has been devoted to the biologic interpretation of trace fossils, although we can all point quickly and proudly to a few famous examples in which biologic properties (identity of the trace producer, behavioral adaptation or ecologic interaction) have been demonstrated convincingly (one of my favorites is the wonderfully detailed work by Richard Bromley and colleagues on burrowing echinoids [e.g. Bromley et al., 1995; Bromley, 1996]). Not everyone will agree, but I see the interpretation of biologic processes and patterns lagging rather far behind the purely descriptive work and practical applications. Nowhere is this more obvious than in the study of the complex trace fossils (Fig. 1), which include: (1) large, intricate structures that record complicated, variable behavior or adaptations of trace producers; (2) the compound trace fossils consisting of connected parts having different morphologies that would receive different ichnotaxonomic labels if preserved in isolation; and (3) the repeated co-occurrence of different, independent trace fossils constructed at about the same time (*contemporaneous composites*) suggesting recurring ecologic interactions (W. Miller, 1996a, 1998, 2000, 2001, 2002a). These more complicated kinds of biogenic structure are not so much taxonomic anomalies or preservational rarities as they are a large, essentially unexploited source of information about the ethology, ecology and evolution of trace producers.

Expansion of the study of complex trace fossils

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Fig. 1. Examples of complex trace fossils, in this case all from Late Cretaceous–Paleogene deep-water limestones exposed near Belluno in northeastern Italy. (A) Bedding-surface view of *Zoophycos* in the Maastrichtian Scaglia Rossa limestone. (From W. Miller and D’Alberto, 2001, fig. 3A.) (B) *Thalassinoides*–*Phycodes* compound burrow systems in the Paleocene Scaglia Cinerea. (From W. Miller, 2001, fig. 5.) (C) Association of *Chondrites* with the *Thalassinoides*–*Phycodes* systems shown in B. (From W. Miller, 2001, fig. 6A.) Scale in all photographs marked in centimeters.

would broaden the scope of ichnology, increase the biologic sophistication of our discipline, and possibly lead to the solution of some very old and stubborn problems. What kind or kinds of organism build the large helicoidal structures we call



*Zoophycos* and why do they go to all that trouble? Why are there so many different kinds of graphoglyptids and what makes them? Did the trace producers of *Chondrites* repeatedly invade bigger structures like *Thalassinoides* simply to process the leavings within any available abandoned burrow, or was there something about the occurrence of the one trace-maker that controlled or limited the occurrence of the other? We do not know, and what is a bit exasperating is that we do not know in spite of the fact that we have studied these patterns for a long time. It simply is not satisfying any longer to claim that *Zoophycos* specimens were produced by a worm that ate mud in a complicated foraging pattern, that graphoglyptids probably were growing crops of microbes to supplement ambient food supplies at the deepsea floor, or that *Chondrites* simply recycled contents of old burrows. We have been saying these things for too long without knowing much about their general validity and biologic accuracy. Focusing special attention on complex trace fossils could lead to solution of these problems.

In this series of papers, we address some of these fascinating issues. Although the approaches differ and the kinds of trace fossils are varied, the emphasis is on the complicated biogenic structures that have always been hard to interpret, and the methods of analysis and interpretive models – in many cases – have more to do with biologic properties than with classification or geologic utility. Not all the authors in this volume would agree with my views on complex trace fossils or even adopt the same terminology that I use, but all will acknowledge the importance of giving special attention to complicated animal artefacts. In this introduction, I will discuss some of the general properties of complex traces, attempt to show how they differ from simpler biogenic structures, and illustrate their possible significance to paleobiology.

## 2. On being complex

The designation ‘complex’ has more than one implication. Several of the concepts of complexity

apply to trace fossils. I have listed below and defined briefly the concepts that are related potentially to complex trace fossils, or the possible ways biogenic structures might be construed to be complex.

