

2. Ethological interpretation of the trace fossil *Zoophycos* in the Hikoroichi Formation (Lower Carboniferous), southern Kitakami Mountains, Northeast Japan

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Abstract. The trace fossil *Zoophycos* was newly discovered in the lower part of the Hikoroichi Formation (Lower Carboniferous) distributed in the southern Kitakami Mountains, Northeast Japan. It consists of a helically coiled spreite, in which black-colored, chevron-shaped lamellae occur in cross section as an internal structure. Apart from the absence of distinct pellets and axial shaft, morphological features of the Hikoroichi *Zoophycos* are similar to those of *Zoophycos* known from Tertiary deep-sea sediments.

X-ray diffractational analysis and microscopic observation in thin section revealed that the black material of the lamellae in the spreite appears to be derived from a higher level as a result of downward conveyor activity by tracemakers. This inference and morphological similarity to Tertiary specimens imply that the black material in the spreite of the Hikoroichi *Zoophycos* is probably of fecal origin, although there is no compelling evidence such as pellets. According to this interpretation, the producing animals of the Hikoroichi *Zoophycos* fed in surface and/or subsurface sediments and deposited fecal matter deep in sediment, as did *Zoophycos* from Pliocene deep-sea sediments of the Boso Peninsula, Central Japan. Such feeding and excretory styles in the *Zoophycos* producer may have already been achieved by at least the Early Carboniferous and have remained unchanged over a long period.

Key words: Ethology, Hikoroichi Formation, Japan, Lower Carboniferous, trace fossil, *Zoophycos*

Introduction

Zoophycos, a complex spreiten structure with several kinds of forms, is known as one of the most striking ichnofossils and has been reported from the worldwide post-Cambrian marine sediments (Seilacher, 1967a, 1967b; Bischoff, 1968; Plička, 1968; Lewis, 1970; Simpson, 1970; Häntzschel, 1975; Ekdale, 1977; Wetzel and Werner 1981; Crimes, 1987; Bromley, 1990; Bryant and Pickerill, 1990; Olivero, 1994). In the post-Cretaceous, it occurs mainly in deep-sea sediments deposited at bathyal and/or hadal depths (eg., Seilacher, 1967a; Ekdale, 1977; Ekdale and Bromley, 1983, 1984a, 1984b, 1991; Wetzel, 1981, 1983, 1987, 1991; Frey and Pemberton, 1984; Frey and Bromley, 1985; Bottjer *et al.*, 1987; Kotake, 1989; Frey *et al.*, 1990; Wetzel and Wijayananda, 1990). In contrast, the Paleozoic *Zoophycos* is found mainly in the sediments of shallower settings, such as delta, nearshore, and shelf environments (eg., Osgood, 1970; Loring and Wang, 1971; Osgood and Szmec, 1972; Marintsch and Finks, 1978; Miller and Johnson, 1981; Chaplin, 1982; Miller, 1984, 1991; Miller and Knox, 1985; Bjerstedt, 1988a, 1988b; Bryant and Pickerill, 1990). Many authors have discussed its origin and interpreted it to be a product of feeding or foraging behavior by a worm-like,

infaunal deposit-feeder. In contrast, I proposed a different model on the origin of *Zoophycos*: the animals of *Zoophycos* appear to represent surface deposit-feeders which ingested surface and/or subsurface sediments (Kotake, 1989, 1990, 1991, 1992, 1993, 1994).

During field studies of the Lower Carboniferous Hikoroichi Formation distributed in the southern Kitakami Mountains, Northeast Japan, A. Kaneko discovered a number of well-preserved specimens of *Zoophycos* in the lowermost interval of the formation. As a result of field observations following the initial recognition of *Zoophycos*, it was revealed that *Zoophycos* is a common ichnofossil in the lower part of the Hikoroichi Formation.

This article reports the first discovery of the trace fossil *Zoophycos* in Paleozoic strata in Japan. The purposes of this paper are (1) to describe the morphology and mode of occurrence of the Hikoroichi *Zoophycos* and to compare them to those of the North American specimens from the same age, (2) to deliberate on the origin of the Hikoroichi *Zoophycos*, and (3) to examine whether or not the mode of the feeding and excretory styles of the Tertiary *Zoophycos*-producer is applicable to that of the Paleozoic one.

Geologic and sedimentologic background of the *Zoophycos*-bearing interval in the Hikoroichi Formation

The Lower Carboniferous Hikoroichi Formation, which is distributed in the southern Kitakami Mountains (Figure 1), consists of shale, tuffaceous shale, fossiliferous or tuffaceous sandstones, limestone, and tuff. It is subdivided into four stratigraphic units (H-1 to H-4 Members in ascending order) (Kawamura, 1983). The trace fossil *Zoophycos* was found in the H-1 Member in the Chyoanji area and the overlying H-2 Member in the Onimaru area (Figure 1C). In this paper, I follow Kawamura's stratigraphic division.

The *Zoophycos*-bearing interval of the H-1 Member consists mainly of bluish gray tuffaceous shale (10 to 40 cm thick) with interbedded tuffaceous sandstone (less than 3 cm thick), fossiliferous sandstone (less than 5 cm thick), and gray or black shale (less than 5 cm thick). On the other hand, the H-2 Member is well exposed in a cliff at the Onimaru Quarry, west of Hikoroichi (Figures 1, 2). There it comprises mainly alternating beds of thin tuffaceous sandstone (mostly 1 to 2 cm thick), tuffaceous shale (1 to 10 cm thick), and black shale (2 to 20 cm thick) in associated with beds of fossiliferous sandstone (mostly 1 to 2 cm thick) and tuff (less than 7 to 8 cm thick) (Figures 2, 3). In particular, the lower part of the H-2 Member represents a sequence of well-sorted, bluish gray tuffaceous shale with thin tuffaceous sandstone beds (Figures 2, 3).

In the Hikoroichi Formation, *Zoophycos* usually occurs in tuffaceous shale overlying tuffaceous sandstone (Figures 4, 5). Throughout the sandstone bed and the overlying *Zoophycos*-bearing tuffaceous shale, a complete Bouma sequence is occasionally visible (Figure 5B). The basal portion of each sandstone bed exhibits several kinds of erosional structures which may have been produced during deposition of the sandstone. In contrast, black shale lacks any sedimentary structures of hydraulic origin and contains body fossils such as brachiopods, cephalopods, bryozoan fragments, and disarticulated crinoid stems. A series of sedimentary structures recognized in the tuffaceous sandstone and the overlying tuffaceous shale strongly suggests that they are of turbidity current origin. On the other hand, the black shale probably was deposited under low-energy, stable bottom conditions below the storm wave-base.

