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Structure and function of large, lobed *Zoophycos*, Pliocene of Rhodes, Greece

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Abstract

In the Kolymbia limestone facies (upper Pliocene) of the Rhodes Formation of Rhodes, Greece, a study was made of a large, spiral form of *Zoophycos*, named herein *Zoophycos rhodensis*. In the small bay south of Cape Vagia, two individuals were excavated and dissected while several more were serially sectioned in a vertical plane. The upper parts of the *Zoophycos* were missing through modern beach erosion, but in one individual the two lowest whorls were almost completely exposed. These comprised a skirt-like zone of spreite surrounded by a zone of 63 marginal lobes. The diameter of the trace fossils was about 1 m. Vertical sections demonstrated that the spreiten were composed of material advected downward from a higher horizon, indicating that the spreite was produced nearly 1 m below the sea floor. The skirt-like zone of the spreite was constructed of sigmoidal minor lamellae in bundles separated by major lamellae. The radiating major lamellae are not replaced by ridges such as is the case in many other lobed, spiral *Zoophycos*. The marginal tube and, to a lesser extent, the spreite are mineralised with an oxidised iron mineral, probably once pyrite. The marginal tube is completely filled with sediment and shows no signs of collapse or compaction. This is taken to indicate active backfilling, and that the operative burrow was thus J-shaped and not U-shaped. The two zones of the spreite are considered to represent two different modes of behaviour. The skirt-like zone probably represents deposit feeding. The mineralised marginal tube and lobes possibly represent sulphide wells connected with chemosymbiosis between the trace-making animal and sulphide-oxidising bacteria.

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Keywords: *Zoophycos*; trace fossils; Pliocene; Greece; deposit feeding; chemosymbiosis

1. Introduction

Spreite trace fossils of the Group *Zoophycos* (Uchman, 1995) are very variable in morphology. They range from simple, isolated spreite lobes (Miller, 1991) to highly complex spiral structures. Several ichnogenic names are available for this array of forms, but as the necessary revision has yet to be undertaken, the ichnogenus *Zoophycos* will be used for the material published herein.

The spiral forms may reach diameters exceeding 1 m. Study of such large structures is usually hindered by difficulty of observation within, and ex-
traction from, the rock matrix. Bedding-plane exposures tend to be far from complete and vertical cross-sections tell little of the overall construction. However, in recent years several advances have been made in our understanding of these complicated trace fossils and their ethological interpretation (e.g., Lewis, 1970; Kotake, 1989; Bromley, 1991; Ekdale and Lewis, 1991; Olivero, 1994; Bromley et al., 1999). Nevertheless, several of the many different types of Zoophycos remain little known. This article presents a close look at the structure of a multi-lobed spiral form from the Upper Pliocene of Rhodes and discusses the possible function of the trace fossil. Multi-lobed Zoophycos appear to be characteristic of the late Palaeogene and Neogene (Seilacher, 1986; Chamberlain, 2000).

2. Location and geological setting

At Cape Vagia, near the village of Kolymbia, the basement is composed of the slightly metamorphic Salakos limestone (Mutti et al., 1970). This limestone was karstified during an Upper Miocene to Upper Pliocene period of subaerial exposure. The karst surface is overlain by Upper Pliocene to Pleistocene marine sediments (Lovlie et al., 1989; Moissette and Spjeldnæs, 1995; Hanken et al., 1996; Spjeldnæs and Moissette, 1997; Kovacs and Spjeldnæs, 1999). The most complete geological record of these young deposits of the Rhodes Formation is preserved in a topographic depression in the underlying karst landscape southwest of Cape Vagia (Fig. 1), and a composite profile of the succession is shown in Fig. 2.

The oldest marine sediments above the Pliocene karst surface consist of shallow-water carbonate deposits, the Haraki limestone. This facies is only patchily preserved owing to subaerial exposure and karstification before renewed deposition of the overlying, Kolymbia, limestone (Ronholt, 1996; Hanken et al., 1996). The Pliocene karst surface is thus overlain elsewhere at the locality by the Kolymbia limestone.

The lower part of the Kolymbia limestone is characterised by shallow-water faunas, but these are progressively replaced upward by deeper-water forms, indicating a bathymetric deepening. According to the terminology of Kendall and Schlager (1981), the Kolymbia limestone represents a start-up phase where carbonate accumulation lagged behind the relative rise in sea level. As the water depth increased, there was a gradual decrease in carbonate production and a transition to deposition of fine-grained terrigenous sediments, the Lindos Bay clay.

The transition between the Kolymbia limestone and the Lindos Bay clay is gradational over a few centimetres and the boundary is placed where the carbonate content falls below 50%. The clastic material in the Lindos Bay clay is dominated by clay and silt fractions with a grain size resembling that of the deep-water Plio–Pleistocene deposits of the Eastern Mediterranean (cf. Kidd, 1978).

