Evolutionary trend of *Zoophycos* morphotypes from the Upper Cretaceous–Lower Miocene in the type pelagic sections of Gubbio, Italy

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**LETHERIA**


**Abstract**

About 200 *Zoophycos* specimens, including 90 specimens studied in detail, have been analysed in the continuous Upper Cretaceous–Lower Miocene pelagic sedimentary type sections of the Gubbio area (the Contessa Highway, Contessa Quarry and Bottaccone sections, Northern Apennines). The sediments are reddish to grey limestones and marls of the Scaglia Group and marls with volcaniclastic deposits of the Bisciaro Formation. The aim was to examine the evolutionary trend of what is probably the most debated trace fossil of all time, from the Upper Cretaceous to Lower Miocene. Despite having been found in beds ranging from the Cambrian to the present, no consensus has been reached regarding mode of construction, tracemaker or ethological explanation for *Zoophycos*. Four *Zoophycos* morphotypes are recognized at Gubbio showing variations of major and minor lamellae, apex, lobes and whorls: the Cretaceous–Eocene cone-shaped type 1, the Upper Eocene–Middle Oligocene helicoidal type 2, the Oligocene lobate type 3 and the Upper Oligocene–Lower Miocene flat type 4. The very high ichnodensity in some beds (hundreds of specimens in discrete levels of the Bisciaro Formation, now destroyed by quarrying) seems to find explanation in abnormal concentrations of phytodetritus and organic matter on the seafloor in some periods. This very high abundance in discrete levels reflects a change in sedimentation and seafloor conditions at pre-flysch deposition. Due to such high ichnodensity, many adjacent specimens display deformed outer margins. Taphonomic analysis shows a variation of whorls, laminae and U-shaped lobes, reflecting ontogenetic development of the tracemaker(s) (?sipunculid worms).

Introduction

The trace fossil *Zoophycos* Massalongo (1855) is one of the most important multi-level, spreite structures in the deep-sea sediments. Since the original description by Massalongo (1855), many studies have presented its strong variability with different ichnogenera that can be ascribed to the *Zoophycos* group. *Zoophycos* is the eponymous trace fossil of the *Zoophycos* ichnofacies, essentially it referred to stable depositional settings (mainly slope and distal basin plain areas) in quiet environmental conditions (Bischoff 1968; Hántzschel 1975; Wetzel & Werner 1981; Bellotti & Valeri 1987; Bromley 1991; Bromley & Asgaard 1991; Ekdale & Lewis 1991; Pemberton 1992; Wetzel 1992; Gaillard & Olivero 1993; Olivero 1996; 2003, 2007; Olivero & Gaillard 1996, 2007; Gaillard et al. 1999; Bromley & Hanken 2003; Miller 2007; Monaco & Checconi 2008; Knaust & Bromley 2012; Zhang et al. 2015a,b). In many cases, as observed in the deep-sea calcareous sediments in the present study area (Monaco et al. 2012, 2015), the *Zoophycos* ichnofacies replace basinward the *Nereites*
ichnofacies typical of deep-sea siliciclastic deposits. Most varieties of *Zoophycos* include a central shaft connecting the burrow with the sediment surface (cylindrical tunnel in Zhang *et al.* 2015b, fig. 1) and a marginal tube along the outer margin of the spreites (Häntzschel 1975; Zhang *et al.* 2015b, fig. 1). *Zoophycos* s.l. is generally assumed to be a trace of unknown deposit feeders (or partly chemichnia), among which sipunculids, polychaete annelids, arthropods or enteropneust hemichordates are the most commonly invoked tracemakers (Wetzel & Werner 1981; Kotake 1989, 2014; Ekdale & Lewis 1991; Olivero & Gaillard 1996, 2007; Löwemark & Grootes 2004; Löwemark *et al.* 2004; Löwemark 2012). *Zoophycos* is one of the most problematic burrow systems to study and interpret in the fossil record (Seilacher 2007). Its macroevolution over 541 Ma was presented by Zhang *et al.* (2015b).

The aim of this paper was to show the evolutionary trend of four morphotypes of *Zoophycos* recovered in continuous pelagic successions of the Gubbio area from the Upper Cretaceous (Cenomanian) to Lower Miocene (Burdigalian). Fortunately, the material was collected in the Contessa Highway section, before the destructive action of quarrying since the year 2003. The morphotypes probably reflect ethological variations and environmental changes of pelagic sedimentation.

**Geological setting**

The Umbria–Marche Basin of the central Italy offers extensive exposures of pelagic carbonate rocks that are nearly continuous and span more than 100 myr from the Early Jurassic to the Early Miocene. The most complete successions of the Upper Cretaceous to Lower Miocene pelagic sediments of the Tethyan type crop out in the Bottaccione Gorge and the Contessa Valley located close to Gubbio. Owing to the continuous, pelagic deposition, a rather modest tectonic overprint, and the availability of excellent age control through magneto, bio, chemo and tephrostratigraphy, and direct radioisotopic dates from interbedded volcanioclastic layers, these sediments have played a prominent role in the establishment of the standard Cretaceous and Palaeogene time-scales (Lutherbacher & Premoli Silva 1964; Lowrie *et al.* 1982; Coccioni *et al.* 2013; Coccioni & Premoli Silva 2015; and references therein). A detailed integrated stratigraphy of these deposits was summarized in several papers (Napoleone *et al.* 1983; Premoli Silva *et al.* 1988a,b; Coccioni 1996; Montanari *et al.* 1997; Coccioni *et al.* 2013; Coccioni & Premoli Silva 2015; R. Coccioni, R. Catanzariti, F. Frontalini, B. Galbrun, L. Jovane, A. Montanari, J. Savian & M. Sideri, submitted and references therein).