Usually an incompletely bioturbated, mottled fabric transition zone is recognizable between the black shale and tuffaceous shale, both of which occupy the uppermost part of a single turbidite unit (Figures 4, 5). The thickness of this zone varies between 1 cm and 10 cm. In this zone, the mottled background fabric contains a diverse association of biogenic sedimentary structures, including *Chondrites*, *Phycosiphon*, *Planolites*, *Scalartuba*, *Teichichnus*, *Thalassionoides*, and *Zoophycos* (Figures 4, 5). In most cases, these trace fossils are crosscut by the black spreiten of

Zoophycos. The upper portion of the transition zone is more heavily bioturbated than the lower part. Judging from the ichnofabrics in the transition zone, the zone appears to be a product of reworking and mixing activities by benthic organisms during deposition of mud. In contrast, there is no apparent evidence of biogenic activity in either the sandstone or the lower part of tuffaceous shale.

These lithological aspects suggest a low-energy off-shore environment related to the influx of turbidity currents for the Hikoroichi basin at the *Zoophycos*-bearing interval, although Kawamura (1984) assumed shallow, temperate, and high-energy conditions above the wave-base as a background situation.

Morphology of *Zoophycos*

General characteristics

The ichnogenus *Zoophycos* usually includes two basic forms; helicoidal form and planar form (Seilacher, 1967b; Häntzschel, 1975). The former is characterized by a three-dimensional morphology and consists of a lobate, spirally coiled spreite around the central portion or axial shaft (Figure 6). The latter consists of a planar spreite developed along the bedding plane (Figure 7). In both forms, the marginal tunnel sharply bounds the spreite and the spreite-bearing host rock (Häntzschel, 1975).

In the spreite of helicoidal form, there are two kinds of lamella structures; major and minor lamellae (eg., Bischoff, 1968; Simpson, 1970). The major lamellae spirally radiate from the axial portion of the spreite (Figure 6A). On the other hand, the minor lamellae branch off the major lamella at an acute angle (10 to 35 degrees). In vertical section these two lamellae show chevron-shaped, lunate, or meniscate structures. In contrast, the spreite of the planar form *Zoophycos* has only a single lamella structure, which is less complex than that of the helicoidal form (Figure 7).

Zoophycos from the Hikoroichi Formation

In the case of *Zoophycos* from the Hikoroichi Formation, the spreite usually is arranged in parallel to the bedding plane, but toward the central portion it becomes inclined at an acute angle of 20 to 30 degrees to the bedding plane (Figure 5C). This fact indicates that the Hikoroichi *Zoophycos* is of helicoidal form. No distinct axial shaft, however, was found in the specimens examined.

The thickness of the spreite ranges from 1 mm or less to approximately 4 mm. In a cross section, the spreite is made of black sheets or systematically arranged chevron-shaped lamellae in a light-colored host rock (Figures 5, 8). In plan view, on the other hand, they are composed of densely packed lamellae of black sediment in blue-gray rock (Figure 9). The Hikoroichi specimens lack pellets in the spreite, which are often preserved in the Tertiary and Quaternary *Zoophycos* (Ekdale, 1977; Wetzel and Werner, 1981; Kota-

Figure 1. Fossil locality maps. **A:** Index map showing the Hikoroichi area in the Kitakami Mountains (dotted). **B:** Map showing the distribution of the Hikoroichi Formation in the Hikoroichi and Choanji areas. **C:** Geologic map of the Hikoroichi Formation in the Hikoroichi area. The geologic map was simplified from Kawamura (1984). Asterisks indicate *Zoophycos*-bearing stratigraphic units in the formation.

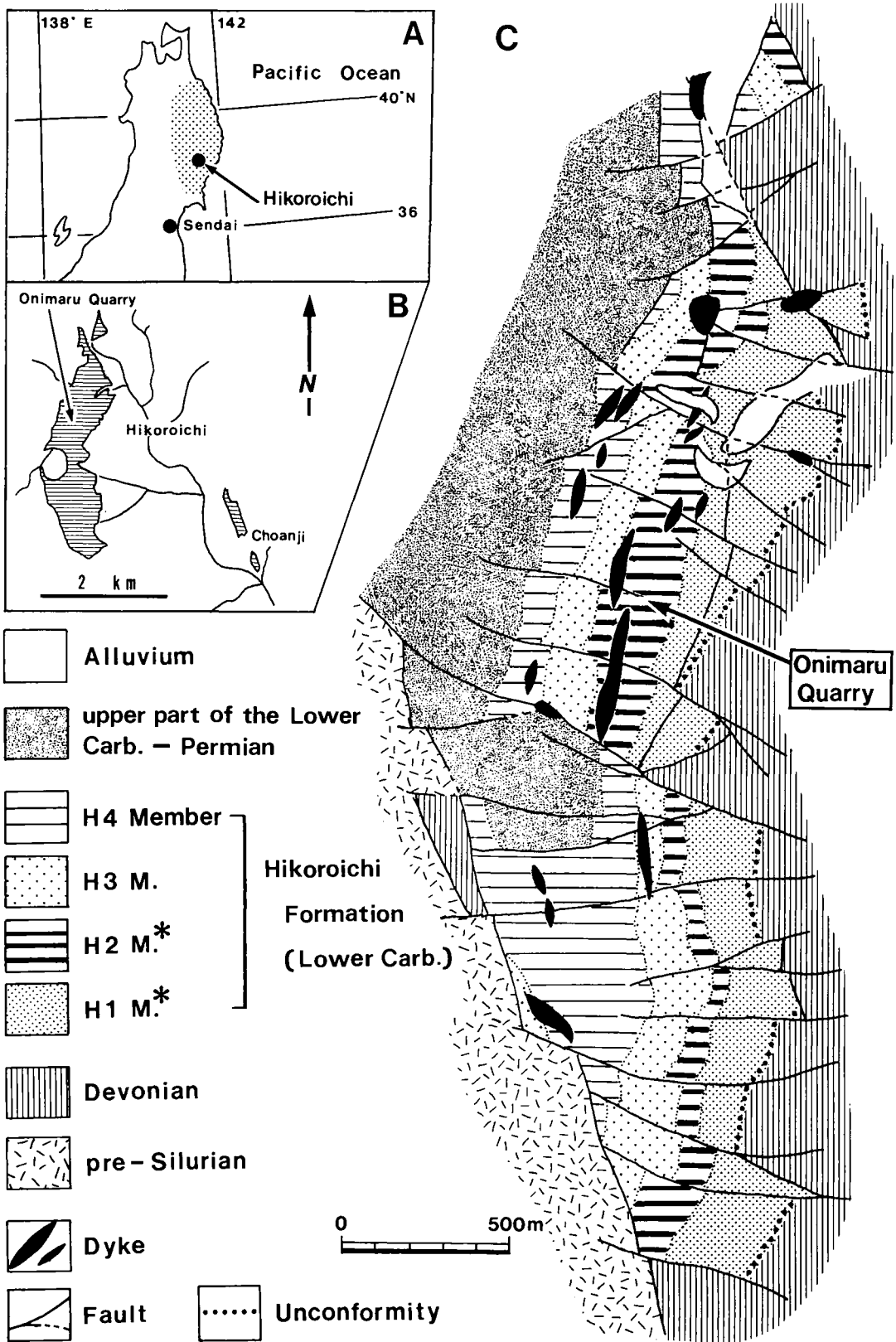




Figure 2. Outcrop photograph of the *Zoophycos*-bearing interval in H-2 Member of the Hikoroichi Formation exposed at a cliff of the Onimaru Quarry (Figure 1). Scale bar=1 m.

