LOWER CARBONIFEROUS *ZOOPHYCOS* FROM THE TOURNAI AREA (BELGIUM): ENVIRONMENTAL AND ETHOLOGIC SIGNIFICANCE

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ABSTRACT - The aim of this work is to describe and interpret well preserved Lower Carboniferous *Zoophycos* from Belgium. They are compared to other similar *Zoophycos* studied by the same authors from Jurassic and Lower Cretaceous from France. Finally, some general conclusions are proposed which are also supported by data from the literature. Lower Carboniferous deposits in the Tournai area (Belgium) are characterized by the abundance of well preserved *Zoophycos* previously described as *Spirophyton*. The upper unit of the Tournai Limestones, the Antoing Formation (Ivorian), was studied here. It is usually made of fine-grained carbonate mudstones or wackestones, occasionally passing to packstones. The paleoenvironmental setting is typical of the deep part of a carbonate ramp, with occasional storm deposition. The general organization of Tournaisian *Zoophycos* is the same as that seen in Jurassic and Lower Cretaceous specimens of southeastern France: a single open tube and a lamina with an upward helicoidal growth. This similar organization suggests a similar ethology for the corresponding tracemaker considered as a deep sediment feeder with an efficient mining program. The more simple morphology of the Tournaisian burrow system suggests that this program is less complex than for the Mesozoic equivalents. *Zoophycos* is best developed in fine-grained sediments. In opposition to the Jurassic examples of southeastern France, this sediment must have still been soft, never slightly firm, when colonized. In addition, the abundance of *Zoophycos* at the top of locally frequent storm deposits could indicate a fairly opportunistic behavior. Considering the above mentioned assumption, the increasing complexity of the morphology and the modification of the related ethology, a possible evolution from an r-strategy to a K-strategy is suggested for the *Zoophycos*-creating organism during geologic time.

KEYWORDS: *ZOOPHYCOS, SPIROPHYTON,* CARBONIFEROUS, PALEOECOLOGY, DEEP WATER, BELGIUM.

RÉSUMÉ - L'objectif de ce travail est de décrire et d'interpréter des *Zoophycos* très bien préservés du Carbonifère inférieur de Belgique. Ils sont comparés à d'autres *Zoophycos* semblables, étudiés par les mêmes auteurs et provenant du Jurassique et du Crétacé inférieur de France. Enfin, quelques conclusions d'ordre général sont proposées en s'appuyant aussi sur des données issues de la littérature. Les séries du Crétacé inférieur de la région de Tournai (Belgique) sont caractérisées par l'abondance de *Zoophycos* très bien conservés, précédemment décrits comme *Spirophyton.* Ce travail concerne l'unité supérieure des Calcaires de Tournai, la formation d'Antoing (Ivoirien). Elle est constituée de calcaires fins de type mudstone ou wackestone, passant éventuellement à des packstones. Le contexte paléoenvironnemental corrrespond à la partie profonde d'une rampe carbonatée montrant occasionellement des dépôts de tempête. L'organisation générale des *Zoophycos* tournaisiens est la même que celle des spécimens observés dans le Jurassique et le Crétacé inférieur du Sud-Est de la France: un tube simple ouvert et une lame montrant une croissance hélicoïdale vers le haut. Cette organisation commune suggère une éthologie semblable pour l'animal correspondant considéré comme un limivore profond doté d'un programme d'exploitation efficace. La morphologie un peu plus simple des terriers tournaisiens suggère que ce programme est moins complexe que pour les spécimens mésozoïques. Les *Zoophycos* sont plus développés dans les sédiments fins. Contrairement à ce qui a été observé dans le Sud-Est de la France, le sédiment devait être mou, et non déja légèrement ferme, au moment de la colonisation. De plus, l'abondance des *Zoophycos* au sommet des dépôts de tempêtes par ailleurs localement fréquents, pourrait indiquer un comportement assez opportuniste. En prenant en compte les considérations ci-dessus, la complexité croissante de la morphologie et la modification correspondante du comportement, il est suggéré une possible évolution d'une stratégie r vers une stratégie K pour le type d'organisme responsable de la formation des *Zoophycos* au cours des temps géologiques.

MOTS-CLÉS: *ZOOPHYCOS, SPIROPHYTON*, CARBONIFÈRE, PALÉOÉCOLOGIE, MILIEU PROFOND, BELGIQUE.

INTRODUCTION

Zoophycos is a common and complex trace fossil that has attracted much interest (Simpson 1970; Wetzel & Werner 1981; Ekdale 1985, 1988; Bottjer et al. 1988; Bromley 1990, 1991; Miller 1991; Ekdale & Lewis 1991; Kotake 1989, 1991, 1992, 1994; Gaillard & Olivero 1993; Olivero 1994; Olivero & Gaillard 1996). More detailed studies of *Zoophycos* and *Zoophycos*-bearing strata from various origin in space and time are still needed because many questions remain concerning the geometry of the burrow system, the nature and ethology of the trace-making animal, and the paleoenvironmental, mainly paleobathymetric, significance of the trace. Help in answering these questions may come from abundant well preserved *Zoophycos* in the Lower Carboniferous limestones of the Tournai area (southwestern Belgium).

In the Tournai area, the Carboniferous limestones, which are normally hidden by Mesozoic and Cenozoic cover, are uplifted along the Mélantois-Tournaisis Anticline and cut by the Escaut River and its tributaries (Fig. 1a,b). The studied exposures are three active quarries (Milieu, Lemay, and Antoing) and one old quarry (Prince's) in limestones of Ivorian (Upper Tournaisian) age lying in the axial zone of the anticline (Fig. 1c and appendix). More detailed data on the geologic setting are available in Camerman (1944), Mortelmans (1963, 1969), and Hennebert & Doremus (1997).

Despite a rich macrofauna, these rocks have proved difficult to correlate with other Lower Carboniferous sections in Belgium, principally because the foraminifera and conodonts necessary for modern biostratigraphic correlation are rare or absent. Moreover, in the Tournai area, the Ivorian is much thicker (more than 200 m) than its lateral equivalents (e.g., in the Dinant Synclinorium: 90 m at Yvoir and 100 m at Dinant) suggesting a deposition in deeper water.

The sequence is divided into two stratigraphic units: the Tournai Formation and the overlying Antoing Formation (Fig. 2) which are separated by a thin argillaceous marker probably of volcanic origin (the "Gras délit"). The Tournai Formation mainly consists of dark-micritic limestones of variable bioclastic content, cemented by microcrystalline silica. These limestones are generally only moderately argillaceous, except for the basal stratigraphic subunit (Crampon Member), which comprises the passage from the predominantly argillaceous rocks of the underlying Orient Formation. The Antoing Formation consists mainly of argillaceous, micritic limestones that are weakly bioclastic in the lower part and are also cemented by microcrystalline silica. Fine-grained detrital quartz is occasionally present.