The sediments of the Gubbio area included in this study belong to the Scaglia Bianca (Late Albian–Early Turonian), the Scaglia Rossa (Early Turonian–earliest Lutetian), the Scaglia Variegata (earliest Lutetian–Late Priabonian) and the Scaglia Cinerea (Late Priabonian–Early Aquitanian) formations that are parts of the Scaglia Group and the Bisciaro Formation (early Aquitanian–Middle Burdigalian). The dominant lithotypes include fine-grained, bioturbated limestones, marly limestones, calcareous marls and marls, which are nannofossil–planktonic foraminiferal oozes. Other lithological components are present in some portions of the succession, such as cherts (Scaglia Bianca, Scaglia Rossa, Bisciaro formations), black shales (Scaglia Bianca), glauconitic–sandy limestones (Bisciaro Formation), clays and volcanioclastic layers (Scaglia Variegata, Scaglia Cinerea and, mainly, in Bisciaro formations). The biogenic sediments were deposited above the calcite compensation depth at a palaeolatitude ranging from 20° N (Late Albian, ~102 Ma) to 40° N (middle Burdigalian, 17.5 Ma), according to the Ocean Drilling Stratigraphic Network Plate Tectonic Reconstruction Service (http://www.odsn.de) and at upper-middle to lower bathyal depths of about 500–1500 m, in a quiet pelagic setting of the central-western Tethys.

The sedimentation rate (compacted) was ~1 cm/kyr through the Scaglia Bianca, then 0.19–2.09 cm/kyr through the Scaglia Rossa, 0.29–2.11 cm/kyr through the Scaglia Variegata, 0.32–2.5 cm/kyr through the Scaglia Cinerea and ~0.42 cm/kyr through the Bisciaro Formation.

Increased sedimentation rates are observed in the Upper Maastrichtian, lower Thanetian, middle–upper Bartonian, middle Priabonian, upper Rupelian and middle Chattian pelagic deposits.

**Methods**

*Zoophycos* has been studied in three places in the Gubbio area, the Contessa Highway section (mining concession named ‘il Cavaliere’, see Premoli Silva *et al.* 1988a,b), the Contessa Quarry section and the Bottaccione Gorge (Fig. 1). The study is based on 200 *Zoophycos* specimens from Upper Cretaceous to Lower Miocene (mid-Burdigalian; Montanari *et al.* 1997) sediments, which belong to the Scaglia Group (Scaglia Bianca, Scaglia Rossa, Scaglia Variegata and Scaglia Cinerea) and the Bisciaro Formation (Fig. 1B). Most of the studied specimens came from
Fig. 1. The study area with sections (A) and synthetic geological setting (B) (modified from Premoli Silva et al. 1988a) C, D, E. some outcrops of the Contessa Highway section: SV = Scaglia Variegata, SC = Scaglia Cinerea, BI = Bisciario formations. In E, arrows for Zoophycos specimens.
the upper surfaces of some beds of the Scaglia Cinerea (Fig. 1C, E) and from the Bisciaro Formation (Fig. 2); the Contessa Highway quarry, where well-exposed bedding surfaces were available in 1999–2002 (as documented by L. Bracchini in her unpublished thesis), is now completely destroyed. Several morphological elements of Zoophycos were described. The construction of spreites resulted from the successive lateral displacement of the marginal tube (Wetzel & Werner 1981) is here reconsidered on the basis of the specimens studied.

In this paper, the evolutionary trend of morphological features of Zoophycos shows variations of major and minor lamellae (sensu Kotake 2014), apex, lobes and whorls (Fig. 3). In the Echinospira-like, lobate specimens (see Discussion of this ichnogenus in Uchman & Demircan 1999; MacIlroy & Falcon-Lang 2006), the functional morphology of the marginal tube and concave minor lamellae is reconsidered here. Whorl number and whorl disposition (vertical extrusion of whorls) and the ‘exposure of lamellae’ sensu Bischoff (1968), that is, bad or good exposure of lamellae, are also considered.