ke, 1989, 1991, 1992, 1993, 1994; Ekdale and Lewis, 1991; Fu and Werner, 1994). A well-defined marginal tunnel is seen at the outer edge of the spreite (Figure 5C).

The Hikoroichi *Zoophycos* occurs in the upper part of a tuffaceous shale and the overlying transition zone, but it is absent in both the black shale and the lower part of turbidite units such as TU₁ and TU₂ (Figures 4, 5). In the lithological units TU₄ and TU₅, sharply defined black *Zoophycos*-spreiten are visible and stand out against the lighter-colored surrounding rock which is characterized by the sparsity of other trace fossils (Figures 5, 8). In the transition zone, by contrast, the *Zoophycos*-spreiten are vague in outline in comparison with those occurring in the underlying tuffaceous shale (Figure 5C).

These lines of evidence suggest that the *Zoophycos* producer probably occupied the deepest tier within the sediment while the other tracemakers concurrently inhabited shallower tiers. Alternatively, the *Zoophycos* producer simply represents the latest stage of bioturbation activity in a stratum produced by discontinuous sedimentation.

As described in the previous literature, some Paleozoic *Zoophycos* seem to differ from the post-Mesozoic specimens in their overall morphology and internal structural features. Indeed, the three-dimensional morphology of the Pennsylvanian *Zoophycos* reconstructed by Miller (1991) is apparently different from that of the post-Mesozoic specimens (Figure 10). Furthermore, Chaplin (1982) and Miller (1991) pointed out that Paleozoic specimens of *Zoophycos*

are characterized by wider morphological variations than the post-Mesozoic representatives (Figure 11).

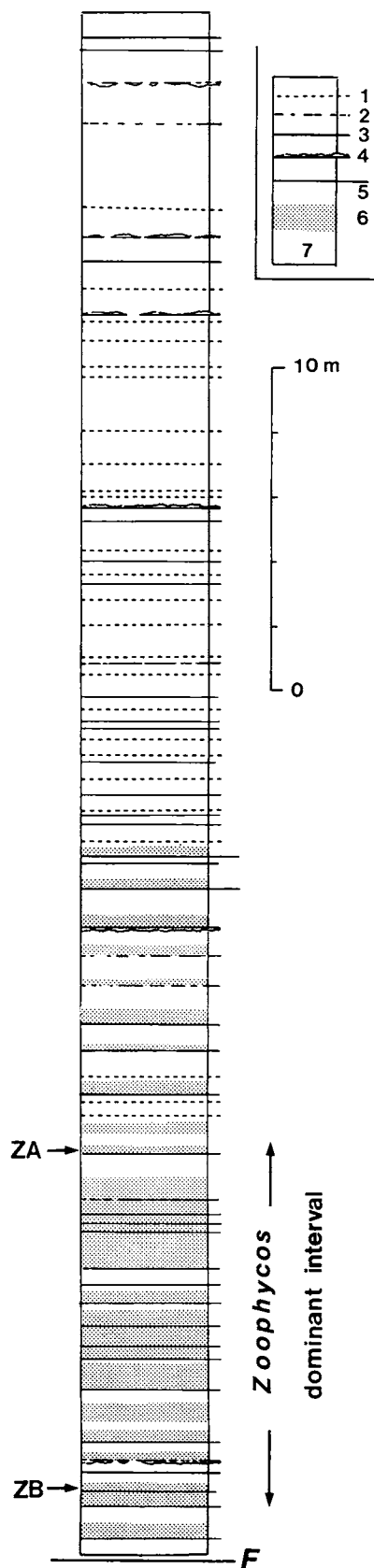
In contrast, apart from the absence of pellets and a distinct axial shaft, morphological features of the Hikoroichi *Zoophycos* are more similar to those of *Zoophycos* from Tertiary deep-sea sediments than to those of the Paleozoic specimens reported by Chaplin (1982) and Miller (1991) (Table 1).

Origin of black material in spreite

The spreite of the Hikoroichi *Zoophycos* is filled with black material. Lithologically, the material superficially resembles the black shale overlying the spreite-bearing bluish-gray tuffaceous shale. Based on well-preserved specimens taken from the lower part of the H-2 Member at the Onimaru Quarry (Figures 2, 3), the component material among the black shale, spreite-bearing bluish gray tuffaceous shale, and the black material in the spreite were compared to one another in order to determine the origin of the black material.

Methods

X-ray diffraction analysis of the three kinds of sediment samples was accomplished to determine the mineralogical composition. Samples (1 g to 2 g each) were taken from three different portions in a single slab (Figure 12). Because the *Zoophycos*-spreite consists of alternating lamellae of black material and bluish-gray host tuffaceous shale (Fig-



ures 5C, 8, 9), it is difficult to completely isolate only the black portion from the spreite. Since contamination with particles originating in the tuffaceous shale portion is unavoidable, the black material dominant portion in the spreite (Figure 12) was used in the present analysis to diminish contamination as much as possible.

In addition, thin sections of the spreite and surrounding host rock were examined to compare microfacies, grain size, and component material between them.

Results

The x-ray diffraction profile of the bluish-gray tuffaceous shale markedly differs in the relative abundance of chlorite, feldspar and quartz from those of the black shale and black material in the spreite (Figure 13). The profiles of black shale and the black material in the spreite closely resemble each other, and they are characterized by the predominance of quartz. Chlorite is more abundant in the black spreite material than in the black shale. This presumably is due to the incomplete isolation of the tuffaceous shale. The bluish-gray tuffaceous shale, by contrast, is rich in chlorite and feldspar but is poor in quartz. Chlorite in the black shale appears to have derived from the bluish-gray tuffaceous shale as a result of reworking and mixing activities by benthic organisms during deposition of muddy sediments.