Polarity stratigraphy suggests that deposition of the Kolymbia limestone commenced at the end of the Gilbert Chron and that the Pliocene/Pleistocene boundary is about 6 m above the base of the Lindos Bay clay (Lovlie et al., 1989). Deposition of the Lindos Bay clay ended probably during Late Brunhes. On the basis of known bathymetric ranges of extant bryozoan species, Moissette and Spjeldnæs (1995) showed that the water depth was 300–500 m for the upper part of the Kolymbia limestone at Cape Vagia. The transgression reached its maximum (at least 600 m higher than at present) just before the Pliocene/Pleistocene boundary and was followed by a very slow, gradual regression.

The ichnogenus Zoophycos is locally abundant at certain horizons in the carbonate-rich silty clay of the upper bathyal Lindos Bay clay facies. This is the case, for example, at the stratotype locality north of Lindos. Although the trace fossil is seen abundantly in cross-section in the Lindos Bay clay, it has not been possible to discern its three-dimensional structure in this facies. However, at the locality on the foreshore of the small bay on the south side of Cape Vagia, Zoophycos also occurs in the uppermost part of the Kolymbia limestone. It is this occurrence south of Cape Vagia that is the concern of this paper, because in this facies it was possible to dissect the trace fossil and examine it in three dimensions.
Fig. 1. Locality map indicating the site of the study.
3. Material and methods

3.1. Detecting suitable trace fossils

*Zoophycos* occurs at several levels within the uppermost metre of the little-consolidated Kolymbia limestone. The trace fossil is locally abundant and in the wet season (November–April) is seen in nearly horizontal cross-sections on the gently sloping exposure surfaces (Fig. 3). Two criteria were essential in making a choice of specimens for dissection.

1. Individuals should be selected that were as complete as possible. That illustrated in Fig. 3 has lost too much to erosion. Unfortunately, the shaft could not be identified in horizontal section, so search was made for the highest identifiable section of the spreite.

2. Successful dissection was limited to individuals that occurred in the highest level of the Kolymbia limestone, about 1 m below the base of the Lindos Bay clay. These individuals were lightly mineralised by iron impregnation, suggesting oxidised pyrite, unlike the *Zoophycos* occurring immediately below (Fig. 3) and in the Lindos Bay clay. This mineralisation caused sufficient hardening of the trace fossil relative to its matrix to allow its dissection.

Two individuals were found that answered these requirements, and it was possible to dissect out the large trace fossils whorl by whorl and to study them in detail. The whole spreite had a slightly iron-stained discoloration, but certain la-

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Fig. 2. Lithological log at the site in the bay south of Cape Vagia, indicating the stratigraphic occurrence of the *Zoophycos*.

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Fig. 3. The modern erosion surface showing the exposure of a *Zoophycos* at the study site. The section in the upper part of the Kolymbia limestone is slightly oblique to the horizontal plane, and shows the three lowest whorls (arrows).
mellae of the spreite and most of the marginal tube had a strong impregnation of a rust-like substance.

Choosing brushes having nylon bristles hard enough to remove the matrix but softer than the iron mineral, and washing with copious amounts of seawater, the preserved parts of the trace fossils could be exposed almost in their entirety. It

Fig. 4. Zoophycos, specimen I. (A) Photographed in shadow (of a parasol). Note the slight grooves marking the major lamellae. (B) Numbering of the lobes.
should be noted, however, that the upper portions were not recovered because of the recent fore-
shore erosion mentioned above. The shaft and uppermost whorl or whorls were thus missing.

As the trace fossil has a multi-whorled struc-
ture, the remaining parts of the trace fossil could
not be exposed completely at any one time, but
had to be dissected whorl by whorl in order to
reveal the deeper parts. Exposing the two fairly
complete Zoophycos that were dissected, each oc-
upied about 170 person-hours. Several more in-
dividuals were serially sectioned in a vertical plane
so that the two sources of information could be
correlated.

4. Description

The two dissected Zoophycos specimens are
numbered herein Specimen I (worked on in May
1991) and Specimen II (April–May 1992). The
general characteristics of the two specimens are
very similar and they clearly belong to the same
ichnospecies. However, the individuals also differ
in several major respects. They will therefore be
described separately.

4.1. Specimen I

This was the first specimen to be worked on
and the new technique was not mastered at
once. Thus, after 4 days of work, only a single
whorl had been cleaned when the start of the
tourist season stopped work (the site is a tourist
beach).