Another parameter is the density of Zoophycos, which was measured in some larger outcrops of the Scaglia Cinerea (Fig. 1E) and the Bisciaro formations (Fig. 2), where bedding surfaces (now destroyed by quarrying after 2002) exhibited hundreds of specimens per 40 m² (Fig. 2, Table 1). Here, the ichnodensity ranges from 1 to 4 specimens/m². Only one specimen is crossed by Planolites. Other trace fossils, such as Thalassinoides, Chondrites and Trichichnus, are present. Among these traces Thalassinoides is the most abundant. The maximum diameter of Zoophycos specimens varies from 25 to 65 cm; exceptionally, it attains up

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**Fig. 2.** Ichnodensity in the top of a 40-m-long exposure of a bed (A, B, C are contiguous portions in the photograph from 2003 because all beds are now destroyed by quarrying) of the Bisciaro Formation (BI) in the Contessa Highway section. Note very high density of Zoophycos (arrows) in every bed of the formation.
Evolution of Zoophycos morphotypes

Fig. 3. Morphological features with symbols used in this work: A. ML = major ‘lamella’, IL = internal lamellae; scale bar = 3 cm. B. Up to 4 whorls (WH) in flattened morphotype 2 specimen from the Oligocene Scaglia Cinerea Formation; scale bar = 15 cm. C. Large flat morphotype 4 specimen with the central apex (AP) and bended laminae; Lower Miocene Bisciaro Formation; scale bar = 15 cm. D. *Rhizocorallium*-like lobes (LB) with wide marginal tube (MT) and the internal U-shaped lamellae, Type 3 in the Scaglia Cinerea Formation, scale bar = 5 cm.

divergence from the central apex. Other parameters here considered are the thickness and shape of internal lamellae, the extension of lobes and their number, the length of the lobes from their apex and the distance between adjacent lamellae (Table 1).

Ethological and tracemaker interpretations

Zoophycos is probably the most debated of all trace fossils and despite having been found in strata ranging from the Cambrian to the present, no consensus has yet been reached regarding mode of construction or its ethological explanation. Papers on Zoophycos and Zoophycos-like trace fossils are numerous and include recent studies using new techniques (see Kotake 2014; Zhang et al. 2015a); but important questions remain unsolved, including the ichnotaxonomic assignment, the morphological interpretation, the tracemaker identification and the ethological pattern or the evolutionary trends. Löwemark et al. (2004) investigated modern Zoophycos from the Celebes Sea and excluded a significant role of gardening of bacteria (Bromley 1991), because of the minimal difference in values of δ^{13}C_{org} between Zoophycos spreites and the host surrounding sediment. Therefore, the cache model (Jumars et al. 1990; Bromley 1991) was favoured, as supported by an increase of TOC, carbonates and ^{14}C ages within the spreites (Löwemark & Schäfer 2003). In this model, the food is squirrelled away for poorer times (Löwemark et al. 2004; Fig. 2). The cache model was also applied by Miller & D’Alberto (2001) in the Cretaceous–Palaeogene Zoophycos in the northern Italy.

Zoophycos is produced by as an yet-undetermined organism(s), probably a worm-like animal, commonly referred to as being sipunculid (Wetzel & Werner 1981; Olivero & Gaillard 2007), echiuran (Kotake 1989) or polychaete annelids (Ekdale & Lewis 1991; Ekdale 1992), among others (see Knaust 2009 and Zhang et al. 2015a,b for reviews).

Zoophycos is recognized from Palaeozoic sediments (see citations in Knaust 2009; Zhang et al. 2015a,b for reviews).
Table 1. Morphological features of 90 *Zoophycos* specimens (morphotypes 1–4) studied in detail (see text for explanation).

<table>
<thead>
<tr>
<th>Type</th>
<th>90 Samples studied</th>
<th>Dimensions/diameter (cm)</th>
<th>External shape</th>
<th>Direction of rotation</th>
<th>Presence of marginal tunnel</th>
<th>MT = Marginal tunnel (mm)</th>
<th>IL = Internal lamellae</th>
<th>AP = Apex (mm)</th>
<th>LB = Lobes</th>
<th>WD = Whorls</th>
<th>Formations</th>
</tr>
</thead>
<tbody>
<tr>
<td>TYPE 4</td>
<td>31</td>
<td>420 to 1160 mm</td>
<td>Complex spiral form-slight conical shape</td>
<td>Mainly counter clockwise</td>
<td>Not present</td>
<td>Many tens; thickness 8–12 mm</td>
<td>Presence of internal lamellae on spirals</td>
<td>Apex pointing upwards</td>
<td>Not present</td>
<td>Presence of one or more whorls of considerable amplitude</td>
<td>BISCIARO</td>
</tr>
<tr>
<td>TYPE 3</td>
<td>7</td>
<td>300 to 980 mm</td>
<td>Complex lobate form. Lobed coils which increase the size upwards</td>
<td>Clockwise and counter clockwise</td>
<td>Presence tunnel marginal from 5 mm to 8 mm</td>
<td>15 to 25 mm</td>
<td>Presence of internal lamellae on lobes</td>
<td>Apex pointing upwards</td>
<td>Lobes that increase their extension upwards</td>
<td>Spirals lobed</td>
<td>SCAGLIA VARIEGATA AND SCAGLIA CINEREA</td>
</tr>
<tr>
<td>TYPE 2</td>
<td>29</td>
<td>150 to 580 mm</td>
<td>Spiral cone and funnel-shaped spiral</td>
<td>Clockwise and counter clockwise</td>
<td>Visible only in lobes</td>
<td>Many tens; 8 to 10 mm</td>
<td>The lamellae plow through the loop for all its breadth. The lobes are furrowed by the lamellae until you reach the margin</td>
<td>Apex pointing upwards and downwards (from 10 mm to 50 mm)</td>
<td>Present with specimens with half-moon lobes or flower</td>
<td>The amplitude of the spire rises upwards</td>
<td>SCAGLIA ROSSA SCAGLIA VARIEGATA AND SCAGLIA CINEREA</td>
</tr>
<tr>
<td>TYPE 1</td>
<td>23</td>
<td>180 to 600 mm</td>
<td>Simple planar form and spiral cone form</td>
<td>Clockwise and counter clockwise</td>
<td>Not present</td>
<td>Not visible because not preserved</td>
<td>In some cases present only near the apex</td>
<td>Apex pointing upwards and downwards (from 15 mm to 40 mm)</td>
<td>Not present</td>
<td>Visible in some specimens</td>
<td>SCAGLIA ROSSA - SCAGLIA VARIEGATA</td>
</tr>
</tbody>
</table>
2015b), with scarce records from the Cambrian, including the oldest occurrence in the lower Cambrian of the southeastern California (Sappenfield et al. 2012), and other occurrences in middle Cambrian shales from the Czech Republic (Doucek & Mikuláš 2014). Pre-Palaeozoic (late Ediacaran) spreite structures, morphologically comparable to the Palaeozoic Zoophycos from shallow water environments, have been documented recent (Macdonald et al. 2014). Modern records have been recognized in several deep-sea environments (e.g. Wetzel & Werner 1981; Löwemark 2015).