- *Compositional complexity.* Biogenic structures could be regarded as complex simply because they consist of many different parts or elements. A list of compositional elements making up a specimen of *Zoophycos* or a compound burrow system would be longer and have more entries compared to a list for a typical *Skolithos* or *Planolites*. (It takes more words to describe comprehensively a complex trace fossil than a simple biogenic structure.)
- *Structural complexity.* The spatial arrangement, integration or repeated patterns of organization of compositional elements are demonstrably more complex in some biogenic structures than in others.
- *Developmental complexity.* The ‘growth’ or expansion and subsequent operational and maintenance routines recorded in biogenic structures could involve many steps or subroutines, or could be relatively simple and consist of only one major developmental sequence. In complex animal artefacts, a complicated sequence of major developmental stages is anticipated, together with minor sequences forming the dominant trajectory.
- *Operational or algorithmic complexity.* Instead of an inventory of developmental stages, complexity could be detected by analyzing the ‘software’ or behavior required to construct, operate and maintain a biogenic structure. The algorithmic text describing these processes for a complex trace fossil would be significantly richer than the algorithm describing a simple animal artefact, like a footprint or escape structure. (It is helpful here to think about computer models: those attempting to replicate simply the spatial patterns of some complex trace fossils like graphoglyptids have been shown to be much more complicated than those for simple meandering burrows or trails.)
- *Hierarchical or modular complexity.* Dynamic hierarchies consist of nested sets of systems in which any entity in the overall pattern simultaneously interacts with similarly scaled entities,

its own component systems or functional elements, and with the enclosing dynamic system. Large, intricate biogenic structures constructed and operated in a modular fashion might demonstrate this kind of dynamic complexity. Pictured from the point of view of static pattern, this would be a variant or extension of developmental complexity.

- *Complexity associated with ecologic interaction or physiologic/phenotypic projection.* Repeated spatial associations of biogenic structures obviously produced by different organisms, perhaps not at exactly the same time, could be records of ecologic interaction. Interaction networks could consist of two or more local populations of organisms producing artefacts. In the view that complex trace fossils represent extensions of the phenotypes of trace producers or projections of their physiologic processes, trace producers could control the occurrence, condition and fitness of other trace-making organisms. This ‘projected’ ecologic complexity is obviously different compared to a picture of trace fossil assemblages produced by organisms having essentially ‘unaffiliated adaptations’, making up happenstance associations controlled exclusively by extrinsic environmental factors.

Most assessments of complexity of trace fossils focus on compositional or structural properties (as with descriptions of *Zoophycos*, graphoglyptids and terrestrial artefacts like termite ‘nests’), developmental or modular patterns (descriptions of compound ichnotaxa, constructional models of graphoglyptids), and possible interactions (regular, apparently intimate associations of different ichnotaxa). The other kinds of complexity are rarely identified in the interpretation of complex biogenic structures, but represent interesting possible perspectives that need to be explored.

### 3. What are complex trace fossils?

Several of the contributions in this volume focus on *Zoophycos*, a group of large, complicated spreite structures that have inspired (or aggravated) ichnologists for many years. Despite the

fact that we have known for over a century that these elaborate structures are really burrow systems (Fuchs, 1893) – not algae or body fossils of animals – and even though a great deal of recent attention has been focused on these structures (see the recent reviews and opinions in Bromley, 1991; M.F. Miller, 1991; Ekdale, 1992; Olivero, 1994; Fu and Werner, 1995; Olivero and Gaillard, 1996; Kotake, 1997; W. Miller, 1998, 2002a; W. Miller and D’Alberto, 2001), there is still no consensus or general explanation that accounts for the organism(s) that produced *Zoophycos* or the function(s) of the structures collected under this ichnogenus. This is one of the best examples of a group of complex trace fossils anyone can point to: they are structurally and developmentally complex (compared to simpler burrow systems like *Skolithos* and *Planolites*), probably represent a long period of occupation and ‘operation’, and probably record complex, variable behavior (instead of one dominant behavior or interaction). Looking at *Zoophycos* in this way, it is easy to see why so many workers have been drawn to the study of this amazing trace fossil. The descriptions and interpretations of biogenic structures like *Zoophycos* are more challenging (and arguably more interesting) than those of comparatively simple structures; and solving the mystery of *Zoophycos* (or for that matter working out the taxonomic problems associated with this ichnogenus!) would be an enormous accomplishment in ichnology. But from a theoretical point of view, there are even more important things going on here – the *Zoophycos* problem is just the tip of the iceberg.