The whorl has an oval outline and the spreite
lamina is developed as a low, conical skirt-like
zone, distally extended as a large number of mar-
ginal lobes (Fig. 4). The widest diameter of the
whorl from lobe tip to lobe tip measured about 90
cm. The marginal tube is continuous around the
lobate perimeter and has a circular cross-section.
For most of its length it is more strongly miner-
alised than the spreite, having a dark brown to
black colour when wet. The circular cross-section
indicates that the tube had suffered no compac-
tion and was thus filled with sediment by the
trace-maker. Thin-walled skeletal material at this
locality commonly shows considerable compac-
tion.

A second spreite intersected the main one. This
was at first thought to belong to another individ-
ual and was removed. As work progressed, how-
ever, it became clear that the extra spreite was in
fact that of the next whorl down, and that these
two whorls intersected each other. This realisation
came too late to photograph the effect, but
sketches were made (Fig. 5). Thus, the whorl
shows protrusive, i.e., downward advance, but
the next whorl has aberrantly cut upward some-
what. Sarle (1906) also described cases where low-
er whorls of Zoophycos cut upward through over-
lying whorls.

As seen from above, spreite construction ad-
vanced in a clockwise direction (dextral). The
spreite can be said to comprise two zones: a
skirt-like zone proximally and a lobate zone around the edge (Fig. 6). Accretion in the skirt-like zone was by sigmoidal increments (term from Seilacher, 1986), which gave rise to major and minor lamellae in the sense of Simpson (1970). The surfaces of the conical skirt slope at 8–22°, but mostly around 18–20°.

The outer part of the spreite consists of separated marginal lobes of more or less the same width (2–3 cm) but of extremely variable length. The attitude of some of the lobes is straight and radiating. In most cases, however, they are curved backward or trailing with respect to the direction of growth of the spreite. A peculiar feature of the lobes is that most of them dip downward about 2° more steeply than the slope of the skirt at their proximal part but tend to level out somewhat at the distal end. Moreover, each lobe twists by 20–40° or more, in an anticlockwise direction so as to face somewhat forward relative to the growth direction of the trace fossil.

Development of lobes varies extremely, from very long to hardly detectable. A marginal structure is defined as a lobe if its contours are more convex than those of a sigmoid increment. On this basis, the whorl carried at least 23 lobes. The skirt is composed of radiating bundles of sigmoidal minor lamellae bounded on either side by major lamellae. Where these reach the margin of the spreite, they either simply terminate, or they continue onward to grow as a marginal lobe. In this way, usually the radiating bundles of the skirt alternate as lobate and interlobate, whereby lobes occur on every other bundle (Fig. 6). But there are a number of irregularities. Lobes 7 and 8 have no interlobe area between them (Fig. 4), and likewise 12 and 13. Lobes 9 and 10 seem to have two interlobes between them, and between

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![Diagram of the spreite edge to show terminology used in this paper.](image)

![Image of lobes 1–4 of specimen I.](image)

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Fig. 6. Diagram of the spreite edge to show terminology used in this paper.

Fig. 7. Lobes 1–4 of specimen I. These are straight, long marginal lobes. Note the strong mineralisation of the marginal tube and the less strong mineralisation of the lobate lamellae of the spreite.
19 and 20, perhaps three. The area beyond 23 is quite abnormal.

Some lobes are regular in their development, such as lobes 2–5 (Figs. 7 and 8). Lobe 13 (Fig. 9), on the other hand, is aberrant, being minimally developed. The best-developed lobes, i.e., 12, 14, 15 (Fig. 10) and 18, are long and curved.

Of special interest are the stunted lobes 6, 7 and 8 (Fig. 11). In the crowded Zoophycos substrate, the individual under study encountered its close neighbour. The lobate spreite of the neighbour acted as a deterrent to further development to lobes 6, 7 and 8 of the cleaned Zoophycos. In fact, the marginal tube in each of these lobes has actually retreated, leaving a retrusive spreite behind it. Horizontal retrusion has not been previously reported in Zoophycos.

4.2. Specimen II

In the following year a second individual was dissected. With the experience of the first Zoophycos, work was more efficient and two whorls were exposed. The general morphology was similar to specimen I, but there were significant differences. It is not possible to provide meaningful measure-
ments of the diameter, but a little more or less than 1 m is representative.

Like the other specimen, this individual also was protrusive (Fig. 12). Perhaps the most striking difference was the direction of coiling, this individual being sinistral, i.e., accreting anticlockwise as seen from above. The lobes thus trail and twist in the opposite direction to those of specimen I. The clockwise twist of the lobes is greater than the corresponding anticlockwise twist in specimen I, the steepest twist being seen in lobe 45, which reached 63° from the horizontal at its distal end. The longest lobe was no. 38, measuring 48 cm (Fig. 13). The skirt zone sloped more steeply than that in specimen I, ranging from 10° to 36°, but generally around 20–25°.