Studies on evolutionary changes of Zoophycos morphology (Zhang et al. 2015b) show comparatively simple, shallow marine (shelf) structures during Palaeozoic and a lineage of more complex, offshore structures during post-Palaeozoic times (e.g. Seilacher 2007). The Palaeozoic Zoophycos occurs in marginal marine, shallow and deep-sea deposits, while the Mesozoic forms are found mostly in the deeper shelf and deeper sediments and the Cenozoic Zoophycos mainly occurs in deep-sea facies (see also Miller et al. 2009 and references therein). Evident morphological and bathymetric trends through geological time, with special attention to Mesozoic, have been analysed, but variable interpretations have been proposed (Seilacher 1986; Bottjer et al. 1987, 1988; Chamberlain 2000; Olivero 2003; Baucon & Avanzini 2008; Kotake 2014; Zhang et al. 2015b).

The palaeoenvironmental significance and interpretation of environmental conditions of the Zoophycos tracemakers are controversial, resulting in the usefulness of this trace fossil as a palaeoenvironmental indicator being disputed (Kotake 2014). Fossil forms have been related to energy changes, sedimentation rate, food content, symbiotic micro-organisms (e.g. sulphate-reducing bacteria, Zhang et al. 2015a) or bottom-water oxygenation; sediments of different and diverse lithology, with comparative low oxygenation of pore waters, can be colonized by the Zoophycos tracemaker (e.g. Rodríguez-Tovar & Uchman 2004, 2006, 2008). A variable life strategy has been proposed, from an opportunistic strategy in unstable environments for highly lobed Zoophycos to a more specialized strategy in stable environments for simple, unlobed forms (Olivero & Gaillard 2007). Zoophycos and Zoophycos-group trace fossils have been also interpreted in a sequence stratigraphical context (i.e. MacEachern & Burton 2000; MacIroy & Falcon-Lang 2006).

Modern deep-sea Zoophycos have been also extensively studied using X-ray radiographs (Wetzel & Werner 1981; Löwemark & Schäfer 2003; Löwemark et al. 2006; see Löwemark 2012, 2015 for recent reviews), and recently by a high-resolution digital image treatment (Dorador & Rodríguez-Tovar 2014; Dorador et al. 2014a,b; Rodríguez-Tovar & Dorador 2014, 2015). Zoophycos is restricted to water depths below 1000 m in modern deep-sea sediments, even being present in cores from about 5000 m (Löwemark & Werner 2001). According to Löwemark (2015, and references therein), modern deep-sea forms are closely related to particular palaeoenvironmental parameters, calm conditions, relatively low sedimentation rates, and intermediate organic carbon content. The relationship with seasonal shifts in the food flux (Jumars et al. 1990; Löwemark et al. 2006), in cases associated with changes in upwelling conditions during glacial/interglacial periods (Wetzel et al. 2011) and Milankovitch-scale climatic variations (Rodríguez-Tovar et al. 2011), is of a special interest.