Zoophycos occurs sporadically but is abundant only in the Antoing Formation (Fig. 2), from which it was first reported by Legrand (1948). Our study concerns the lower part of the Antoing Formation (mainly the Lower Calonne Member).

ICHNOLOGY OF THE *ZOOPHYCOS* - BEARING STRATA

DESCRIPTION OF *ZOOPHYCOS*

Well preserved specimens are often entirely exposed in the Antoing Formation. Therefore, the detailed in situ observation of many *Zoophycos*

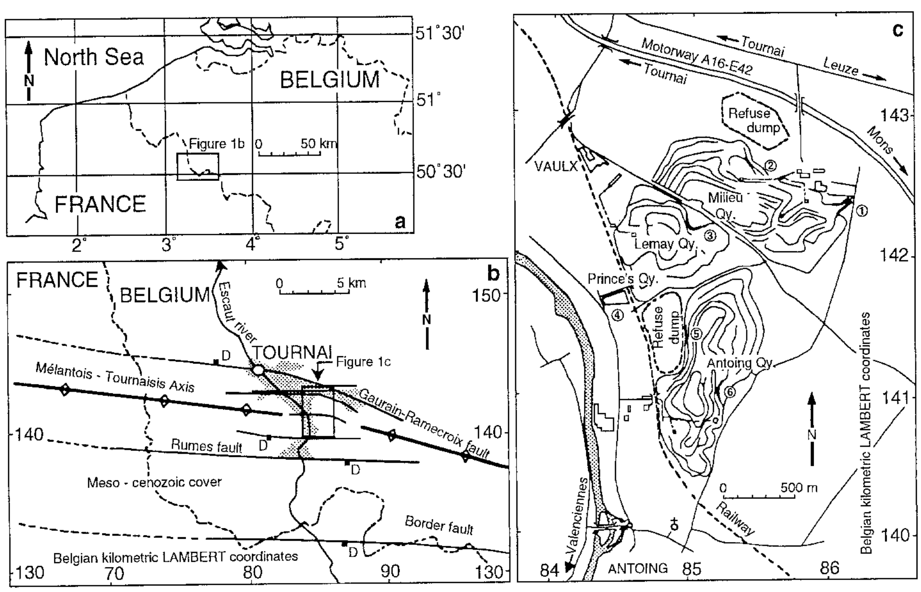


FIGURE 1 - **a.** Location of study area. **b.** Geologic setting of the Lower Carboniferous outcrops on the Mélantois-Tournaisis Anticline. The stippled areas correspond to outcrop of Tournaisian rocks. **c.** Location of the quarry sites (see appendix). ***a.*** *Situation de la région étudiée.* ***b.*** *Contexte géologique des affleurements du Carbonifère inférieur au droit de l'anticlinal du Mélantois-Tournaisis. Les zones grisées correspondent aux affleurements tournaisiens.* ***c.*** *Situation des sites étudiés dans les carrières (voir l'annexe).*

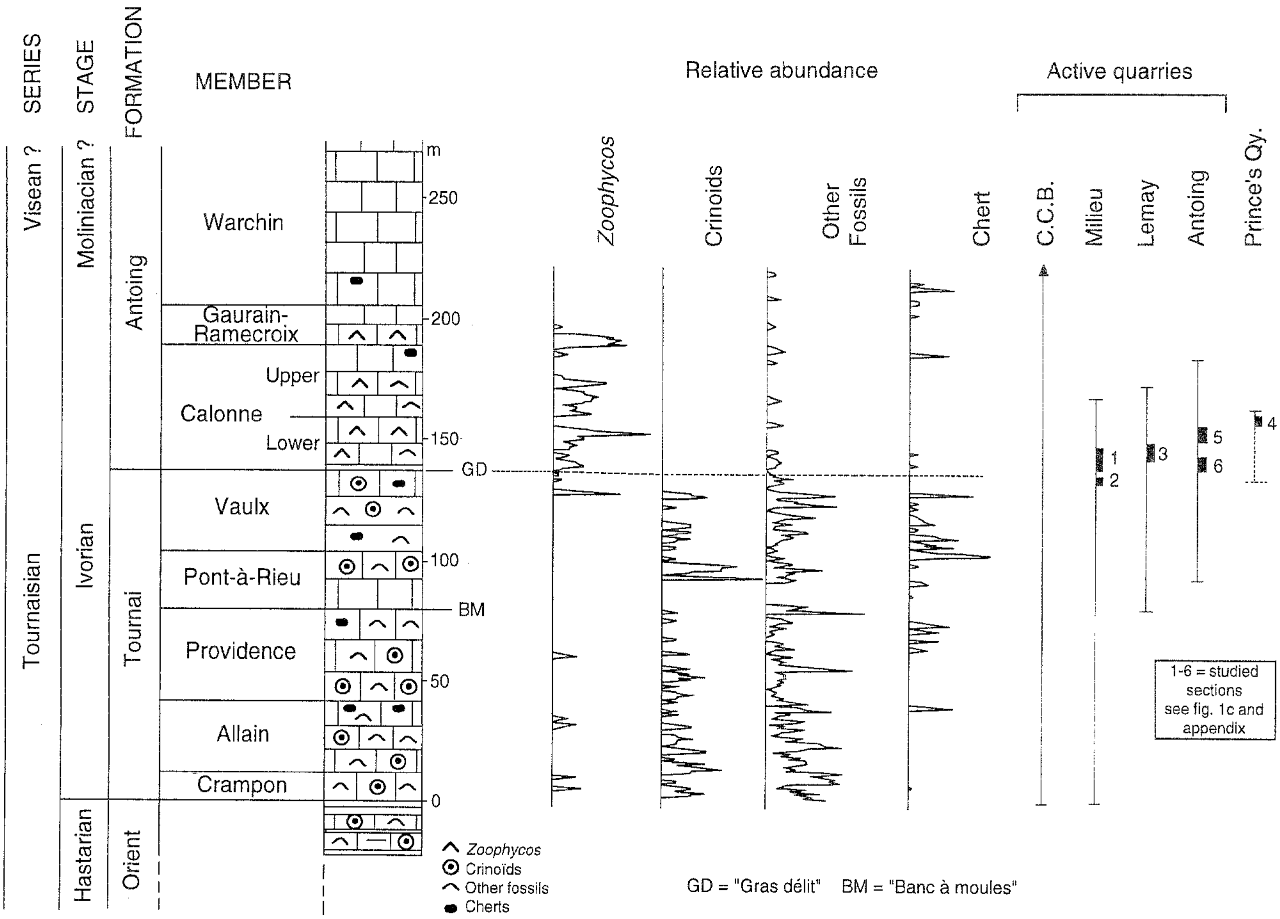
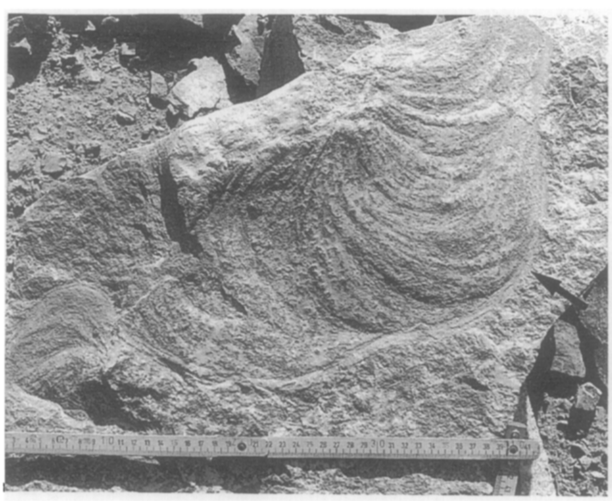