The uppermost preserved whorl had been damaged by tourist activities and the upper right quadrant was missing. A beach-levelling bulldozer destroyed lobes 1–3 before they could be photographed. The upper whorl had about 32 lobes; the missing quadrant was estimated, probably correctly, on the basis of the number of lobes in the subjacent whorl quadrant (Fig. 12A). The lower whorl had 31 lobes (Fig. 14). The ferruginous mineralisation of the marginal tube in the upper whorl was not as continuous as in specimen I, and some lobes were poorly visible. Nevertheless, as in specimen I, the tube could be seen to have a circular cross-section and showed no signs of compaction.

The general outline of the trace fossil was more circular than in specimen I, and the development of the lobes was more regular. In most cases the lobate and interlobe bundles alternated regularly. However, two lobes appear to have been branched (12–13 and 58–59), a feature that was not seen in specimen I.

4.3. Death of trace-maker II

As the spreite accreted to lobe 54, the structure showed considerable regularity and the lobes were long and well developed (Figs. 14 and 15). Lobes 55 and 56, however, are under-dimensioned, while 57–63 may be considered definitely subnormal. Lobe 63 is the trace-maker’s last attempt at constructing a lobe. After this, minor lamellae were restricted to the sigmoidal type, comprising three or possibly four bundles, the marginal tube coming to lie along the radial path of the major lamellae, and spreite construction ceased (Fig. 16). At this point, the spreite had risen up to and cut through the overlying whorl. From lobe 55 to the

Fig. 10. Lobes 13–15 of specimen I. Lobes 14 and 15 are well developed, curved, but very little twisted. The damage to lobe 15 was incurred during preparation.
end, the trend of deterioration would seem to represent the advance of senility in the trace-maker.

Unfortunately, during excavation of the trace fossil, a supposedly foreign spreite was seen to cut the spreite being cleaned, having a very steep attitude unusual in Zoophycos. This spreite was removed as it impeded work and was not considered to have any connection with the whorl being excavated. Only when the final whorl was exposed was it revealed to be the terminal part of the specimen. Its further upward course is unknown, but the tube appeared to be headed toward the axial region as would be expected.

4.4. Vertical sections

Several Zoophycos individuals were sectioned vertically, but owing to the abundance of the trace fossil, neighbouring individuals overlapped and produced a confusing picture. However, axial sections indicated that the Zoophycos have at least four whorls (Fig. 17).

The sediment comprising the spreite was more muddy and darker in colour than the ambient sediment. This indicates that the spreite material has been advected downward from the topmost Kolymbia limestone. The darker material occurs as ovoid pellets in millimetre size. More extensive darker patches of sediment in the spreite appear to be Lindos Bay clay (Fig. 17B). This would indicate a colonisation surface as much as 1 m above the lowest whorl. This figure agrees with the burrowing depth estimated by Fu and Werner (1995) for Quaternary Zoophycos, based on similar evidence.

The Lindos Bay clay material occurs as patches within the spreite, or as a group of a few minor lamellae, usually in the higher whorls. Thus, increments of spreite composed of Lindos Bay Clay are followed downwards by later lamellae composed of high Kolymbia Limestone sediment. This suggests that material was not being collected at the seafloor, but rather at several levels close beneath it, subsequent to the initial deposition of the Lindos Bay clay.

4.5. Association with other trace fossils

The Zoophycos cross-cuts most of the other trace fossils occurring with it in the completely bioturbated sediment. These include Thalassinooides, a Taenidium 5 mm in diameter seen only where iron mineralised, pale-filled Planolites and oblique, straight structures that may be Teichichmus.

Rustily mineralised, extremely fine, branched trace fossils 0.5 mm in diameter are locally visible.
These may be *Chondrites*. In places these are common within and running over the surface of the *Zoophycos* spreiten and clearly belong to a deeper tier.

Finally, the heavily iron-mineralised spirals of *Helicodromites mobilis* are common at the *Zoophycos* horizon. No case was seen of cross-cutting relationships between *Zoophycos* and *H. mobilis*. However, several cases were seen where *Zoophycos* avoided contact with *H. mobilis* (Fig. 12B), suggesting that *H. mobilis* was emplaced at the same or a slightly deeper tier than *Zoophycos*. 
5. Systematics

The described Zoophycos possess several distinctive characters that have not been seen in combination in other named ichnospecies. In the following, therefore, we designate a name to the Rhodes Pliocene Zoophycos.