Several ethological models have been proposed: as deposit feeding, detritus feeding, refuse dump, cache, gardening or chemosymbiosis, among others (Seilacher 1967; Wetzel & Werner 1981; Kotake 1989, 1991; Bromley 1991; Ekdale & Lewis 1991; Olivero & Gaillard 1996; Bromley & Hanken 2003; Löwemark et al. 2004; Knaust 2009; Zhang et al. 2015a). Younger Zoophycos has been interpreted as a result of a few feeding strategies, such as surface detritus feeding, cache behaviour or gardening (Löwemark & Werner 2001; Löwemark & Schäfer 2003; Löwemark & Grootes 2004; Löwemark et al. 2008; see recent revision by Löwemark 2015). There have only been a few papers on the evolutionary trend of Zoophycos (e.g. Olivero & Gaillard 2007; Seilacher 2007; Zhang et al. 2015b). The work of Zhang et al. (2015b) highlights the macroevolution of Zoophycos since 541 Ma, with scarce data on the Cretaceous–Palaeogene boundary interval and the Palaeogene–Neogene transition, supposedly because of a general absence of continuous sections containing this trace fossil. These authors pointed out: that the high occurrence frequencies of Zoophycos in the Cretaceous–Cenozoic were closely linked with the ever increasing shelf areas and with plankton blooms, most importantly coccoliths, which enhanced the nutrient supply to the deep sea. Unlike the three aforementioned two-direction radiations, the radiations after the K-Pg mass extinction took only one direction from the shallow bathyal to deep bathyal (Zhang et al. 2015b, p. 7). Zhang et al. (2015b), in summary, focused only on the large-scale bathymetrical shift of the Zoophycos group, from littoral–neritic to bathyal environments during the Phanerozoic. The Cenozoic macroevolution of Zoophycos can be more completely documented on the basis of the continuous pelagic section of the
Gubbio area (Bottaccione and Contessa) that offers excellent age control through magneto, bio, chemo and tephrostratigraphy, direct radioisotopic dating and the continuous occurrence of Zoophycos, as presented in this paper for the first time.

Morphological features of Zoophycos in the Central Apennines

Only a few studies contain reports or descriptions of Zoophycos in the Central Apennines (Valeri 1975; Bellotti & Valeri 1987; Uchman 1995; Montanari & Koebel 2000; Monaco & Checconi 2008). Recently, Monaco et al. (2012, 2015) analysed this important trace fossil in the Upper Cenomanian and in the Cretaceous–Palaeogene (K-Pg) boundary intervals showing its distribution in association with other trace fossils, such as Chondrites, Planolites, Thalasinooides and Trichichnus. The overlying deposits, such as the Palaeogene Scaglia Rossa, Middle–Upper Eocene Scaglia Variegata, Upper Eocene – Lower Miocene Scaglia Cinerea and the Lower Miocene (Aquitanian to mid-Burdigalian) Bisciaro Formation at Gubbio, contain a high concentration of Zoophycos, with a morphology that is different from the older strata. The differences in morphology of Zoophycos in the Gubbio area through the Lower Cretaceous to Lower Miocene interval were never analysed. The most conspicuous difference is the variation in morphology in relation to stratigraphical position.

(A) Major ‘lamellae’. The term ‘lamellae’ widely used in the literature is misleading in describing only the surficial expression of the structure (‘primary lamellae’, Löwemark & Schäfer 2003; Löwemark et al. 2004; Olivero & Gaillard 2007; Zhang et al. 2015a,b, fig. 28.9; ‘generic laminae’ in the modern Zoophycos from the Celebes Sea by Löwemark et al. 2004). In fact, the ‘lamellae’ exhibit features of overlapping ‘tunnel’ or ‘tubs’; therefore, the term ‘tunnels’ or ‘tubes’ should be more appropriate (the thickness of a lamella is <2–3 mm, see Colacicchi & Monaco 1994). These ‘tunnels’ or ‘major lamellae’ migrate laterally in a radial manner, clockwise, being fixed in the apex in all Zoophycos studied. The resultant cumulative structure (Bromley 1996) is a radial structure composed of numerous, partly overlapping J-shaped spreite structures that originally can be U-shaped. These structures, when the worm completes the work, form cumulative structures (spreites in Zhang et al. 2015b; see the cumulative structures in Bromley 1996, fig. 6.7, pp. 151–152). In lobate/tongued specimens, the J-shaped tunnels change into U-shaped protrusive burrows along the margin of the whorls, where they encircle tongue-like lobes. In epichnial view, the major ‘lamellae’ are preserved as semicircular, string-like, preferentially cemented, positive reliefs (Fig. 3A–C). Usually, about ten or more major ‘lamellae’ descend radially down from the apex (Fig. 3C). At the beginning and turning progressively clockwise (60% of specimens) or counterclockwise (40% of specimens). Usually, they assume a J-shaped form at some distance from the apex. In most specimens (40%) from the Scaglia Cinerea to Bisciaro units, the major ‘lamellae’ are straight near the apex then, they turn gradually producing a marked concavity near the margin of whorls (Fig. 3C). In other specimens (30%), they are sinusoidal, exhibiting convexity followed by a concavity (Fig. 4A). Rarely, the major ‘lamellae’ are nearly straight (Fig. 4C), or with a slight concavity only in some whorls or close to the outer margin (Fig. 4B). 20% of specimens they are disposed along a curved path directly from the apex to the margin with the same concordant concavity (Fig. 4A). The distance between two adjacent major ‘lamellae’ (in the middle of the whorl, where they are parallel or nearly parallel) is 20–35 mm. It is very interesting to note an abrupt increase in concavity (40%) in nearby specimens within the same bed (Fig. 4D). This indicates that the shape of lamellae is function of burrow construction and free space availability.