Microscopic observation revealed that the spreite-bearing bluish-gray tuffaceous shale consists mostly of clay-sized particles, in which no bioclasts were found. In contrast, component materials of the black sediment in the spreite and black shale closely resemble one another in grain size (ranging from clay to medium-grained sand) and are much coarser than the spreite-bearing host rock (Figure 8). In rare cases, fine to medium sand-sized bioclasts, which are dominant in the black shale, are contained in the black portion in the spreite.

These data strongly suggest that the black sediment in the spreite of the Hikoroichi *Zoophycos* originated in the black shale just above the spreite-bearing horizon.

Discussion

Most previous authors believed that the *Zoophycos* producer systematically moved through the substrate to search for and ingest organic matter for food (Bischoff, 1968; Simpson, 1970; Häntzschel, 1975; Ekdale, 1977; Wetzel and Werner, 1981; Ekdale and Lewis, 1991). In other words, the component material of the fillings in the spreite in this interpretation originated in the sediment at the site of spreite emplacement. However, Ekdale and Bromley (1983) pointed out that some *Zoophycos* occurring in the Danish Cretaceous chalk were filled with sediments derived from a higher

Figure 3. Columnar section of H-2 Member of the Hikoroichi Formation exposed at the Onimaru Quarry. The *Zoophycos*-bearing rock samples for this study are indicated by arrows ZA and ZB. 1: sandstone bed less than 0.5 cm thick, 2: sandstone bed between 0.5 cm and 1 cm thick, 3: sandstone bed between 1 cm and 2 cm thick, 4: sandstone bed more than 2 cm thick, 5: tuff, 6: tuffaceous shale, 7: shale.

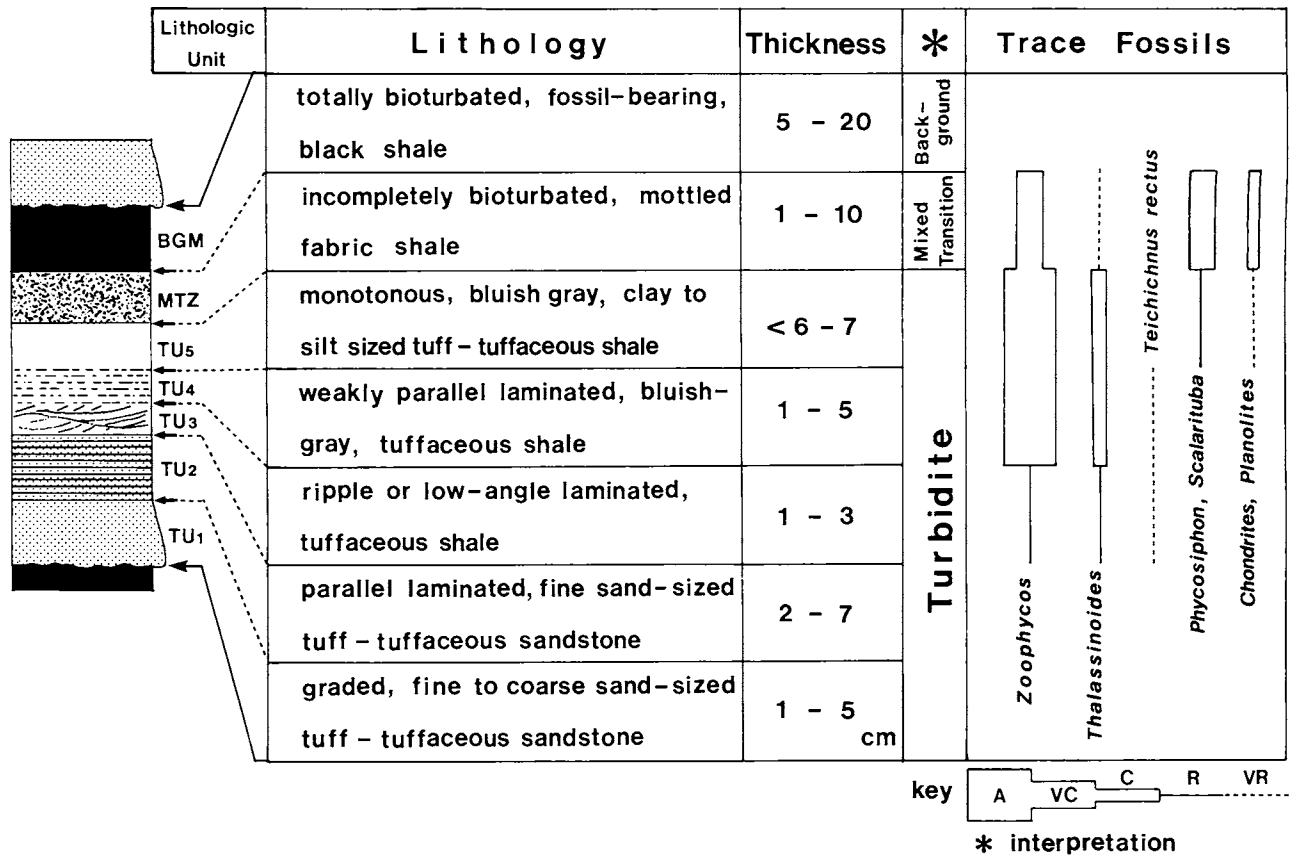


Figure 4. Lithological characteristics of the *Zoophycos*-bearing bed and tiering patterns of *Zoophycos* and related trace fossils in H-2 Member of the Hikoroichi Formation. BGM: background mud, MTZ: mixing transition zone, TU: lithological unit in a single turbidite bed, Key: A=abundant, VC=very common, C=common, R=rare, VR=very rare.

level.

Based on *Zoophycos* in Pliocene deep-sea sediments (Shiramazu Formation) of the Boso Peninsula, central Japan, I proposed another interpretation, that *Zoophycos* was produced by the excretory behavior of a deposit-feeder, which fed on surface and/or subsurface nutrient sediment at the sea floor and deposited its fecal matter deep in sediment (Kotake, 1989, 1991, 1992, 1993, 1994). This interpretation emphasizes that sediment in the spreite is of fecal origin and was derived from the sediment surface through the feeding and excretory process of the producer.

As mentioned above, mineralogical and microscopic observations suggest that the *Zoophycos* from the Hikoroichi Formation is a product of downward conveyor activity by its producer. This interpretation is consistent with that for the *Zoophycos* from the Pliocene deep-sea sediments of the Boso Peninsula. The morphological similarity between the Hikoroichi *Zoophycos* and the Pliocene specimens, furthermore, proves that the black sediment in the spreite of the Hikoroichi *Zoophycos* is probably of fecal origin.