5.1. Ichnogenus Zoophycos Massalongo 1855

The ichnogenus Zoophycos is in need of revision. It covers a broad morphospace of forms from simple tongue-shaped spreiten and antler-shaped forms to highly complex spiral spreite trace fossils (Seilacher, 1986; Miller, 1991). Details both of the construction of the spreite and the general morphology vary widely. Some forms that diverge variously from Massalongo’s (1855) forms have valid ichnogenus names such as Tao-nurus von Fischer-Ooster (1858), Cancellophycus De Saporta (1873), Echinospira Girotti (1970) and several others (Häntzschel, 1975). These names are usually considered junior synonyms of Zoophycos, but possibly they should be revised and reinstated to cover these divergent forms. The broad collection of related forms at present grouped as Zoophycos are covered by the ichnofamily Alectoruridae (Schimper and Schenk, 1879; Fuchs, 1895).

Despite our lack of knowledge of the upper part of the Zoophycos under study, we consider that its structure differs significantly from previously named ichnospecies, and we therefore designate it as a separate ichnospecies.

5.2. Zoophycos rhodensis, isp. nov.

**Diagnosis:** Large, spiral Zoophycos having at least four whorls, a smooth spreite comprising radiating bundles of minor lamellae separated by major lamellae and developed at the perimeter into numerous elongated lobes. The lobes normally extend from every second bundle. These lobes are twisted so as to tilt downward towards the direction of accretion of the spiral spreite. A single marginal tube runs around the entire perimeter. The direction of coiling may be sinistral or dextral.

**Holotype:** A representative piece of specimen I, comprising parts of lobes 2, 3 and 4, is deposited in the Geological Museum, University of Copenhagen, as no. MGUH 26390. Fig. 7 shows this part of the trace fossil in the field prior to collection.

**Type locality:** Small bay on the south side of Cape Vagia, Rhodes (Fig. 1).

**Type horizon:** About 1 m below top of the Kolymbia limestone, 7 m below the Pliocene/Pleistocene boundary as determined by Lovlie et al. (1989).

**Remarks:** Most lobate spiral Zoophycos lack the clear distinction between major and minor lamel-
Zoophycos rhodensis in their spreite construction. Bischoff (1968) defined the structure of these more simple, lobed spreiten in some detail (see also Plička, 1968, pl. 107, fig. 3; Uchman, 1999, pl. 14, fig. 1). The remarkable form described by Uchman and Demircan (1999) lacks major and minor lamellae and is constructed of a series of broadly overlapping lobes.

The Zoophycos described by Kotake (1989, 1991, 1992) has a spreite composed of major and minor lamellae that somewhat resembles that of Zoophycos rhodensis. However, in contrast, the margin has far fewer lobes, these are not twisted, and the spreite is relatively coarsely pelleted. Furthermore, the Japanese form also has far more numerous whorls than the Rhodian form. Nevertheless, it should be emphasised that
Fig. 15. Oblique view of specimen II, giving an impression of the overall conical form of the trace fossil. Visible are marginal lobes 41–62. The twisted attitude of the lobes is clear, those on the left facing perpendicularly to the camera.

Fig. 16. The last phase of spreite construction in specimen II, no. 63 being the last lobe produced. The next three swings are sigmoidal, terminating interlobe spreite bundles, after which the well-mineralised marginal tube follows a major lamella and curves steeply upward (see also Fig. 14B). The ridge connecting this to the axis is a cross-section of the spreite, which must have led up to the axial shaft, whence the tube continued to the seafloor. Note the two Helicodromites mobilis beside the penultimate sigmoidal interlobe.
the complete number of whorls is unknown in the Rhodes form.

Many lobate spiral Zoophycos appear to have radiating ribs or spokes crossing the spreite between the bundles of minor lamellae, and thereby replacing the major lamellae. This is the case with Zoophycos funiculus Sacco (1886) (Olivero, 1994, pl. 1, fig. 4 published a photograph of the holotype). The marginal lobes of Z. funiculus seem to have a slight twist reminiscent of that of Zoophycos rhodensis. Echinospira pauciradiata Girotti (1970) also has radiating ribs. However, most impressive in this respect is the New Zealand Zoophycos, Cretaceous–Oligocene Amuri Limestone Group (Stevens, 1968; Lewis, 1970; Seilacher, 1986; Ekdale and Lewis, 1991; Ekdale, 1992), where the spokes are numerous and the whorls look like wheels (see Section 5.3). The presence of the spokes and the significantly lesser development of marginal lobes distinguish these forms from Z. rhodensis.

The whorls of Zoophycos rhodensis are in the form of a simple cone, and the trace fossil does not resemble the coiling mode of Zoophycos (Cancellophyx) as described by Olivero (1994, 1996), Olivero and Gaillard (1996) and Gaillard et al. (1999). In that form, a central, more or less vertical, axial structure extends to the deepest point of the trace fossil. Such a central structure is not developed in Z. rhodensis (Figs. 3, 16 and 17A).