(B) Minor or internal lamellae. We prefer to use the term ‘minor’ or ‘internal lamellae’ (Simpson 1970; Bromley & Hanken 2003; Zhang et al. 2015a, b) instead of the ‘secondary lamellae’ (e.g. Olivero & Gaillard 2007) even if they are the second-order lamellae (see discussion about retrusive and protractive structures in Zhang et al. 2015a,b). The internal lamellae are indicated in Figure 3A. In the Gubbio Cenozoic deposits, Zoophycos is composed of alternating, crescentic, light- and dark-coloured minor lamellae, with or without faeces (Zhang et al. 2015b). Their thickness (1–2 mm in 70% of cases and >1.5 mm in 30% of cases) falls in the typical width range of laminae. The thicker laminae are probably swollen by diagenetically crystallized calcium carbonate affecting two or more contiguous lamellae (Colacicchi & Monaco 1994). The shape of internal lamellae varies from ‘sigmoidal’ to ‘lobate’ (Seilacher 2007, plate 38). Olivero & Gaillard (2007) indicated ‘secondary lamellae’ as effectively feeding lamellae, located obliquely between ‘major lamellae’ and revealed by an alternation of raised and grooved linear structures, locally having dark-/light-coloured alternation. They are disposed between adjacent major ‘lamellae’ and their length and shape (sigmoidal to concave) are largely variable in different
in the lobate specimens. The angle between the two types of lamellae varies from $30^\circ$ to $45^\circ$ (Fig. 3A). Usually, internal lamellae are poorly visible in limestones of the Scaglia Bianca, Scaglia Rossa and lower part of the Scaglia Variegata formations due to diagenetic obliteration of these structures in rocks of very high calcium carbonate (Colacicchi & Monaco 1994). In contrast, in the upper part of the Scaglia Variegata, Scaglia Cinerea and the Bisciaro formations, where clay content is very high, these lamellae are well preserved (Figs 3, 4). Thus preservation seems to be enhanced by the clay content, as described in some mixed deposits by Colacicchi & Monaco (1994). In the Rhizocorallium-like, U-shaped, protrusive burrow, internal lamellae are concordant, strongly convex outwards, in accordance with the disposition of the marginal tube (Fig. 3A–C; see also Seilacher 2007; plate 38, and Olivero & Gaillard 2007; Zhang et al. 2015b); they tangentially join the limbs (Fig. 5B).

(C) Lobes. Lobes protrude from the Zoophycos whorl margins or run from the apex beyond the whorl margin. They represent another important morphological component that has been noted mainly in marly limestones of the Palaeogene Scaglia Variegata, Cinerea and the Bisciaro units (Fig. 5A, B). Zhang et al. (2015b) showed Cenozoic Zoophycos with complex, helicoidal lobate spreites with several whorls (Zhang et al. 2015b, fig. 1c, d). The lobes are U-shaped, Rhizocorallium-like structures, 5–15 cm wide (average 7 cm, Fig. 5B) and up to 40 cm long (exceptionally up to 46 cm starting from the apex, Fig. 5B). The lobes usually are horizontal or slightly oblique. These structures are very similar to some U-shaped Rhizocorallium (see Knaust 2013 and some Triassic specimens of La Mancia in Spain) or Echnospira (fodinichnion of the Zoophycos group, see Uchman & Demircan 1999; Seilacher 2007). Many lobate Zoophycos have been described, although their ichnotaxonomy is not yet clarified (Bischoff 1968; Kotake 1989; Bromley 1991; Wetzel 1992, 2008; Olivero 1996, 2003, 2007, 2007; Olivero & Gaillard 1996, 2007; Uchman 1998; Uchman & Demircan 1999; Seilacher 2007; Zhang et al. 2015b). Many
authors follow Książkiewicz (1970), Książkiewicz (1977), who used Zoophycos brianteus Massalongo for oval whorls and Zoophycos insignis Squinabol for lobate forms, but the case of Zoophycos rhodensis Bromley & Hanken and some Zoophycos s.l. from France (Olivero & Gaillard 1996, 2007) show both morphologies in one structure [Zhang et al. 2015b indicated only Zoophycos brianteus and Zoophycos insignis].