FIGURE 2 - Stratigraphic framework indicating the distribution of *Zoophycos* and other constituents of the Tournai Limestone (relative abundance after Mortelmans 1963). *Contexte stratigraphique montrant la répartition des* Zoophycos *et de quelques autres composants des Calcaires de Tournai (abondances relatives d'après Mortelmans 1963).*



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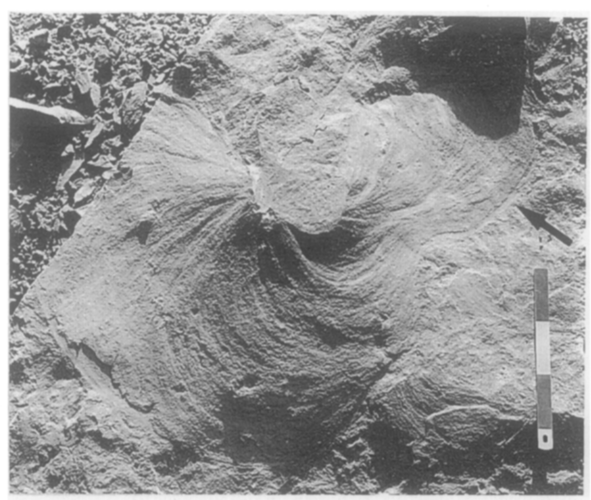

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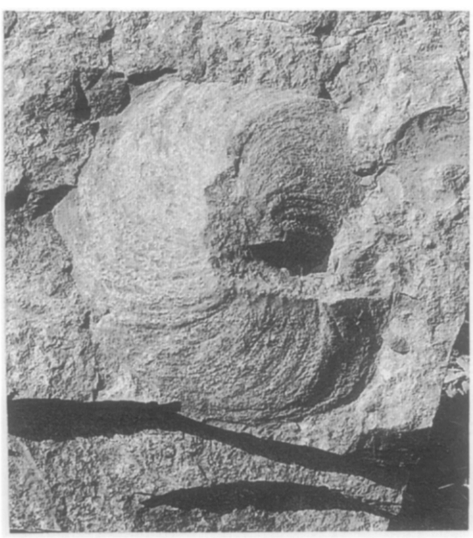
FIGURE 3 - **a.** Organization of the *Zoophycos* burrow system: the marginal tube (arrow) and, backwards, arched lamellae are clearly visible. East of Milieu Quarry. Scale in centimeters. **b.** Similar specimen but more lobate. Milieu Quarry. Scale = 15 cm. **a.** *Organisation d'un* Zoophycos: *le tube marginal (flèche) et, en arrière, les lamelles arquées sont nettement visibles. Est de la carrière du Milieu. Echelle en centimètres.* ***b.*** *Autre spécimen semblable, mais à contour plus lobé. Carrière du Milieu. Echelle = 15 cm.*

FIGURE 4 - Cross sectional view of *Zoophycos* with 3 visible whorls and a lamina becoming more horizontal in its upper part. East of Milieu Quarry. Hammer = 33 cm. *Vue en section verticale d'un* Zoophycos *montrant 3 tours d'enroulement et une lame de plus en plus horizontale dans sa partie sommitale. Est de la carrière du Milieu. Longueur du marteau = 33 cm.*

specimens allowed a precise description of the burrow system. The observed traces exhibit a growth pattern with a marginal tube corresponding to the external border of a lamina formed by numerous arched lamellae. Each lamella corresponds to a deformed, filled tube, which marks the previous position of the same single tunnel moving through the sediment. The marginal tube indicates the last position of this tunnel (Fig. 3). It is the only part of the burrow system which remained open during the life of the trace-maker. This spreite organization corresponds to the more classic constructional model for *Zoophycos* (Seilacher 1967a,b; Bromley & Ekdale 1984). However, the tube is not a true "U" form; it has only one opening at the seafloor, similar to the "J tube" model of Wetzel & Werner (1981) and to the model of Gaillard & Olivero (1993).

The lamina is spirally coiled around a vertical axis (never preserved as a tube) which is approximately perpendicular to bedding. Each whorl resembles a flattened cone with its apex pointing upwards. The diameter and degree of flattening of each successive whorl increases upwards (Fig. 4). The convexity of the lamellae, as demonstrated by the backfill structures visible in sections of the lamina, shows that the burrow system grew upwards (Fig. 5). The direction of coiling may be dextral or sinistral (Fig. 6). For example, of the 78 well preserved *Zoophycos* observed on the upper surface of a single bed in the Antoing quarry, 55% are dextral and 45% sinistral; they appear to be mixed at random. Measurement of the trace fossil is often difficult because many specimens cross one another. However, the diameter of the lamina generally ranges from 20 to 70 cm (maximum 85 cm), the diameter of the marginal tube ranges from 3 to10 mm and the total height of the trace ranges from 10 to 20 cm.

These *Zoophycos* clearly correspond to the constructional model of Gaillard & Olivero (1993) and are very similar to specimens from the Jurassic (Toarcian to Oxfordian - Olivero 1994; Olivero & Gaillard 1996) and Cretaceous (Berriasian to Hauterivian - Olivero 1996) of southeastern France.