Fig. 17. Vertical sections of Zoophycos rhodensis. (A) Axial section showing the basal part of the shaft and four whorls of spreite. In the upper parts, darker sediment in the spreite is Lindos Bay clay, piped nearly 1 m downward. (B) Spreite of another Z. rhodensis. The pale sediment is more clayey than the host sediment and derives from near the top of the Kolymbia limestone. The darker region of a whorl (arrowed) comprises Lindos Bay clay sediment from above the Kolymbia limestone.
Some Zoophycos have been reported having extra tubes, similar in size to the marginal tube, cutting and following the spreite discordantly to the system of lamellae. These may belong to the Zoophycos itself, as suggested by Bromley et al. (1999), or may represent the work of other deep-tier animals (Olivero and Gaillard, 1996; Miller, 2000; Miller and D’Alberto, 2001). No such tubes were seen to intersect Zoophycos rhodensis.

5.3. Zoophycos from Rhodes and New Zealand compared

The New Zealand Amuri Limestone Zoophycos has been interpreted by Ekdale and Lewis (1991) as having accreted by means of successive Rhizocorallium-like excursions of the marginal tube, each excursion having overlapped and destroyed half the width of the previous one. In this way, only the final Rhizocorallium-like excursion is preserved whole. One of the limbs of each of the previous excursions is preserved, however, as a radiating rib or spoke across the spreite skirt. The multi-whorled structure rises retrusively through the sediment from a deep-seated starting point. This double reworking of the sediment seems inefficient (Wetzel, 1992). More probably, the New Zealand Zoophycos accreted in the same way as Zoophycos rhodensis. However, the Z. rhodensis trace-maker obliterated its previous radial tube as it produced the next bundle of sigmoidal lamellae, whereas the New Zealander, in contrast, preserved the outline of the radial tube as a sediment-filled rib (Fig. 18). A close look at the minor lamellae reveals that they are not arcs of a circle representing half Rhizocorallium lamellae, but are sigmoidal shapes having a long, straight central portion. In cross-section (Lewis, 1970, fig. 6), the minor lamellae are seen to continue into the ribs, as would be the case where the tube that gave rise to the rib was shifted laterally. However, why the rib should have a wider diameter than the thickness of the spreite and its causative tube is not explained.

This more or less follows Seilacher’s (1986) interpretation of the New Zealand Zoophycos, the interpreted direction of accretion being the opposite of that of the Ekdale and Lewis (1991) model; the coiling is again considered retrusive but the Rhizocorallium element now represents the start-point and not the conclusion. In Seilacher’s interpretation, the Rhizocorallium-like element (‘starter tongue’) lies at the lower termination of the spreite, not the upper as in the Ekdale and Lewis model. Zoophycos having a Rhizocorallium-like starting point are known also from the Permian of Svalbard (Bromley and Hanken, unpublished).

This starter Rhizocorallium-like feature suggests that, in these forms, the spreite does not represent the lifetime work of the trace-maker, but that the animal makes many Zoophycos structures in a lifetime. This is in strong contrast to those Zoophycos that show a gradual size increase that appears to represent ontogeny; a good example of this is the Bozo Peninsula material (Kotake, 1989). As the upper parts of the Rhodes Zoophycos were missing, it is not known whether there was a Rhizocorallium-like starting point in Zoophycos rhodensis. No obvious ontogenetic enlargement was seen in either the dissected or sectioned individuals.

The New Zealand Zoophycos is therefore close to Zoophycos rhodensis, differing in the preservation of radial ribs, retrusive versus protrusive spiral accretion, and in the much greater marginal lobe development in Z. rhodensis.

The New Zealand form also has far fewer marginal lobes than Zoophycos rhodensis, and these are not twisted. Seilacher (1986) pointed out that, owing to the inclination of the sigmoidal lamellae being less than 90°, the occurrence of several bundles of sigmoidal minor lamellae in succession tends to reduce the radius of the spreite (Fig. 19). Seilacher (1986) proposed that, to counteract this effect, the function of the lobes in this form was to permit recovery of radius length by allowing the next bundle to extend further outward along the lobe. He pointed out that the length of these reset lobes was excessive for this purpose, and that the lobes therefore probably had an additional function. In Z. rhodensis, the occurrence of a lobe on every second bundle avoids this problem of radius reduction; these lobes also appear to have an additional function.
6. Discussion