In the Gubbio area, the lobes show a thick (up to 20 mm, exceptionally up to 25 mm), U-shaped major ‘lamella’ with parallel limbs, which increases in its thickness at the distal part (Fig. 3D, see also Fig. 5A, B). In some Zoophycos-rich intervals of the Eocene–Oligocene, the vertical development of lobes in different superimposed whorls is difficult to observe, especially when overlying individuals are present and compaction is strong. Thus it can be very difficult to tell whether lobes belong to different structures. The lobes correspond to U-shaped Rhizocorallium or Echinospira specimens presented by Uchman & Demircan (1999); for the Neogene, Zhang et al. (2015b, fig. 2) indicated two types of Zoophycos: the Rhizocorallium-like spiralling spreite form from the Oligocene of New Zealand or the irregularly spiralling spreite form with long lobes from the Miocene of Turkey. Lobes are also present, but less developed, in the large ‘Amuri’ Zoophycos from New Zealand (Ekdale & Lewis 1991). Lobes with J- to U-shaped spreites also occur in lophoctenids (Lophoctenium and Phycosiphon, Seilacher 2007; plate 40), but they are joined only from one side to the limb. The role and length of lobes in the Zoophycos group remain unsolved (Simpson 1970). Olivero & Gaillard (2007) suggested that the worm fed between obstacles in the sediment, for example bivalve shells (their fig. 28.2); however, this explanation requires an unrealistic regular distribution of the obstacles, which is not present at Gubbio. This is rather an expression of a predicted behaviour of the tracemaker for cache surface detritus in depth or for chemosymbiotic activity. Bromley & Hanken (2003) noted that the lobes protrude from the lowest whorl and are steepened and that they may be structures for partly chemosymbiotic feeding (see also Pervesler & Uchman 2004).

(D) Apex. The apex is another important feature and can vary in many specimens (Figs 3C, 4B). In the white limestone level of the uppermost Maastrichtian and in the reddish limestones and marls of the Palaeogene, it appears as an elevated pinnacle (70% of specimens), which is oval, round or irregular in outline (Fig. 4B). In some beds of the Scaglia Cinerea and the Bisciaro formations, the apex, if not mechanically destroyed (30%), appears as a downwards depression. It is located in the centre or near the cen-

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Fig. 5. Lobate, U-shaped radiate specimens of Zoophycos morphotype 3 from the Scaglia Cinerea Formation Contessa Highway section (now destroyed). A. radiate and whorled morphotype 3 with up to 46-cm-long lobes developed in bed, bar = 10 cm. B. Two specimens with some measures of angles and distribution of major ‘lamellae’, internal lamellae and length of lobes from the apex, scale bar = 10 cm.
tre of the structure; often, in clay deposits of the Scaglia Ciner ea and Bisciaro formations, the apex, the nearby major ‘lamella’ and the internal lamellae are bent towards the lower part of the bed, probably due to compaction (e.g. Figs 3C, 4D). It is not clear if the mechanism of this downwards curvature is primary (Olivero & Gaillard 2007) or diagenetic, because in some specimens this depression can be mainly developed in the central part of Zoophycos and less in the other parts (e.g. sample 77; see Fig. 3C).

(F) Whorls. The convex Zoophycos that is very common in mudstones/wackestones of the Scaglia Rossa and Scaglia Variegata is a typical helicoidal structure that exhibits up to 8 (exceptionally 10) whorls (Fig. 6A). The margin of each whorl is commonly regular and helicoidal in shape, and the major ‘lamellae’ of the margin are the only structure preserved (forming helicoidal structures). The general shape exhibits a marked convexity of whorls, up to 25 cm high from the apex to the whorl margin, with the larger whorls deep and the smaller shallower in the Cretaceous–Eocene interval (Fig. 6A–C). The helical whorls have been found continuously from the Upper Cenomanian (Monaco et al. 2012) up to the Upper Maastrichtian limestones, where several whorled Zoophycos specimens occur in a white, 40-cm-thick limestone bed (Fig. 6D), just below the K–Pg boundary (Montanari & Koeberl 2000; Monaco et al. 2015). In reddish mudstones of the Palaeogene Scaglia Rossa Formation, whorls show major ‘lamellae’ while internal lamellae are partially preserved due to weathering and diagenetic processes. Many whorls point to an asymmetrical shape of Zoophycos (Fig. 6C; see helicoidal shape of whorl 6).

Stratigraphical distribution

The study of about 200 Zoophycos specimens from the Scaglia Group and the Bisciaro Formation of the Gubbio area, including 90 specimens studied in detail (Table 1), brings a new contribution to the knowledge of this mysterious trace fossil (e.g. Bischoff 1968; Bromley 1991; Löwemark & Schäfer 2003; Olivero & Gaillard 2007; Seilacher 2007 among many others). Four types of morphological variants of Zoophycos can be recognized in the Gubbio area as summarized in Figure 7.