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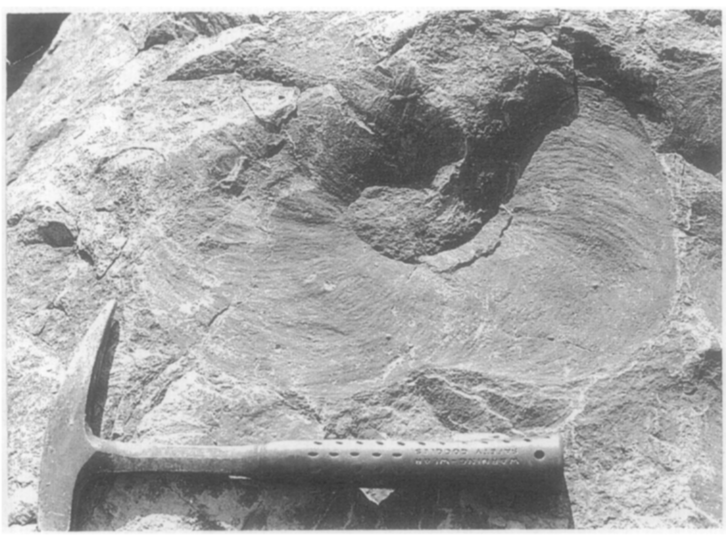

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FIGURE 5 - Two plan views of *Zoophycos* with upward growing lamina in a circular outline. **a.** Upper surface of a bed. East of Milieu Quarry. Magnification: the same as in fig. 5b. **b.** Lower surface of a bed. Lemay Quarry . Hammer = 33 cm. *Deux vues en plan de* Zoophycos *dégagés, à contour circulaire et montrant clairement la croissance de la trace vers le haut.* ***a.*** *Surface supérieure d'un banc. Est de la carrière du Milieu. L'échelle est la même que pour la fig. 5b.* **b.** *Surface inférieure d'un banc. Carrière Lemay. Longuer du*

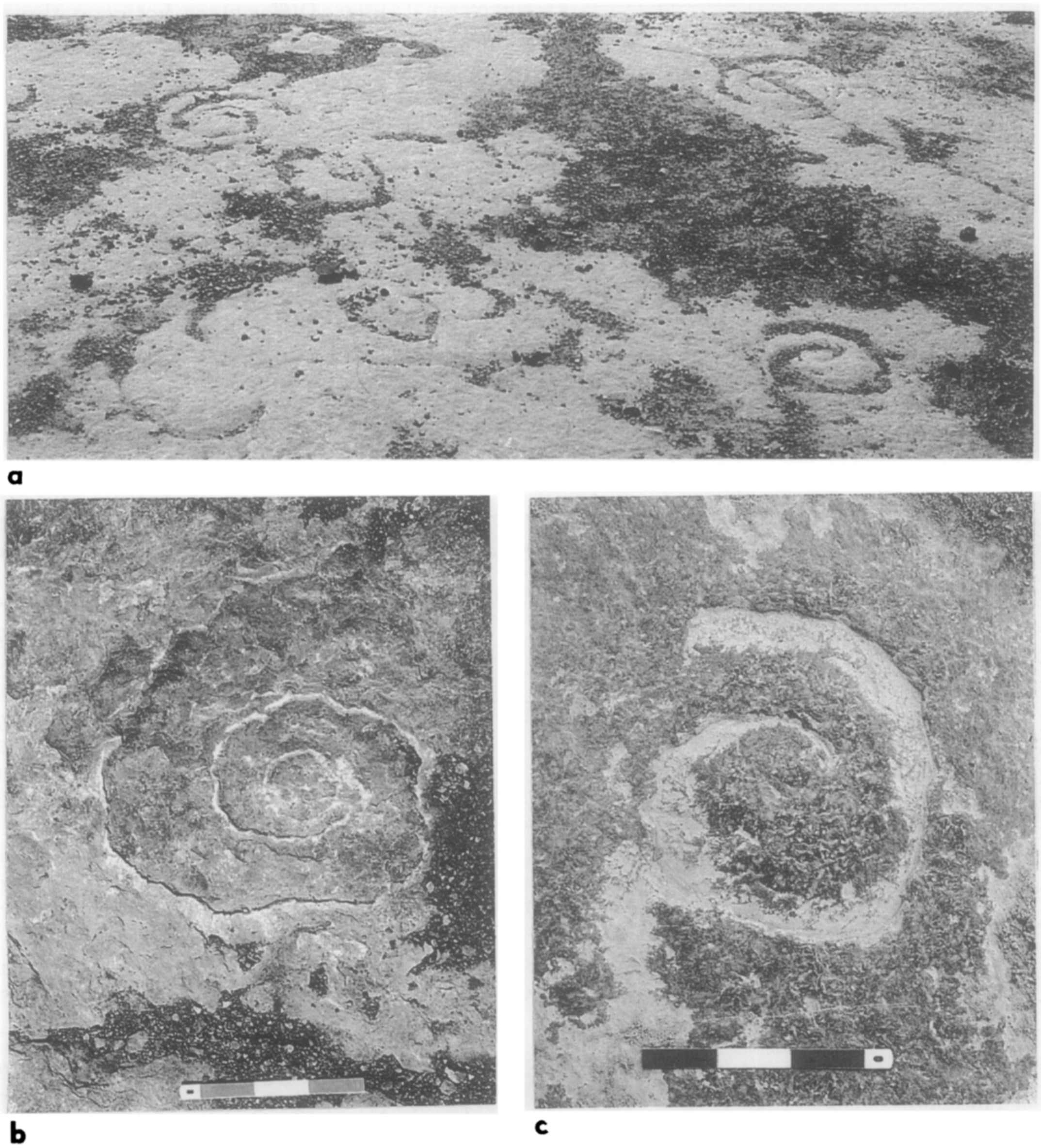

FIGURE 6 - Upper floor in the Antoing Quarry with eroded *Zoophycos* exposed on the surface. **a.** General view. **b.** Dextral *Zoophycos.* Scale = 15 cm. **c.** Sinistral *Zoophycos.* Scale = 15 cm. *Plancher supérieur de la carrière d'Antoing montrant des* Zoophycos *érodés à sa surface.* ***a.*** *Vue générale.* ***b.*** Zoophycos *à enroulement dextre. Echelle = 15 cm.* ***c.*** Zoophycos *à enroulement senestre. Echelle = 15 cm.*

The general organization of the trace is the same but, in detail, the pattern of the Mesozoic specimens is slightly more complex than that of the Carboniferous ones. In the Tournaisian material, secondary lamellae are not visible, perhaps because they are poorly preserved, but more probably because they are absent. The general outline of the trace is simple, being generally circular (Fig. 5) and only rarely exhibiting short lobes (Fig. 3b). In contrast, Mesozoic specimens usually exhibit highly lobate outlines.