This interpretation suggests a functional similarity in feeding and excretory styles of the producers of *Zoophycos* in the Hikoroichi and Shiramazu Formations. It is assumed

that the producer of the Hikoroichi *Zoophycos* segregated the feeding and excretory places in Early Carboniferous time and retained such an ethological style until at least the latest Tertiary.

Based on specimens of *Zoophycos* found in Devonian and Pennsylvanian strata deposited in shallow marine settings, Miller (1991) considered that the material filling in the spreite was transported downward from the overlying layer or sediment surface by the tracemaker activity. This is consistent with my interpretations for Tertiary *Zoophycos* from the Boso Peninsula and the Carboniferous specimens from the Hikoroichi Formation. However, Miller (1991) did not clarify whether or not the material in the spreite was of fecal origin. This is because these specimens lack the direct evidence, such as identifiable pellets. Furthermore, it might also be difficult to apply the feeding and excretory model based on the Boso Tertiary *Zoophycos* to the Devonian and Pennsylvanian specimens illustrated by Miller (1991) because of the presence of morphological and structural dissimilarities between them. Thus, it may not be easy to judge whether or not the material filling in the spreite of the Devonian and Pennsylvanian *Zoophycos* examined by Miller (1991) was of fecal origin.

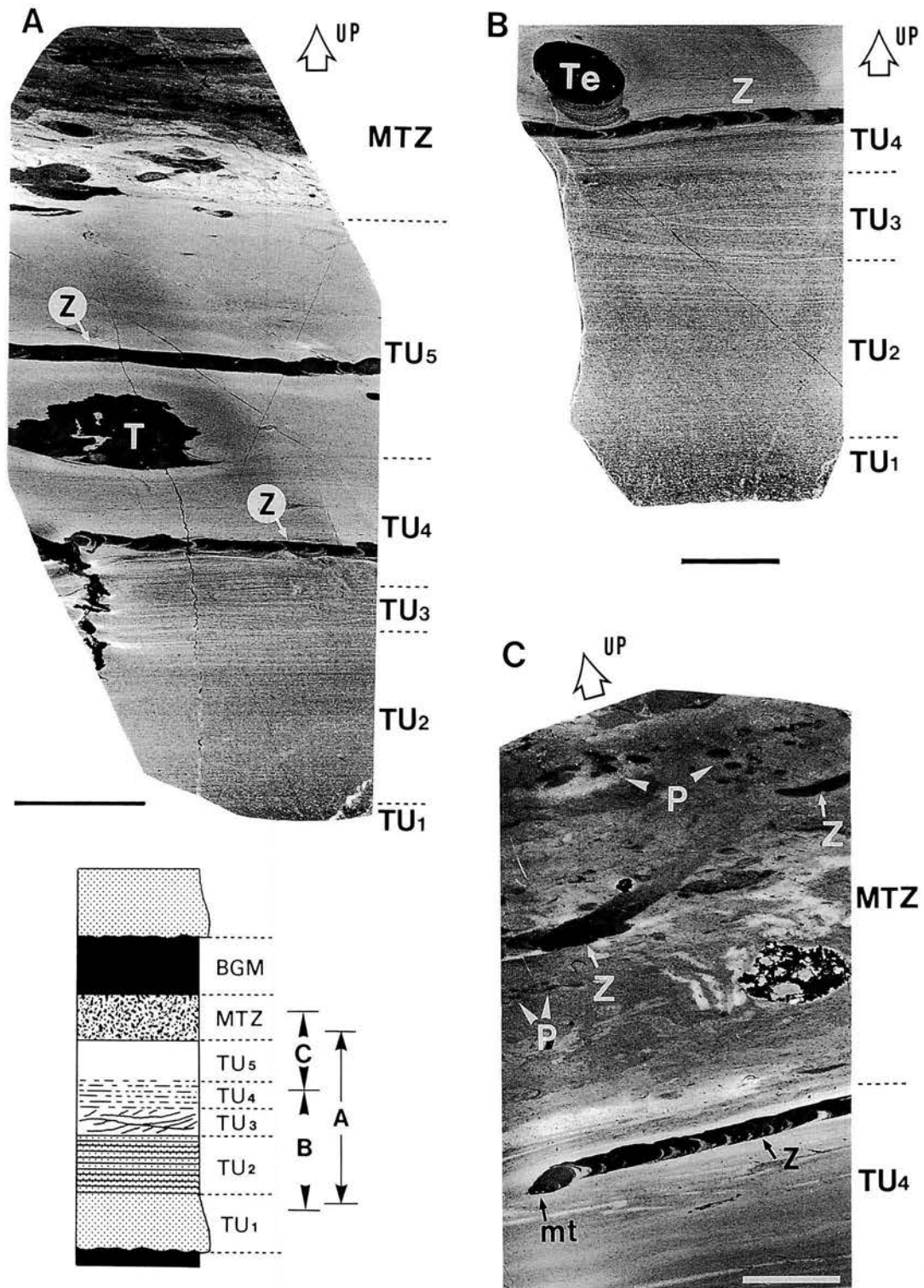


Figure 5. Specimens of the Hikoroichi *Zoophycos* on the polished surface of slabs. Note that the well-preserved, sharply defined *Zoophycos* spreiten (Z) are restricted to the lithological units in TU₄ and MTZ. Specimens A and C and specimen B were collected from the horizon ZB and ZA in Figure 3, respectively. Z: *Zoophycos*, T: *Thalassinoides*, Te: *Teichichnus rectus*, P: *Phycosiphon incertum*, mt: marginal tunnel. Scale bars = 2 cm (A), 1 cm (B, C).

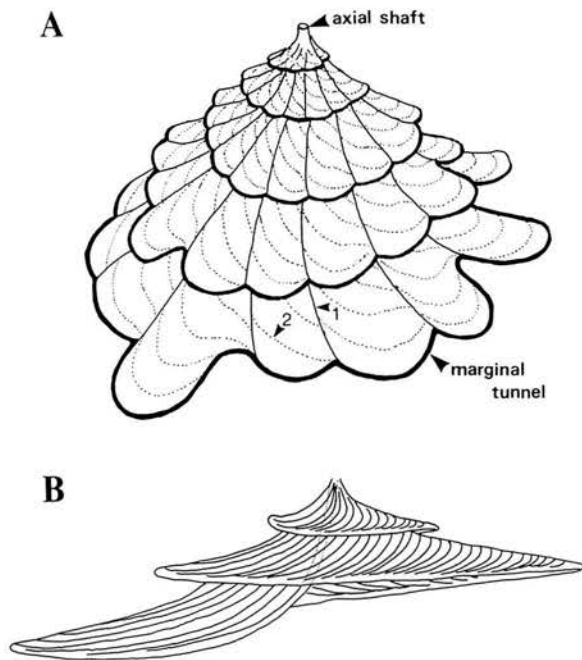


Figure 6. General morphology of the helicoidal form of *Zoophycos*. This form is characterized by a spirally coiled spreite around the axial shaft (A) or central portion (B). B is modified after Sarle (1906). Arrows 1 and 2 indicate major and minor lamellae, respectively.