Trace fossils like these point to the limitations inherent in the application of some of the traditional approaches used to describe and interpret biogenic structures. The most obvious limitation is that complex trace fossils cannot be shoehorned into the ethologic classification proposed by Seilacher (1953) and used by many investigators. This scheme has worked well for morphologically simple structures and in geologic applications (see Ekdale et al., 1984), but has not helped in the interpretation of complex structures like *Zoophycos*, graphoglyptids, and compound systems. It appears to me that new ways of thinking about

Table 1

Distinction between ‘deliberate’ and ‘incidental’ biogenic structures (based on W. Miller, 1998, table 1; W. Miller and Vokes, 1998, table 2)

	Deliberate structures	Incidental structures
Characteristics	<ul style="list-style-type: none"> <li>– Complex structure</li> <li>– Multiple functions</li> <li>– Rich in behavioral tokens</li> <li>– Long occupation?</li> <li>– Too complex for Seilacher’s classification</li> </ul>	<ul style="list-style-type: none"> <li>– Simple structure</li> <li>– One main function</li> <li>– Record of simple behavior</li> <li>– Fleeting interaction</li> <li>– Fits one category in Seilacher’s scheme</li> </ul>
Examples	<ul style="list-style-type: none"> <li>– <i>Zoophycos</i></li> <li>– Graphoglyptids</li> <li>– Compound ichnotaxa</li> <li>– Termite nests</li> </ul>	<ul style="list-style-type: none"> <li>– <i>Skolithos</i></li> <li>– <i>Planolites</i></li> <li>– Escape structures</li> <li>– Footprints</li> </ul>
Significance	<ul style="list-style-type: none"> <li>– Failure of traditional methods and concepts</li> <li>– Habitat re-engineering and control of food supplies</li> <li>– Extended phenotypes, projected physiologies (= characters of the trace producer, not independent structures)</li> </ul>	<ul style="list-style-type: none"> <li>– Snapshot of simple behavior or interaction</li> <li>– No habitat, disturbance or resource controls</li> <li>– Not vital extensions of the organism’s body</li> </ul>

complicated animal artefacts are needed before any further progress can be made (W. Miller, 2002a). Traditional methods are unlikely to yield a definitive interpretation of complex trace fossils in terms of the identity of trace producers or their behavioral ecology.

### 3.1. ‘Deliberate’ vs. ‘incidental’ biogenic structures

There are probably many ways to expand the study of complex traces. I have proposed that they be given a special conceptual status as structures rich in behavioral information and referred to them as deliberate biogenic structures (W. Miller, 1996a,b, 1998, 2002a). This kind of animal artefact appears in many cases to have been inhabited and utilized for long intervals (relative to generation times of the trace producers), and to record elaborate behavioral adaptations involving (but not limited to) habitat re-engineering, disturbance modulation, and control or modification of food supplies (Table 1). These animal-produced structures are obviously different compared to the morphologically simple structures that seem to represent one kind of behavior or a single, dominant interaction or adaptation, which I called incidental biogenic structures.

The object of making the distinction was not to introduce an additional complication to ichno-

taxonomy, but simply to make the first formal step in drawing attention to the salient properties of complex biogenic structures (initially identified as complex using any of the criteria described earlier). One difficulty with the deliberate vs. incidental distinction is that some compound trace fossils are structurally complex and represent more than one kind of behavior, but are not occupied for long periods and do not represent efforts of the trace-maker to control or significantly re-engineer its immediate environment (e.g. Ekdale and Bromley, 2001). Another difficulty involves examples of trace fossils that fall in between the designations of deliberate and incidental, and possibly cases in which undetected complex behavior or ecologic interaction is associated with apparently incidental (compositionally/structurally simple) structures. Notwithstanding the potential difficulties, any attempt to open up the study of complex trace fossils and to introduce biologic concepts and methods would seem to me to be a step forward. The distinction is useful if it brings attention to complex trace fossils.