TAXONOMIC IMPLICATIONS

Legrand (1948) identified the traces described here as *Spirophyton* and interpreted them as imprints of undetermined organisms. He wrongly considered this ichnogenus as synonymous with *Zoophycos.* The trace fossil *Spirophyton* is distinguishable from Zoophycos according to the difference in basic morphology and overall size. *Spirophyton* HALL, 1863 is mainly characterized by a large axial tube corresponding to the vertical part of a basic J tube. This tube turns down in the sediment as a result of downward development of the burrow system. In addition, the average diameter of the whole trace never exceeds 5-6 cm (Antun 1950; Simpson 1970; Häntzschel 1975; Miller 1991). These morphological characteristics are not consistant with those of the studied specimens. Therefore, we attribute them to *Zoophycos*

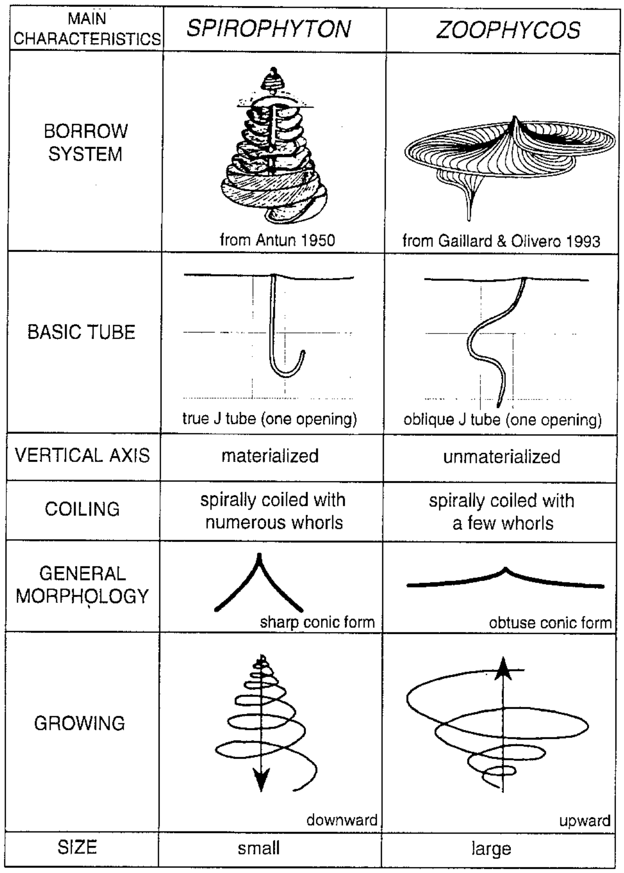

FIGURE 7 - Major differences between *Zoophycos* (studied specimens) and *Spirophyton*. *Principales différences entre Zoophycos (d'après les spécimens étudiés) et Spirophyton.*

MASSALONGO, 1855 although this complex ichnogenus (Häntzschel 1975; Olivero 1995) needs revision. Differences between the studied specimens and *Spirophyton* are summarized in figure 7.

ASSOCIATED TRACE FOSSILS

Zoophycos generally is the only well-preserved trace fossil occurring in the studied limestones. The *Zoophycos*-producing organism probably often formed a thriving population well adapted to live in the corresponding substrate. Other burrows sometimes occur faintly. Beds with abundant *Zoophycos* occasionally alternate with thin beds characterized by a dense, monospecific assemblage of small irregularly sinuous, unbranched tubes (2 - 4 mm in diameter, 2 - 5 cm long - Fig. 8) which could be *Helminthopsis* or, more probably, large *Phycosiphon* according to Wetzel & Bromley (1994, 1996). These traces are preferentially developed parallel to bedding and are clearly visible at the top of the bed. They are endichnial infilled burrows probably representing feeding structures. It is possible that these abundant *Phycosiphon*-like traces were formed rapidly following sudden influxes of organic material by opportunistic shallow burrowing organisms. These organisms may have been adapted to conditions unfavorable to the *Zoophycos*-producing organisms. This could be a lack of oxygenation because undiversified ichnofauna, small burrow size and slight penetration depth often reflect dysaerobic conditions (Savrda & Bottjer 1986, 1989, 1991; Savrda et al. 1991). However, *Chondrites,* which commonly thrives in poorly oxygenated environments, is absent here. Another explanation is the elimination of the *Zoophycos*-producing organisms resulting from a competition whith the *Phycosiphon*-producing organisms.

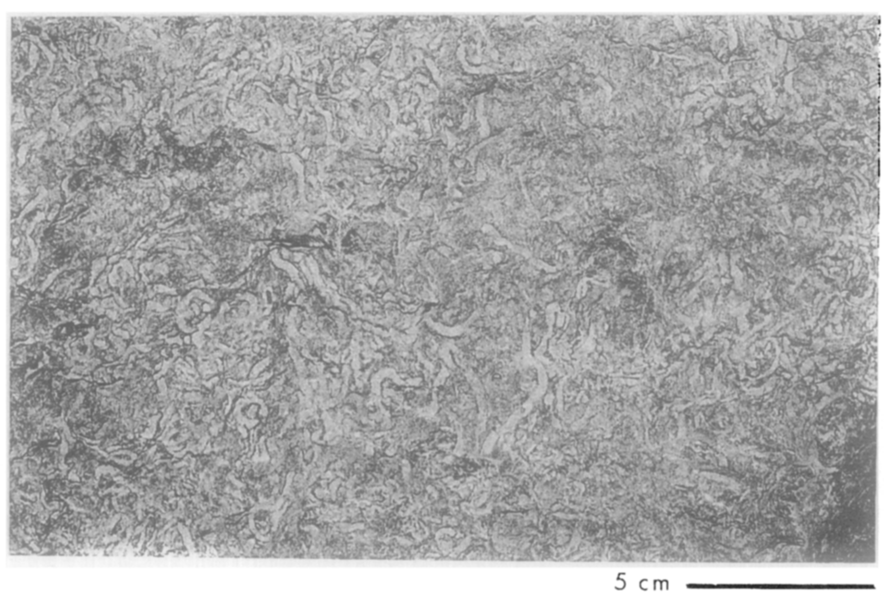

FIGURE 8 - Plan view of a bioturbated layer containing unidentified sinuous traces resembling *Helminthopsis* or *Phycosiphon* after Wetzel & Bromley (1994, 1996). East of Milieu Quarry. *Vue en plan d'un banc bioturbé contenant de nombreuses traces sinueuses ressemblant à* Helminthopsis, *ou, d'après les révisions récentes (Wetzel & Bromley 1994, 1996), à* Phycosiphon. *Est de la carrière du Milieu.*

DEPOSITIONAL ENVIRONMENT OF THE TOURNAISIAN *ZOOPHYCOS*

The limestones of the Tournai succession are mainly monotonous mudstones and wackestones with occasional packstones. Those of the *Zoophycos*-bearing Lower Calonne Member are characterized by dominance of lime mudstones (approx. 90%; Bindels 1995). Throughout the Tournai succession, the beds are generally about 30 cm thick, only rarely ranging up to 1 m. The relatively lime-rich and uncompacted cores of the beds pass upwards and downwards into thin argillaceous seams or shale beds via fissile zones with fitted fabrics and/or dissolution seams. Stylolites are not present. Although Bathurst (1987, 1991) proposed a mainly diagenetic origin for such features, they have been interpreted in terms of an oscillation between hemipelagic calcareous input and clay input (Hennebert 1996). Erosional bases, graded bedding and cross stratification are rarely observed. Thin (1 to 3 centimetres thick) shell beds or crinoidal layers occur and thin shell layers occasionally alternate with mudstone layers. These deposits accumulated in deep water on a carbonate ramp where the orbito-climatic signal is not significantly altered (see Hennebert,