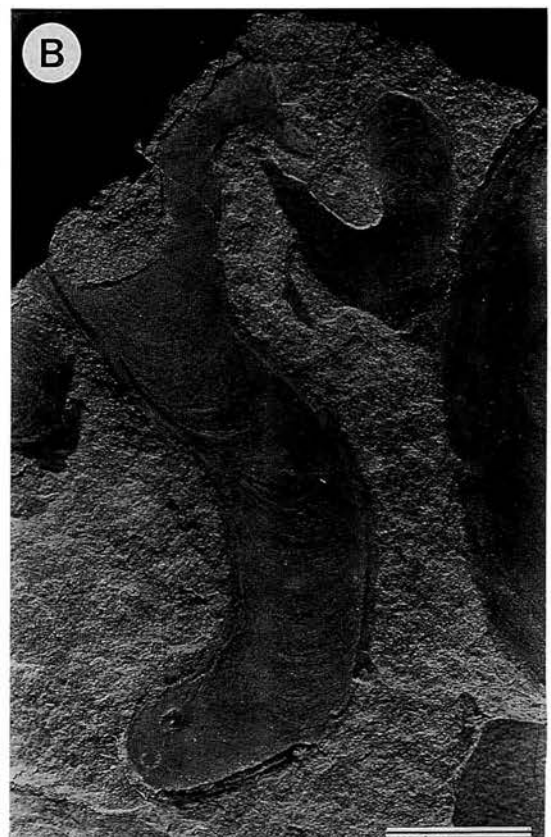
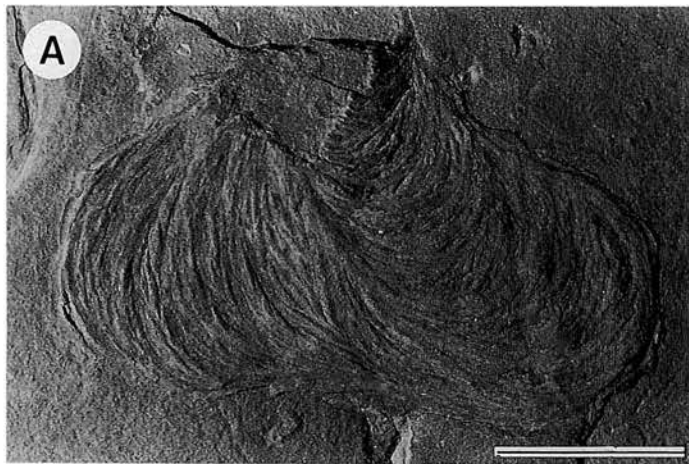


Figure 7. Plan view of the selected specimens of the planar forms of *Zoophycos* from the Mississippian Borden Formation distributed in the northeastern part of Kentucky, U.S.A. This form represents wide morphological variations ranging from the simple type (A) to the extremely lobate type (B, C). Scale bars = 4 cm (A), 3 cm (B, C).

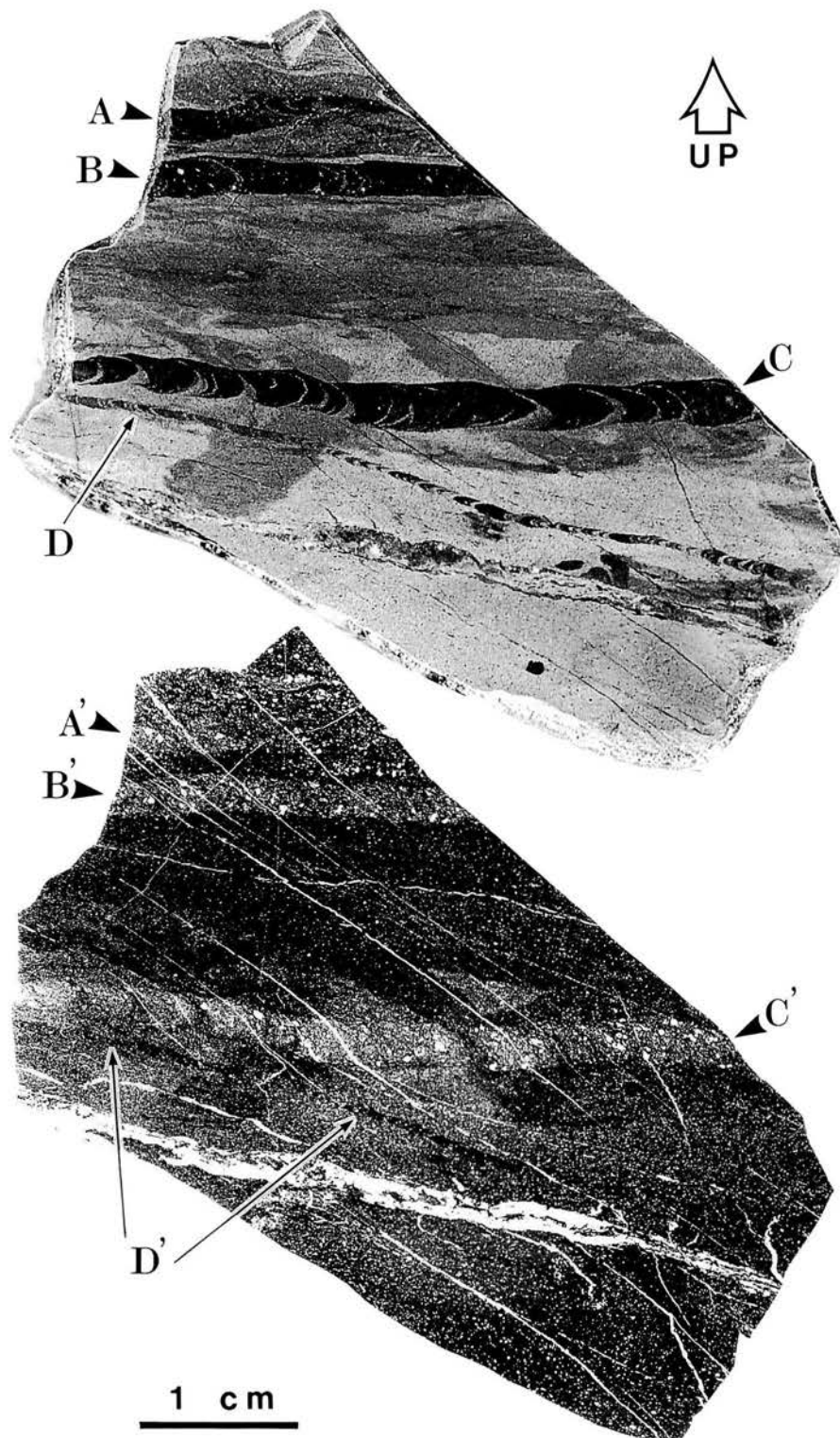


Figure 8. Cross-sectional view of the polished specimens of a *Zoophycos*-bearing slab (upper) and thin section of the same specimen (lower). Four spreiten (A-D, A'-D') are visible. Component material in the black fill in the spreite represents ill-sorted, coarser grains in comparison with those of the spreiten-bearing rock. This specimen was collected from the horizon ZB (see Figure 3).