### 3.2. Fabrication analysis and formalization of ethologic inventories

As a special approach, I proposed using fabrication analysis to describe and interpret complex

trace fossils, which involves the identification and interpretation of embedded records of behavioral adaptations or interactions that I called behavioral tokens. Each token represents a particular activity of the trace producer that could be interpreted based on actualistic comparisons (both field observations and experimental manipulations), mechanistic interpretations, computer models, or possibly on association/connection with other tokens whose functions are known. As a way to portray results, I recommended using a kind of systems diagram or flow chart to summarize the spatial position and temporal order of tokens – a paleoethologic ‘blueprint’ or comprehensive inventory of artefact-related behavior that could be used in systematic comparisons with other trace fossils and modern biogenic structures (W. Miller, 1996a,b, 1998; W. Miller and Aalto, 1998; W. Miller and Vokes, 1998). Such a blueprint would contain information in the following categories, which obviously could overlap in terms of function and spatiotemporal order:

- *Construction* involving the primary fabrication of the system: initiation of the structure; excavation, moving material, adding/attaching structural elements, stacking, stuffing; initial development of the branching order in burrow systems, spatial positioning of components; construction of tunnels, galleries, runways, outlets, linings and initial arrangement of special features.
- *Operation* including the ‘normal’ hour-to-hour, day-to-day routines of utilization of the system: manipulation and modification of structural elements; re-entries, movement of materials in tunnels and galleries; gradual expansion/movement of working faces, storage areas, processing centers; recycling or restocking contents, removal of waste material; irrigation, ventilation and gardening activity; possible brooding of young or communication functions.
- *Maintenance* involving repairs and extensions of the system not included in normal routines of operation: various forms of minor damage control; intermittent repairs to ventilation/irrigation systems, tunnels and galleries, work on sally ports; rebuilding sections after disturbances caused by physical erosion or bioturbation; re-

plenishment of stocks after minor instances of plundering or erosion; catching up with backlog of waste disposal.

My experience has been largely with marine biogenic structures, which accounts for the examples of function that I listed. Although different specific functions could be documented for terrestrial artefacts, like termite nests or beaver dam-lodge-impoundment systems, the same general categories ought to apply. Special elements or tokens could be produced by trace-makers forced to depart from the round of normal behavioral routines, because of environmental stress, radical change in trophic regime or a catastrophic encounter with another organism (e.g. radial tunnels in *Zoophycos* probably recording periods of starvation, described by W. Miller and D’Alberto, 2001). An example of fabrication analysis of the branching burrow system *Phymatoderma*, summarized in a paleoethologic blueprint, is shown in Fig. 2.

#### 4. Significance of complex trace fossils: possibilities and prospects

What I am probably expected to say here is that complex trace fossils represent a significant challenge to the future development of ichnotaxonomy (which they do) and that they hold promise as sensitive indicators of environmental parameters of depositional settings in which they occur (which is almost certainly the case). I will let the taxonomically and geologically oriented ichnologists explore these topics. I prefer to emphasize the biologic significance of these remarkable animal-produced structures. This is a facet of paleobiology that remains practically untouched. Here are some possibilities.

##### 4.1. *Paleoethology of trace producers*

The most significant property of complex trace fossils of all kinds is the richness of behavioral information recorded in the structures. In other words, complex artefacts are more complete ledgers of the activities and adaptations/exaptations

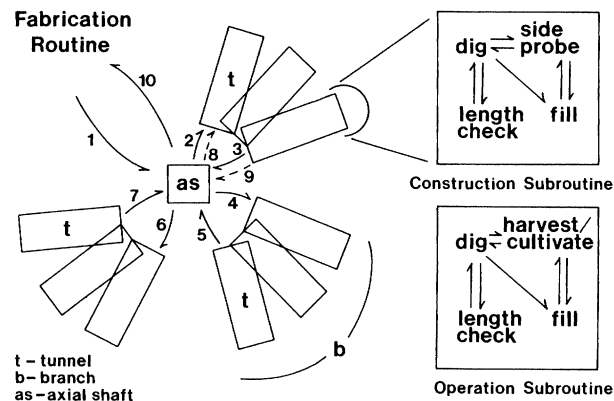
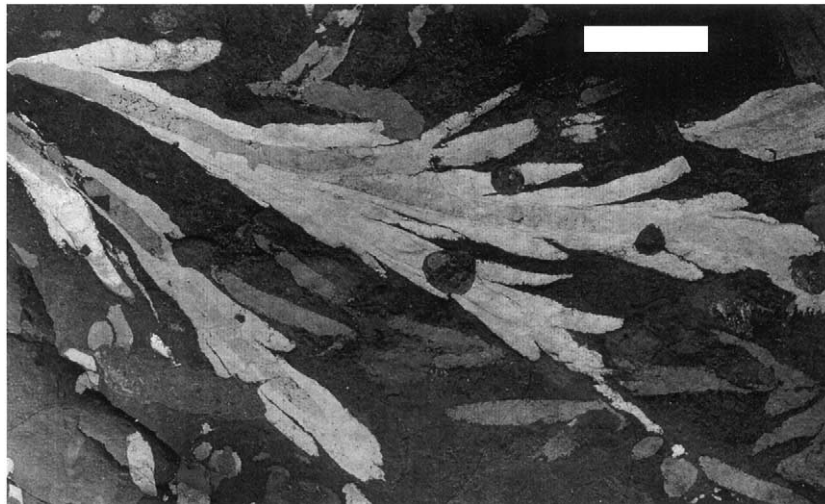