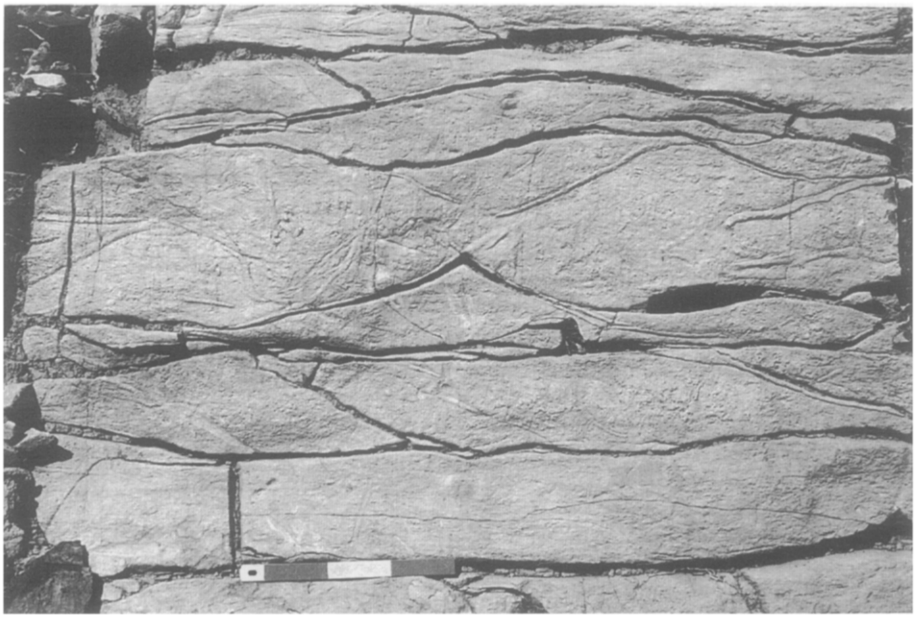

FIGURE 9 - *Regularly distributed* Zoophycos *in the fine-grained limestones. Scale = 15 cm. Prince's Quarry.* Zoophycos *régulièrement répartis dans des calcaires fins. Echelle = 15 cm. Carrière du Prince.*

FIGURE 10 - *Zoophycos* (small arrows) concentrated in the fine-grained upper part of a storm-generated succession (the arrow on the left shows the thickness of the storm unit). Northwest of Milieu Quarry. Zoophycos *(petites flèches) concentrés dans la partie supérieure finement grenue d'une séquence de tempête (la flèche de gauche montre l'épaisseur du dépôt de tempête). Nord-Ouest de la carrière du Milieu.*

1996 for discussion) and where storm influence was normally low (prominent storm deposits occur only locally: e.g. sites 2 and 4, Fig. 1).

There are distinct differences in the faunal assemblages between the Tournai and the overlying Antoing Formation. The former represents the nearly in situ accumulation of remains from a crinoid-bryozoan-brachiopod community with associated rugose and tabulate corals, gastropods, bivalves, nautiloids, and trilobites. In the Antoing Formation, the fauna is less abundant and consists mainly of small rugose corals, inarticulate brachiopods, small chonetids, and dissociated crinoid remains. Nautiloids and goniatites also occur at several levels. This change of fauna, together with other changes in allochems and a marked increase in the proportion of the fine fraction heralds the arrival of abundant *Zoophycos*. These are present in fine-grained beds (Fig. 9) and in the fine-grained upper part of the occasional storm deposits (Fig. 10).

In the Lower Calonne Member, where the abundant *Zoophycos* occur, petrographic study reveals the presence of sparse skeletal debris of crinoids, ostracods, brachiopods, echinoids, fenestrate bryozoans, sponge spicules, trilobites, the simple foraminifera *Earlandia*, and the problematic *Sphaerinvia* (Bindels 1995). There are no foraminiferans or algae. Because plurilocular foraminifera were abundant in the shallow and moderately agitated Early Carboniferous marine settings (Mamet & Skipp 1970; Mamet 1977; Gutschick & Sandberg 1983), their absence suggests relatively deep-water conditions (100 m or more). According to Mamet (1977), the Erlandiidae could survive in deeper water than that required by contemporaneous plurilocular foraminiferans. *Sphaerinvia* is an enigmatic calcitic micro-organism normally found in Upper Tournaisian deep environments (Vachard 1980; Hennebert & Lees 1991). Absence of algae suggests a subphotic depositional environment. A similar organism assemblage occurring in Lower Carboniferous rocks of southwest England was interpreted by Hennebert and Lees (1991) to reflect a distal location on the carbonate ramp. *Zoophycos* occurs in this assemblage (Hennebert & Lees 1985). In the Tournai area, the occurrence of *Zoophycos* in beds with storm deposits indicates deposition in an environment close to the storm wave base.

Paleozoic *Zoophycos* have been reported from various paleoenvironments with a wide paleobathymetric range (Bottjer et al. 1988; Bromley 1990; Ekdale 1985, 1988; Miller 1991; Miller & Johnson 1981; Pemberton et al. 1990). Concerning the studied Tournaisian *Zoophycos*, sedimentologic and paleontologic data corroborate the more common interpretation of a deep marine setting (Seilacher 1967a).

The dark micritic sediment, the presence of pyrite, and the relatively poor benthic fauna that characterize the Antoing Formation could reflect dysaerobic conditions. The occurrence of *Zoophycos* in poorly oxygenated sediments is well documented (Ekdale 1988; Savrda & Bottjer 1986, 1989, 1991; Savrda et al. 1991). Dysaerobic sediments could be burrowed by *Zoophycos*-creating organisms that maintained access to the bottom water. The upward (and not downward!) shifting of a simple tube would allow the burrowing activity to remain at a limited distance from the sediment/water interface, where oxygenation could occur (Gaillard & Olivero 1993; Olivero & Gaillard 1996). However, the relatively large diameter of the marginal tube of Tournaisian *Zoophycos* (up to 10 mm) does not reflect poorly oxygenated waters, as the size of burrows generally decreases with decreasing oxygenation. Therefore, the oxygen level of the bottom water was probably not dysaerobic.

Zoophycos are regularly distributed in homogenous fine-grained limestones of the Antoing Formation (Fig. 9). In contrast to the *Zoophycos* of Middle Jurassic of France, the Carboniferous *Zoophycos* are not preferentially concentrated at the top of beds, and they do not correspond to firmgrounds. This does not corroborate the idea that the sediment is burrowed by *Zoophycos* when becoming firmer, after a period of zero sedimentation (Gaillard & Olivero 1993; Olivero 1994, 1996; Olivero & Gaillard 1996). Here, the burrowed substrate probably remained a true softground.