Figure 9. Plan view of polished surface of the spreite of *Zoophycos* from the Hikoroichi Formation. Arrows 1 and 2 indicate major and minor lamellae, respectively. These lamellae, consisting of light host rock, stand out against the dark-colored spreite fill sediments. Scale bar=1 cm.

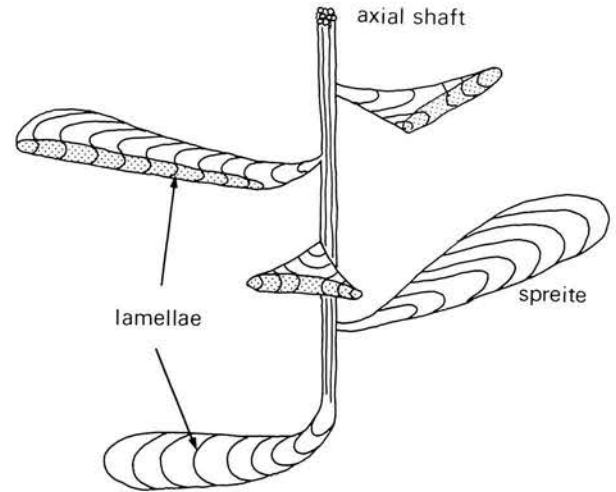


Figure 10. Three-dimensional morphology of the Pennsylvanian *Zoophycos* consisting of some axial shafts with planar spreiten. Meniscate lamellae are present in vertical section of the spreiten (stippled portion). Modified after Miller (1991, fig. 8).

As stressed in this paper, the morphological characteristics of the Japanese Paleozoic *Zoophycos* from the Hikoroichi Formation more closely resemble those of the Tertiary specimens in the Boso deep-sea sediments than do those of hitherto described Paleozoic specimens in North America (eg., Miller and Johnson, 1981; Chaplin, 1982; Marintsch and Finks, 1982; Miller, 1991). This fact demonstrates that the Hikoroichi *Zoophycos* has a different ethology from most Paleozoic *Zoophycos* occurring in shallow-water settings. Indeed, Miller (1991) interpreted wide morphological variations

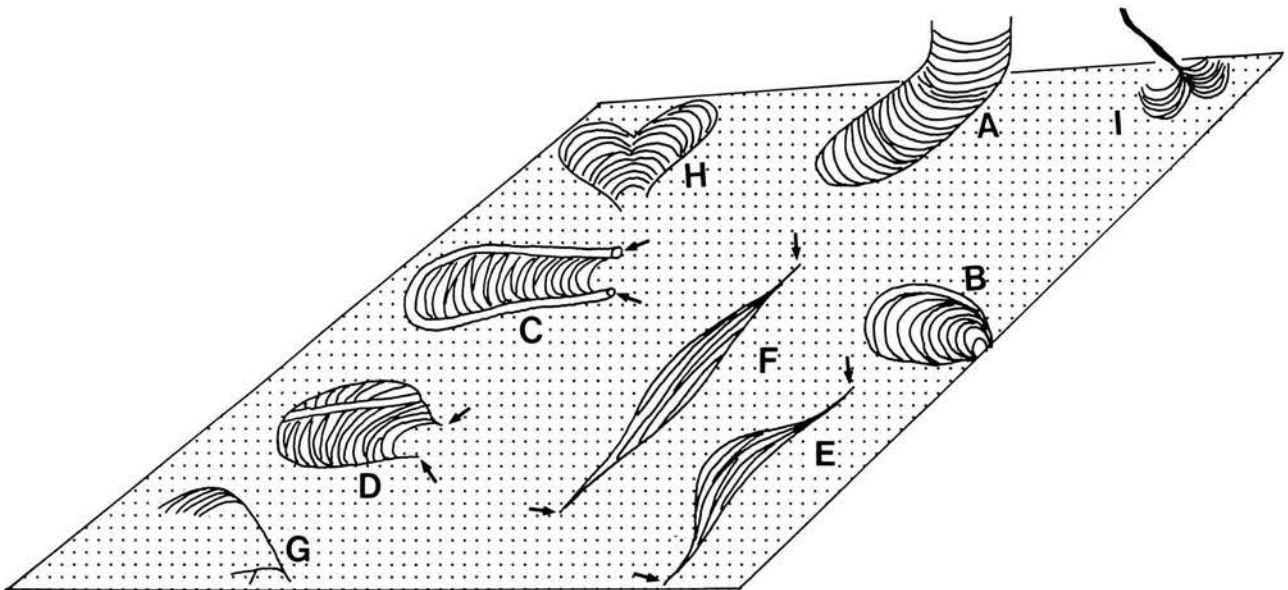


Figure 11. Morphological variations of *Zoophycos* occurring in Devonian storm deposits. Arrows indicate termination points. Modified after Miller (1991, fig. 6).

Table 1. Comparison of morphological characteristics between Tertiary and Lower Carboniferous *Zoophycos*. Morphological data on the North American Paleozoic *Zoophycos* obtained from the Mississippian and Pennsylvanian specimens of Kentucky and Tennessee.

Comparative <i>Zoophycos</i> specimens	type of form	type of lamellae	axial shaft	marginal tunnel	fecal pellet	regularity of internal structures
J.T. DS. <i>Zoophycos</i>	helicoidal	major & minor	Pr	Pr	Pr	high
J.P. <i>Zoophycos</i> (Hikoroichi <i>Zoophycos</i>)	helicoidal	major & minor	N	Pr	None	high
N.A.P. <i>Zoophycos</i>	helicoidal & planar	major >> minor	N>>Pr	N>>Pr	None	poor

N>>P indicates that both type is present but N is the major form.