Fig. 2. *Phymatoderma* from Pliocene bathyal mudstone, Esmeraldas Province, coastal Ecuador. A bedding-surface exposure reveals a particularly complete specimen (top; bar scale represents 4 cm) that can be used to draw a paleoethologic 'blueprint' (below). Within the blueprint, 1 represents initiation of the burrow, 2–7 summarize tunnel construction and stocking with fecal pellets, 8 and 9 are examples of revisiting tunnels and recycling or restocking the contents, and 10 represents abandonment of the system. Even rather complicated sketches such as this can only summarize the elaborate behavior recorded in *Phymatoderma*; complexity can be viewed as compositional, developmental or modular. (Reproduced from W. Miller and Aalto, 1998, figs. 1 and 7, with permission of the Palaeontological Society of Japan.)

of trace producers than are the relatively simple structures – and their significance is ultimately based on this. Pointing out the difference is the purpose of the deliberate vs. incidental distinction (Table 1). Future investigations should attempt more sophisticated ethologic interpretations, comparisons with artefacts produced by modern organisms where possible, and improvements on my fabrication analysis approach (or replacement with a better method). At any rate, some sort of

standard technique is needed to make an accurate inventory of the structural elements or behavioral tokens; illustrate routines and subroutines of construction, operation and maintenance; and to facilitate comparisons with other trace fossils and with modern biogenic structures.

#### 4.2. Paleoecologic patterns

Ecologic interactions (predation, parasitism,

competition, mutualism) usually are inferred for ancient organisms based on co-occurrence of body fossils (especially involving attachments or overgrowths, body penetrations and embedments, repeated patterns of stereotypic skeletal damage, growth reactions, and sometimes gut contents) in the same bedding units and on comparison with living organisms (Ager, 1963; Boucot, 1990; Dodd and Stanton, 1990). The same kind of inferences can be made using recurrent associations of trace fossils, especially when comparisons to modern counterparts are available (Bromley, 1996). Patterns such as tiering, repeated spatial co-occurrence and apparent amensalism are well known in the trace fossil record. Recurrent associations of ichnotaxa that reflect non-antagonistic relationships (facilitation, obligate mutualism, certain types of indirect interaction) are less well known but probably have been preserved just as readily (e.g. W. Miller, 2000, 2001).

A related ecologic problem in ichnology involves the frequently invoked interpretation of ‘gardening’ behavior (some form of microbial cultivation) in complex biogenic structures. Several authors have proposed that deep-marine *Zoophycos* and the more complex versions of graphoglyptids were the burrow systems of ‘gardeners’ that utilized crops of symbiotic bacteria grown in their tunnels and galleries either as a major source of food or as a (seasonal?) supplement (see Seilacher, 1977; Fu and Werner, 1995), and that this kind of trace producer–bacteria relationship developed as an adaptation to life in food-poor environments (e.g. beneath mid-oceanic gyres, in isolated deep basins). It should be remembered that although shallow-marine and terrestrial invertebrates are known to cultivate bacteria and fungi in various ways, this has never been demonstrated convincingly for the trace producers living at the deepsea floor (W. Miller, 1991). It goes without saying that investigation of the probable associations that exist between the *Zoophycos* and graphoglyptid producers and deepsea bacteria is long overdue, and will have to involve recovery and analysis of samples from the modern ocean floor as well as cooperation with deepsea microbiologists.