ETHOLOGIC SIGNIFICANCE OF *ZOOPHYCOS*

ETHOLOGY OF THE TOURNAISIAN *ZOOPHYCOS* PRODUCER

The organization of the Tournaisian *Zoophycos* resembles that of Jurassic to Lower Cretaceous *Zoophycos* from southeastern France in that it exhibits a marginal tube with only one opening at the seafloor and a lamina with helicoidal upward growth. Thus, the main ethologic conclusions of Gaillard & Olivero (1993), Olivero (1994) and Olivero & Gaillard (1996) can be applied here.

The sediment filling the abandoned tunnels constituting the lamina is the same as the enclosing one. Therefore, there is no evidence of a fill originated from the sea floor deposit (as shown by Kotake 1989, 1991) and data are consistant with a fill originated from the deep sediment. Therefore, the organism was probably a deep-tier sediment feeder with a complex and efficient mining program.

The formation of lobate structures as seen in the Mesozoic examples, is not well developed here

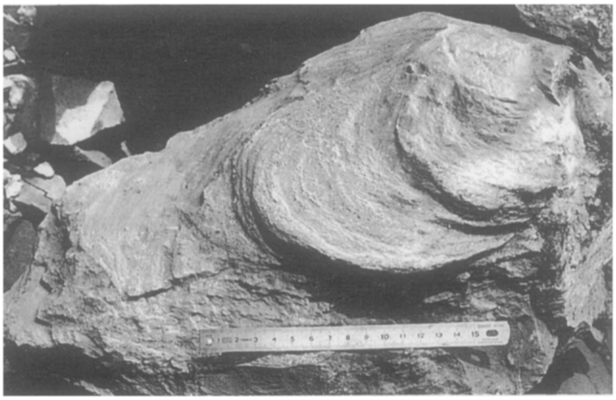

FIGURE 11 - Oblique view of *Zoophycos* exhibiting a lamina with two sharp deepening sectors. Antoing Quarry. *Vue oblique d'un* Zoophycos *dégagé montrant une lame avec deux stades d'approfondissement brutal. Carrière d'Antoing.*

(Fig. 3). Lobate structures of the Tournaisian specimens are deviations seemingly produced only to avoid obstacles such as shells. The lamina of some specimens exhibit undulations (Fig. 11) which disturb the general upward growth pattern and correspond to short periods of deepening in the feeding activity. This behavior probably allowed the animal to feed a longer time in a favorable substrate (Olivero & Gaillard 1996).

Zoophycos is abundant only in dark fine-grained limestones which clearly represented the more favorable substrate of the Tournai area. Here, the maximum density was reached (intensity 5 in the scale of Olivero 1994). Sometimes, neighbouring burrow systems interpenetrated one another (Fig. 9, 12), but some laminae growing at the same level only touched and turned around each other (Fig. 13). This may reflect competitive behavior resulting in maximum exploitation of the sediment.

When storm deposits occur in the Tournai limestones, their fine-grained upper part is systematically burrowed by *Zoophycos* (Fig. 10). Their lower part, which is not bioturbated, is characterized by a coarse-grained, graded unit with entire body fossils and bioclasts (rugose corals, brachiopods, crinoids, etc.) resting on an erosional surface. The *Zoophycos*-producing animal colonized the substrate after the deposition of the whole sequence, rarely penetrating down into the coarse-grained sediment. The colonization occurs even for frequent storm events and may indicate a relative opportunistic behavior. But, as the time interval between two storm-generated deposits is unknown, this hypothesis cannot be substantiated. A very similar occurrence was reported from the Lower Carboniferous of South Wales by Wu (1982). Other *Zoophycos* from various Paleozoic marine environments, which are shallower and characterized by environmental stress and fluctuations, were interpreted as burrows produced by opportunistic animals (Miller 1991).

GENERAL EVOLUTION OF BEHAVIOR OF THE ZOOPHYCOS-PRODUCER

These new data from the Tournaisian of Belgium, the numerous data from the Mesozoic of France reported by the present authors and reference to the literature allow some general considerations.

It is highly likely that a bathymetric shift of *Zoophycos* from shallow to deep marine environments occurred through time. Shallow-water occurrences are common during the Paleozoic, uncommon

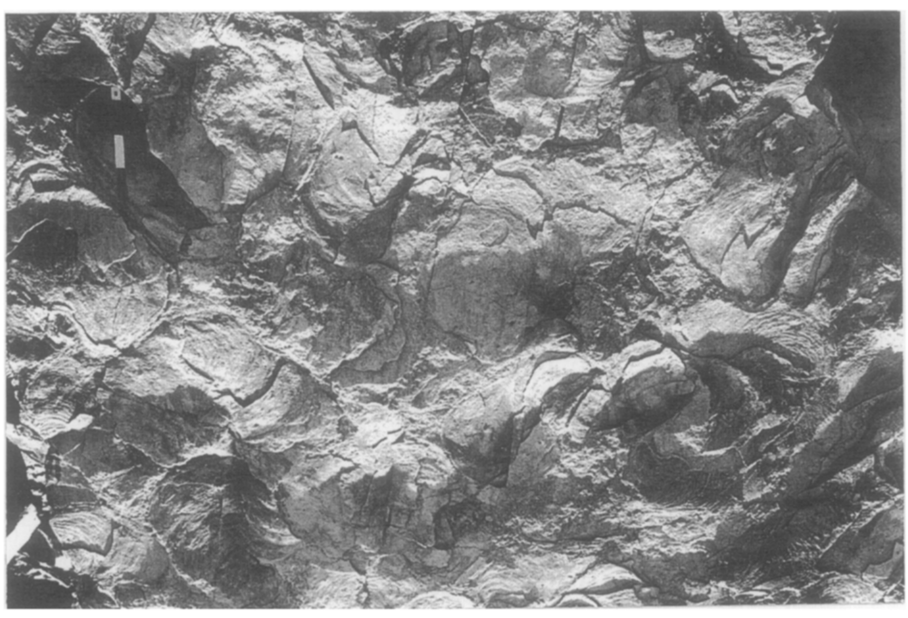

FIGURE 12 - *Top of a bed totally bioturbated by* Zoophycos *(degree 5 of the bioturbation intensity scale after Olivero 1994). Scale = 15 cm. Lemay Quarry. Sommet d'un banc totalement bioturbé par* Zoophycos *(degré 5 d'après l'échelle d'intensité de bioturbation proposée par Olivero 1994). Echelle = 15 cm. Carrière Lemay.*

FIGURE 13 - Three contemporaneous or penecontemporaneous *Zoophycos* arranged for the maximum exploitation of the sediment. The middle and the right specimens clearly avoid each other. Scale = 15 cm. Antoing Quarry. *Trois* Zoophycos *contemporains ou sub-contemporains disposés pour une exploitation optimale du sédiment. Les spécimens du centre et de droite s'évitent clairement. Echelle = 15 cm. Carrière d'Antoing.*

during the Mesozoic, and absent during the Cenozoic times when *Zoophycos* apparently was exclusively a deep-sea ichnogenus (Bottjer et al. 1988; Ekdale 1988; Gaillard 1992; Miller 1991; Miller & Johnson 1981). Competition from other burrowers was less important during the Paleozoic. Later *Zoophycos* could have been progressively eliminated from shallower marine environments by more efficient competitors. However, relatively deep water Paleozoic examples do occur, as the present example shows.