6.1. Marginal tube and oxygenation

Unfilled or incompletely filled marginal tubes of Zoophycos tend to collapse with sediment compaction (e.g., Ekdale and Bromley, 1983, 1984, fig. 2). However, the marginal tube in both Rho- dian specimens was uncompacted. It is not possible for such a long, narrow tube to fill totally with sediment by passive, mechanical means and the sediment fill must represent active backfill by the trace-maker. This means that the marginal tube was J-shaped and not U-shaped. Wetzel and Werner (1981) found both types in Zoophycos in deep-sea boxcores. They suggested that the open U allowed circulation of seawater, which would be necessary in areas of low benthic oxygenation. However, the maintenance of the long tube would be a costly business, and the J-tube would be sufficient in conditions of good oxygenation (Wetzel and Werner, 1981; Wetzel, 1991).
6.2. Ethological interpretation

The spreite construction of Zoophycos rhodensis is basically that described by Simpson (1970), which was interpreted by him and Seilacher (1967) as a paradigm for deposit feeding. In this model, sediment particles were processed and re-deposited within the active front of the spreite. However, several authors have shown that in at least some Zoophycos, sediment comprising the spreite is not derived from the same level, but has been advected down from higher levels, even from the seafloor (Ekdale and Bromley, 1983; Kotake, 1989, 1991; Miller, 1991; Savrda and Bottjer, 1994; Fu and Werner, 1995; Locklair and Savrda, 1998; MacEachern and Burton, 2000). Using AMS$^{14}$C dating of sample pairs in Zoophycos and the ambient sediment from gravity cores of late Quaternary ‘deep-sea’ sediment, Löwemark (2001), Löwemark and Schäfer (in press) and Löwemark and Werner (2001) found spreite sediment always to be several thousands of years younger than the surrounding host sediment. The trace-maker was thus a reverse conveyor animal (Bromley, 1996). The composition of the spreite of Z. rhodensis indicates that the sediment was derived from around the base of the Lindos Bay clay about 1 m above the base of the spreite.

Kotake (1989, 1991) provided evidence of seafloor feeding in the Pliocene Zoophycos mentioned above from Bozo Peninsula, Japan. Some authors have interpreted other Zoophycos as behaving in this way (e.g., Locklair and Savrda, 1998), the trace-maker feeding at or near the seafloor and depositing pelleted excremental material at depth in the spreite. However, Wetzel and Werner (1981) and Wetzel (1991) noted that the presence or absence of Zoophycos in the deep sea was related to the organic content of the host sediment and not to that of the surface sediment. This was taken as evidence for deep deposit feeding rather than surface detritus feeding. As stated, the Bozo Zoophycos has a structure comparable to Zoophycos rhodensis, which also appears to have advected near-seafloor sediment down into its spreite.

The reverse conveyor model in Zoophycos is complicated by the fact that the material was not deposited directly within the sediment but was placed in a preformed cavity (Bromley, 1991). There are now five ethological explanations for the reverse conveyance into a pre-existing cavity by the Zoophycos animal.

1. Cesspit model. The animal feeds at the seafloor and excretes faecal pellets at depth beneath the seafloor (Kotake, 1989). This model begs three explanations. It does not explain why such a highly organised and complexly structured spreite should be produced by mere deposition of excrement; why some Zoophycos spreiten extend lobes into special places such as within Thalassinoides (Ekdale and Bromley, 1983; Bromley...
and Ekdale, 1984; Bromley et al., 1999) or ammonite body chambers (Olivero and Gaillard, 1996); or why the animal should eat volcanic ash (cf. Miller and Vokes, 1998).

(2) Ballast model. The animal deposit-feeds at depth within the sediment and excretes at the seafloor. However, in order not to create a cavity at the site of feeding, which would inhibit efficient water circulation, seafloor material is simultaneously conveyed down and deposited to backfill the cavity (Bromley, 1991; Bromley et al., 1999). This sediment is ballast. It may by chance be rich in refractory organic material or it may be volcanic ash. It may be pelleted to improve transport efficiency. On the other hand, the fact that deep-sea Zoophycos is found in sediment that is poor in organic material and is not found in sediment that is organic-rich (Wetzel and Werner, 1981) does not support deposit feeding. Moreover, enhanced total organic carbon within the spreite sediment relative to the surrounding sediment also argues against deep deposit feeding.

(3) Cache model. Some deep-sea environments are characterised by strong seasonal variation in availability of benthic food. During times of plenty, animals may bury organic-rich sediment deeply within the seafloor for use in times of poverty (Jumars et al., 1990). The deep-tier spreite of Zoophycos may be a cache of nutrient-rich seafloor surface sediment (Bromley, 1991). Clear indication of Zoophycos in which the spreite has been revisited and effectively exploited has been reported by Miller and D’Alberto (2001).

(4) Gardening model. Culture of micro-organisms on an organic-rich substrate in the controlled environment of a burrow is well-known in the marine endobenthos (Bromley, 1996 and references therein). The Zoophycos spreite, composed of surface or near-surface sediment in extended contact at the advancing edge with the oxygenated water of the marginal tube, might represent a site of raised microbial activity (Bromley, 1991; Fu and Werner, 1995). Growth of the spreite would represent continual refreshment of the microbial farm.