T: Tertiary, DS: Deepsea, J: Japanese, P: Paleozoic, N.A.: North American
Pr: present, N: none

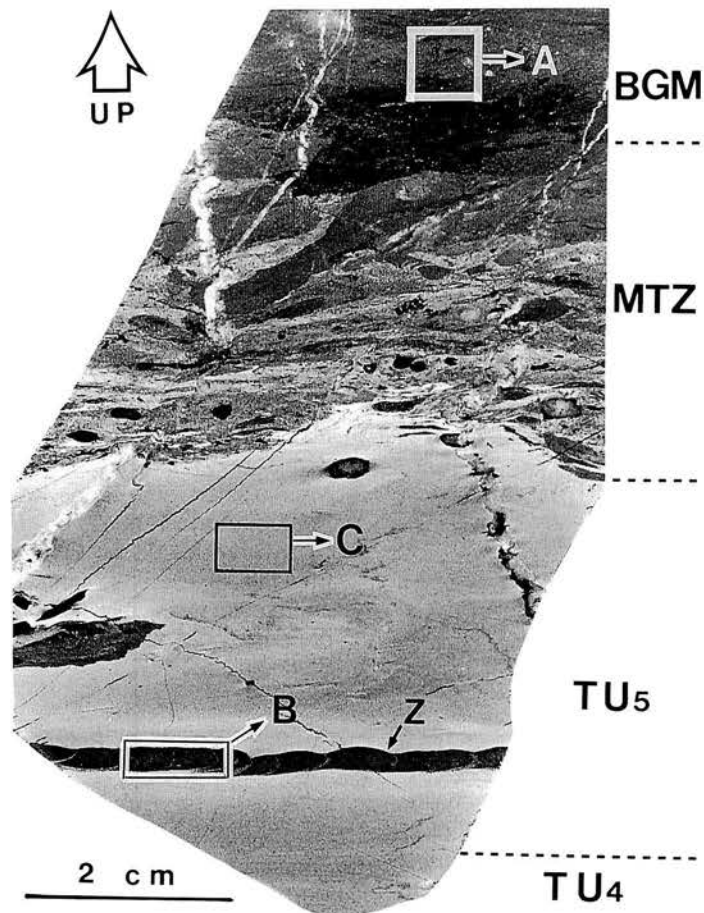


Figure 12. Cross-sectional feature of the typical *Zoophycos*-bearing rock. A to C indicate the sites where samples were taken for determination of the mineralogical composition by mean of x-ray diffractational analysis. This specimen was collected from the horizon ZB in Figure 3. A: intensely bioturbated black shale, B: spreite of *Zoophycos*, C: bluish-gray tuffaceous shale.

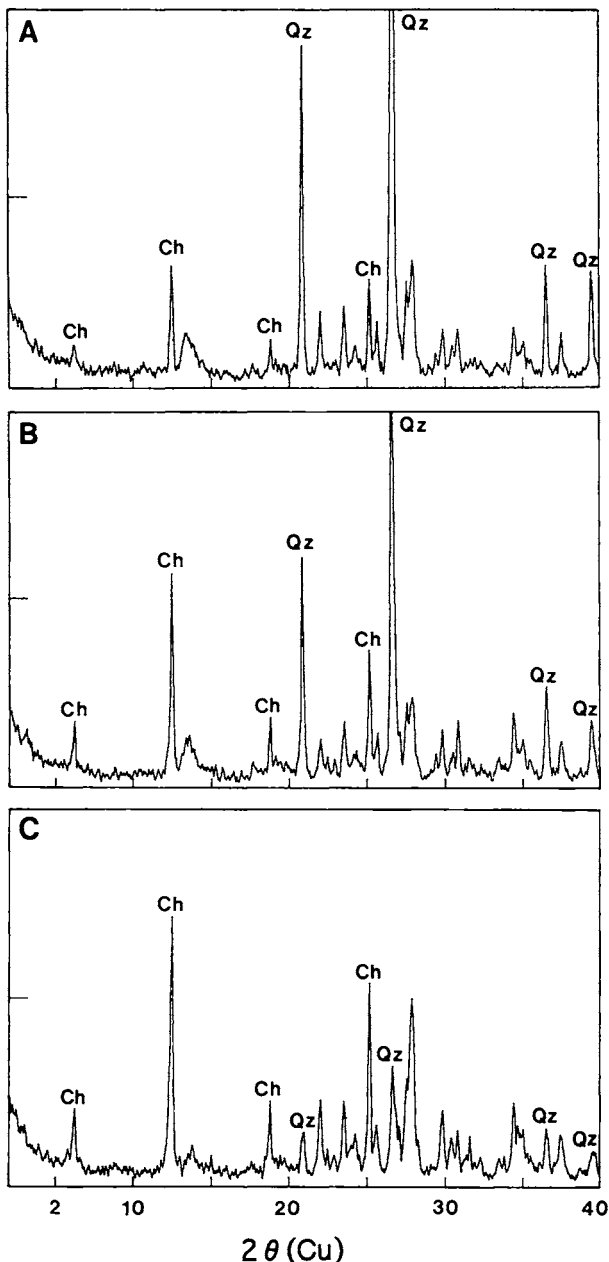


Figure 13. X-ray diffractograms of the bioturbated black shale (A), black material in *Zoophycos*-spreite (B), and *Zoophycos* spreite-bearing host rock (C). Ch: Chlorite, Qz: Quartz. See Figure 12 for analytical portions of A-C.

of *Zoophycos* in the Devonian and Pennsylvanian shallow-marine sediments as being due to the variability of the producer's behavior in response to changeable environmental conditions such as salinity, sedimentation rate, heterogeneity of food material on and/or within sediments. Following her interpretation that the *Zoophycos*-producers could switch their behavior in response to change in environmental conditions, the Hikoroichi specimens characterized by a three dimensional morphology and few morphological

variations might be a product of a specialized behavior of a producer that lived in a more stable habitat.

The inverted conveyor model, by which the *Zoophycos*-producer fed on sediment at the seafloor and deposited its own fecal matter deep in sediment, appears to explain the origin of the *Zoophycos* in the Hikoroichi Formation. However, implicit application of this feeding and excretory model to all specimens from different ages and localities is still debatable, because other workers believe that the producer of *Zoophycos* is an infaunal deposit-feeder, which ingested organic matter at a level deep within the sediment (eg., Wetzel, 1991; Ekdale and Lewis, 1991; Fu and Werner, 1994; Fu *et al.*, 1994), and/or that the *Zoophycos* structure might represent bacterial gardening by the producer (*sensus* Seilacher, 1977, 1990; Bromley, 1991). Apart from the works by Miller (1984, 1991), furthermore, little discussion has been given to the origin and significance of the morphological variation of the Paleozoic *Zoophycos*. Consequently, any comprehensive interpretation of the origin of *Zoophycos* based on many specimens from various depositional settings of different ages is needed not only to evaluate the utility and limitation of these models, but also to consider the evolution of feeding and excretory behavior of the *Zoophycos* animals.

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