The above mentioned environmental shift of *Zoophycos* is probably accompanied by a progressive specialization of the trace making organism. Increasing morphologic complexity of *Zoophycos* through time possibly illustrates the increasing complexity of the mining program of a similar infaunal organism. This evolution is clear from the late Paleozoic to the late Mesozoic: as shown in this paper, Middle Jurassic *Zoophycos* differ from Lower Carboniferous ones in the presence of more lobate laminae and by the development of well preserved secondary lamellae, which probably correspond to a more efficient strategy for sediment exploitation (Gaillard & Olivero 1993; Olivero 1994; Olivero & Gaillard 1996). Cenozoic *Zoophycos* are even more complex in organization (Venzo 1950; Lewis 1970; Bellotti & Valeri 1976; Ekdale & Lewis 1991). The similar evolution of *Zoophycos* is suggested by Seilacher (1986) from Triassic to Tertiary.

The present work suggests that Tournaisian *Zoophycos* could be produced by less specialized organisms than their Middle Jurassic equivalents. In general, the simple *Zoophycos* known from various Paleozoic environments may have been produced by cosmopolitan and more opportunistic organisms, whereas the complex Cenozoic forms, which are restricted to deep sea environments, may have been produced by specialized organisms. This could indicate a progressive shift to a K-selected strategy by the *Zoophycos*-producing organism.

SUMMARY AND CONCLUSIONS

Certain levels in the Antoing Formation of the Tournai area contain abundant *Zoophycos*, previously described as *Spirophyton*. The significant characteristics of these *Zoophycos* are (1) upward helicoidal growth and (2) the presence of a marginal tube with only one opening on the sea floor. This morphological organization corresponds to the constructional model proposed by Gaillard & Olivero (1993) for Mesozoic specimens from southeastern France but the general form of the Tournaisian specimens is simpler, lacking complex lobate structures. The trace maker was a deep-tier sediment feeder with a mining program that became increasingly complex through the Phanerozoic. Tournaisian *Zoophycos* occurred in low-energy environments on a deep carbonate ramp, near the storm wave base and probably in the subphotic zone. This interpretation is based upon: (1) dominant well stratified micritic deposits, (2) occasional storm deposits, (3) relative scarcity of benthic animals, and (4) absence of photosynthetic organisms. *Zoophycos* always colonized softground substrates and developed best in fine-grained limestones. However, the fact that they also occur in the upper fine-grained part of probably frequent storm deposits may indicate a more opportunistic type of behavior than that of some Mesozoic *Zoophycos*.

Considering also data from the literature, a general shift from a r-selected strategy to a K-selected strategy is possible during geologic time.

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APPENDIX

LOCATION OF THE STUDY SITES. *SITUATION DES GISEMENTS ÉTUDIÉS*

Site 1. Milieu Quarry. NE end of the quarry, 230 m SE from the staff building. Ramp down to the first bench. Levels from 4 to 12 m above the "Gras délit". Belgian kilometric LAMBERT coordinates (East-North): 86.04-142.33. *Site 1. Carrière du Milieu. Extrémité nord-est de la carrière, 230 m au Sud-Est des bureaux. Rampe descendant vers le premier palier. Niveaux situés de 4 à 12 m au dessus du "Gras délit". Coordonnées kilométriques LAMBERT belges (Est-Nord): 86.04-142.33.*

Site 2. Milieu Quarry. NW part of the quarry, 100 m SW from the weighting station. 180 m North from the G2 crusher. Just below the "Gras délit". Belgian LAMBERT coord.: 85.38-142.70. *Site 2. Carrière du Milieu. Partie nord-ouest de la carrière, 100 m au Sud-Ouest de la station de pesage. 180 m au Nord du concasseur G2. Juste en dessous du "Gras délit". Coordonnées: 85.38-142.70.*

Site 3. Lemay Quarry. NE face of the quarry, 50 to 100 m SW of the old road from Vaulx to the "N-D au Bois" chapel. Levels from 8 to 14 m above the "Gras délit". Belgian LAMBERT coord.: 85.00-142.24. *Site 3. Carrière Lemay. Front nord-est de la carrière, 50 à 100 m au Sud-Ouest de l'ancien chemin de Vaulx à la chapelle "N-D au Bois". Niveaux situés de 8 à 14 m au dessus du "Gras délit". Coordonnés: 85.00-142.24.*

Site 4. Old Prince's Quarry. 50 to 100 m NE from the road Antoing-Vaulx. At the top of the North face of the quarry. Levels situated about 2 m above the top of the Vignobles Member lentil (about the summit of the Lower Calonne Member in the normal sequence). Belgian LAMBERT coord.: 84.39-141.72. *Site 4. Ancienne carrière du Prince. 50 à 100 m au Nord-Est de la route Antoing-Vaulx. Sommet du front nord de la carrière. Niveaux situés environ 2 m au dessus du sommet du corps lenticulaire de Vignobles (près du sommet du membre inférieur de Calonne). Coordonnées: 84.39-141.72.*

Site 5. Antoing Quarry (Cimescaut). NW part of the quarry. Below the topographic reference stick (borne) B2. Blocks fell from levels situated at about 16 to 20 m above the "Gras délit". Belgian LAMBERT coord.: 85.00-141.52. *Site 5. Carrière d'Antoing (Cimescaut). Partie nord-ouest de la carrière. En dessous de la borne topographique B2. Blocs éboulés provenant de niveaux situés à environ 16 à 20 m au dessus du "Gras délit". Coordonnées: 85.00-141.52.*

Site 6. Antoing Quarry (Cimescaut). East face of the quarry. 320 m North of the primary gyratory crusher. Levels from 4 to 8 m above the "Gras délit". Belgian LAMBERT coord.: 85.25-141.15. *Site 6. Carrière d'Antoing (Cimescaut). Front est de la carrière. 320 m au Nord du concasseur primaire giratoire. Niveaux situés 4 à 8 m au dessus du "Gras délit". Coordonnées: 85.25-141.15.*

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