(5) Chemosymbiosis model. An additional model was suggested by Bromley et al. (1999) for some Zoophycos in Cretaceous chalk. Many invertebrates have a symbiotic relationship with chemosulfotrophic sulphide-oxidising bacteria (Zuschin et al., 2001, and references therein). Such systems involve the availability of sulphides and oxygen for bacterial metabolism. The marginal lobes of some Zoophycos might act as sulphide wells in close combination with the oxygenated water of the marginal tube. The searching behaviour of lobes into Thalassinoides and ammonites may be exploration for sulphide-rich sediment.

More than one trophic style could be represented by a single spreite. Löwemark (2001) suggested that indications of more than a single mode of behaviour in a Zoophycos spreite might suggest varying behaviour according to seasonal variation in availability of food, i.e., surface-detritus feeding in times of organic richness and deep deposit feeding, cache, possibly combined with bacterial farming in times of poverty.

6.3. Ethology of the Zoophycos rhodensis skirt

The skirt zone of the spreite seems to represent deposit feeding as envisaged by Seilacher (1967, 1997), Wetzel (1991) and Ekdale (1992). However, as the spreite sediment derived from higher levels, presumably either the ballast conveyance model, the gardening model or the cache model of Jumars et al. (1990) was in operation. There is no sign of re-exploitation of the spreite, which makes the cache explanation less attractive.

The ballast and gardening activities could occur simultaneously or in alternation. In the first, the ‘significant’ sediment is that which is eaten and which passes up the shaft. That which replaces it is ballast. In the second activity, gardening, the ‘significant’ sediment is the surface sediment that is passed down the shaft. This must have refractive organic material in it for microbial culture. If both activities were to be carried out, the energy budget would be markedly improved. It is suggested, therefore, that the skirt zone is a structure produced by deep deposit feeding and microbial gardening.

6.4. Ethology of the Zoophycos rhodensis lobes

The lobes seem to represent a quite different
behaviour and may represent a gardening or bacterial symbiosis activity. As the marginal tube appears to have been a J-shaped structure, backfilled as the trace-maker moves forward, the individual lobes would have had a limited period of activity, being replaced by new lobes periodically. The peculiar twisted form of the lobes suggests some special relationship to the surrounding sediment quite different from that of the skirt zone. The elongation of the lobes placed the marginal tube in extended contact with the spreite sediment. This sediment, being derived from near the seafloor, would have been relatively rich in combustible organic material and bacteria.

The twist of the lobes would slightly increase the distance between the marginal tubes of successive lobes, thereby increasing their isolation. This would increase the amount of fresh sediment in the vicinity of each lobe for exploitation.

The heavy mineralisation of the marginal tube is probably now-oxidised pyrite and the great depth beneath the seafloor (1 m) at which the animal operated supports this idea. It is therefore suggested that the lobes represent sulphide wells, much along the lines that Fu (1991) and Savrda et al. (1991) envisaged for *Chondrites*. The avoidance strategy with *Helicodromites mobilis* is interesting. *Helicodromites mobilis* is also heavily iron-mineralised. If these trace fossils also represent sulphide wells, but of another animal, the surrounding sediment might be sulphide-poor, and of little interest for the *Zoophycos* animal.

Possibly the lobes, as an extension of the accreting front of the skirt zone, might equally well have been used for culturing microbes for food. It is not known whether both activities could be conducted simultaneously in harmony.

7. Conclusion

The lower parts of two *Zoophycos* have been excavated to show much detail of their spreite structure. The two individuals have the same general bauplan, and are designated as a new ichnospecies, *Zoophycos rhodensis*. Nevertheless, the two individuals show many differences. One is coiled dextrally, the other sinistrally. The axial shaft is unknown. The spreiten consist of two zones: an inner, skirt-like zone and an outer zone of marginal lobes. The marginal lobes vary in development but they occupy a relatively large part of the trace fossil. These lobes show a relatively uniform twisted and bent morphology and clearly represent a behaviour pattern different from that of the skirt-like spreite.

Cross-sections of other individuals show that the spreite material has derived from horizons higher than the spreite, including overlying silty clay occurring about 1 m higher in the succession. This indicates that the base of the trace fossil lay about 1 m below the palaeoseafloor.

The marginal tubes of the two dissected individuals are, for the most part, strongly iron-mineralised, suggesting oxidised pyrite. It is suggested that the skirt zone represents deposit feeding and microbial gardening and the lobes may have been sulphide wells connected with sulphur-oxidising bacteria having symbiosis with the trace-making animal.

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