#### 4.3. *Environmental engineers*

Richard Lewontin’s perspective on the relationships of organism to environment will prove useful in an expanded biologic assessment of complex trace fossils. In his view, ‘organisms not only determine what aspects of the outside world are relevant to them by peculiarities of their shape and metabolism, but they actively construct, in the literal sense of the word, a world around themselves’ (Lewontin, 2000, p. 54). Adaptation is more, then, than organisms proposing solutions to environmental problems, and the environment electing the best solution: organisms to a certain extent control their own ecologic and evolutionary fates (Lewontin, 2001; expansions of this perspective are described in Laland et al., 2001; Sterlney, 2001).

It is rather easy to see the complex, variable behavior recorded in complicated animal artefacts as evidence of a trace producer’s attempts to modify its surroundings, insulate itself from short-period fluctuations in ambient physicochemical processes, and insure a more or less predictable supply of food. This is an area in which comparison with modern biogenic structures has been and will be especially fruitful. In this sense, the producers of structures like *Zoophycos* have re-engineered their habitats to new specifications, instead of taking what comes to them and making the best of it (W. Miller and D’Alberto, 2001; W. Miller, 2002a). Levinton (1995) has evaluated modern endobenthic deposit feeders in exactly these terms.

The producers of large, long-lived, complicated biogenic structures also re-engineer the environment of co-occurring organisms (Jones et al., 1994). Large, persistent structures like *Zoophycos*, extensive compounds, and the large terrestrial structures like termite nests and beaver impoundments (see Hansell, 1984; Meadows and Meadows, 1991; Butler, 1995; Pollock et al., 1995) influence the species composition, abundance, physiologic condition and fitness of co-occurring organisms of all kinds, from bacteria to black bears. Some organisms – including some trace producers – are ecologic ‘kingpins’, entraining an entourage of other organisms wherever and



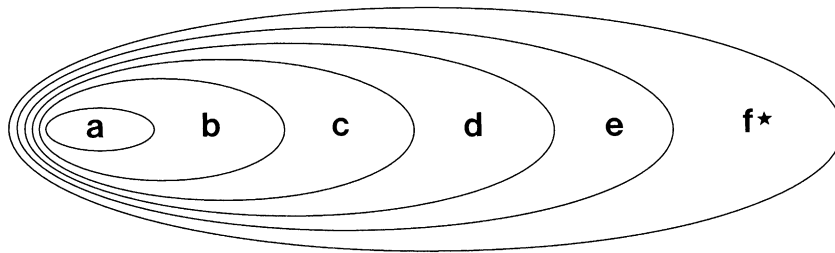


Fig. 3. The extended phenotype of the *Zoophycos*-producing organism. Each zone represents function and adaptive structure at greater distances from the genome: (a) the realm of genes and chromosomes; (b) zone of cellular processes and patterns; (c) cellular integration and tissues; (d) functional integration of tissues into organs; (e) integration of organs and whole-body organization and function; and (f) the periphery or outer reach of the phenotype, including construction, operation and maintenance of the burrow systems we refer to as *Zoophycos*. A pattern of offset, nested ellipses is used rather than nested circles to emphasize structuring ('stretching') of the phenotype through reciprocal interaction with the environment. The long axis of the ellipses represents coordinated adaptations of various functions and structures of the organism; the outer reach of the phenotype (the *Zoophycos* burrow system) is indicated with the star. (Based on W. Miller, 2002a, fig. 2.)

whenever they occur, thereby controlling the development of ecologic systems by biasing the array of ecologic interactions that can be developed (O'Neill et al., 1986; W. Miller, 2002b). The kingpins do not have to be especially dense or numerous, but must have properties that influence strongly other key players in the same ecologic system (e.g. Ziebis et al., 1996).

For example, the Mesozoic and Cenozoic *Zoophycos* producers were probably relatively large, long-lived organisms that lived through times of feast and famine at the deepsea floor; and their large, elaborate burrow systems can be viewed as adaptations or exaptations to such settings (see Jumars et al., 1990; W. Miller and D'Alberto, 2001; W. Miller, 2002a). At any one time actively occupied *Zoophycos* systems may have been uncommon in these areas of sea bottom, if comparison to modern deep-marine ecosystems is a reliable guide (Gage and Tyler, 1991). In terms of the local habitat structure, however, chemical gradients and physical properties of the substratum would have been significantly altered by the direct activity or legacy of these trace producers despite the scarcity of the organisms themselves. And in terms of trophic dynamics, the *Zoophycos* producers were probably 'carbon bankers' (in the sense that their feeding behavior and metabolic processes probably resulted in large quantities of organic carbon being sequestered and localized within the sediment) forming especially important

(and unacknowledged) components of the carbon cycle at the deep-ocean floor, out of all proportion to their relative abundance at any one time. The organisms responsible for the structures we call *Zoophycos* may not have been very abundant at all, but nonetheless could have controlled the organization and development of the surrounding local ecosystems through construction and utilization of their burrow systems.

#### 4.4. Complex trace fossils as extended phenotypes

A closely related idea is that of the extended phenotype, the notion that heritable characters of species may include their artefacts, if these extensions of the body of organisms affect physiologic condition and influence fitness (Dawkins, 1989). In this view, complex trace fossils like *Zoophycos*, in both a functional and evolutionary sense, are parts of the organisms that constructed, operated and maintained them. The structures are not incidental productions or records of a fleeting environmental interaction, but are the indispensable toolkits of the *Zoophycos* animal(s) used in the moment-to-moment survival of the organism and in the leveraging of its genes into subsequent generations (Fig. 3). Turner's (2000) generalizations about extended organisms in terms of physiologic projections of various kinds are an updated, mechanistic version of this same idea. I have already proposed that the processes associ-

ated with utilization of the *Zoophycos* systems changed the local environment in which the structures were located; the functions of endobenthic food mining, food or feces stowage, and cultivation of microbe gardens suggested as interpretations for these structures would be the physiologic projections that resulted in/occurred with the modifications of habitats and ecosystems.

Davide Olivero (personal communication, and his contribution to this volume) has described a peculiar, but by no means rare, version of helicoidal *Zoophycos* that coils upward through the substratum, rather than downward as 'typical' versions do. His examples range from Early Jurassic to Late Cretaceous, and may be limited to a single depositional basin in southeastern France. Olivero has documented environmental shifts in the occurrence of these structures (from shallow to deep water) and what appears to be a related transformation in their constructional morphology (involving size increase and development of marginal lobes). This could be a case in which a succession of complex trace fossils reflects an actual evolutionary transition: the uniqueness of the structures, the regional delimitation of the occurrences, and the extended temporal pattern seem to point to a single clade of Mesozoic *Zoophycos* producers (possibly sipunculans) undergoing evolutionary transformations in step with shifts in their habitats. This kind of reasoning only works if the biogenic structures can be considered as extended phenotypes (*sensu* Dawkins) of phylogenetically related trace-producing organisms, which may in fact be the case here. It would certainly be interesting, from a biologic point of view, to have more examples of this kind of well-documented transition in the fossil record.

## 5. Conclusions

Each contributor to this volume has his/her own concept of what complex trace fossils are and a different opinion about their significance. My approach has been to emphasize biologic properties and concepts. I have said little, for instance, about the geologic utility or the practical taxonomic problems involved in the study of com-

plex biogenic structures. At least we can agree that complex trace fossils deserve special treatment as especially rich records of behavior and interaction. We might also be able to agree that more attention needs to be concentrated on morphologically intricate traces, compound systems, and trace fossil records of ecologic interactions; and that the future expansion of biologic methods and concepts in ichnology could be supported in this way. No one doubts that more descriptive work needs to be done on complex trace fossils and the comparable modern biogenic structures.

There is another kind of conclusion to draw. Complex trace fossils are not so much weird preservational oddities or special taxonomic puzzles as they are a large class of objects in paleobiology that has never received adequate attention. I see them as a sign that ichnology has a lot of growing up to do. Ichnotaxonomy and geologic applications are well developed; it is time to shift some of our time and energy to the more purely biologic questions, like which organism(s) make *Zoophycos*, and how and why do they do it?

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