![Fig. 6. Conical Zoophycos morphotype 1 from reddish limestones of the Upper Cretaceous to Lower Palaeogene Scaglia Rossa Formation in Contessa Quarry and Highway sections. A. One convex specimen with up to eight increasing downwards whorls in size (1–8), bar = 5 cm. B, A partially preserved Zoophycos morphotype 1 with 4 whorls; note very poorly preserved apex (AP), lonely major ‘lamella’ (ML) and internal lamellae due to diagenesis, bar = 8 cm. C, Increasing downwards whorled conical specimen with the deepest elliptical whorls more enlarged (see 1–6), bar = 8 cm. D, Several whorled morphotype 1 specimens (very high ichnodensity) in the white limestone bed of latest Maastrichtian at the Bottaccione Gorge, bar = 10 cm.](image-url)
(1) Zoophycos morphotype 1. Morphotype 1 is represented by simple specimens without lobes, with up to 10, usually 4–8, convex up, steeply inclined whorls around the central, elevated apex, which are sub-circular to elliptical in outline and larger downwards; the internal lamellae are poorly preserved (Figs 6A–D, 7A–D). Type 1 is usually small, up to 30 cm high, with whorls from 20 to 40 cm wide (Figs 6A–D, 7). It is very similar to the ‘type g’ by Seilacher (2007, plate 38). The propagation of the structure is probably from the top to the bottom (downwards following the increase in the worm body size). The morphotype 1 occurs in the Scaglia Bianca and Rossa, especially from the Upper Cenomanian to Middle Eocene interval, abundantly in the white limestone key bed in the Bottaccione Gorge, immediately below the K–Pg boundary (Montanari & Koebel 2000; Monaco et al. 2015; Fig. 6D). The morphotype 1 occurs also less frequently in the Late Eocene of Scaglia Variegata. Due to early diagenetic processes, many of Zoophycos type 1 in the red or white limestones of the Scaglia Rossa exhibit steeply inclined whorls and show poorly preserved internal lamellae (Fig. 6A). The ichnodensity of Zoophycos type 1 can be very high (5 specimens/m²) in some levels, as in the white level immediately below the K–Pg boundary (Fig. 6D). This has been noted in both the Contessa and Bottaccione sections at the same horizon, probably due to a change in sedimentation rate before the K–Pg boundary crisis (this aspect needs further analyses). In the Lower Paleocene, the type 1 is lacking at 6 cm above the K–Pg boundary (Monaco et al. 2015) and then progressively increases in abundance and dimension in the overlying beds (Fig. 7). The sedimentation rate of limestones in the Upper Cretaceous–Lower Eocene interval (maximum 2.11 cm/kyr) and strong early diagenesis of pure calcareous sedimentation (calcium carbonate content about 80%) influenced the preservation of the Zoophycos type 1.

(2) Zoophycos morphotype 2. The morphotype 2 shows a helicoidal, complex arrangement of cumulative structures of regular whorls, each composed of many overlapping J-shaped structures (up to 30 for a whorl, see Bromley 1996, fig. 6.7c), which are less inclined than in the type 1. The major ‘lamellae’ are curved to straight. The internal lamellae are well preserved. The apex is convex. The constructional model of type 2 resembles specimens figured by Löwemark & Schäfer (2003) (partially visible in Fig. 3B); the helicoidal arrangement is not clear. The ‘complex spiral form’ from the Jurassic of France (Olivero & Gaillard 2007, fig. 28.5) is not developed due to the very high compaction of marl sediments at Gubbio. The morphotype 2 is common in the upper part of the Scaglia Rossa and Scaglia Variegata where calcium carbonate decreases and clay progressively increases, in both the Bottaccione and Contessa sections (Fig. 7).

(3) Zoophycos morphotype 3. This is a typical lobate form with long, radially disposed, U-shaped Rhizocorallium-like lobes (Figs 3D, 5A, B). The marginal ‘tube’ (here not ‘lamella’) and internal concave lamellae are often black because of the high content of organic matter; laminae are preserved in about 50% of specimens. Some long lobate specimens are very similar to Echinospira isp. presented of Uchman & Demircan (1999) and Seilacher (2007), but they differ from the forms illustrated by Löwemark et al. (2004, fig. 2). The morphotype 3 shows lesser ichnodensity than types 1 and 2, but it is wider than the previous ones. It is abundant in marl-clay deposits of the upper Scaglia Variegata and Scaglia Cinerea formations (Upper Eocene–Lower Oligocene).

(4) Zoophycos morphotype 4. Zoophycos morphotype 4 is a simple, planar, poorly whorled flat form (Fig. 4A–C), with a reverse or flat apex at the centre of the structure. This form is not indicated in the evolutionary model of Zhang et al. (2015a,b), but it is the most abundant Zoophycos (very high ichnodensity) in the Gubbio sections. Minor lamellae commonly form lunate structures with a curved or straight course (Fig. 4A–D). About 70% of specimens show flattening due to compression or exhibit a downwards trend close to the apex. This type should be analysed in cross-section to observe a complete structure, but now all specimens have been destroyed by quarrying. This is a problem in the Contessa Highway section where all specimens are lost. The poorly whorled flat type 4 is common in the hemipelagic, grey marls of the upper Scaglia Cinerea and Bisciaro formations (Middle Oligocene–Lower Miocene) in the Contessa Highway section where clay-rich sediment was easily flattened by burial (Fig. 7). These deposits very rich in morphotype 4 display an upwards increase in volcaniclastic material that was distributed in the whole Umbro-Marchean Basin during the Oligocene and Early Miocene (Montanari et al. 1997). In many specimens from the Bisciaro Formation (Fig. 2), contiguous Zoophycos can display an abrupt increase in bending of the major and minor lamellae at the contact between specimens (Figs 3C, 4D).

**Evolutionary trend and ichnodensity**

The evolutionary trend from circular to lobate (e.g. the ichnosubgenus Echinospira of Seilacher 2007, p. 110, plate 38) and to flat morphotypes from the
Upper Cretaceous to the Lower Miocene at Gubbio contributes to the stratigraphical knowledge of this debatable trace fossil. The evolutionary trend proposed by Seilacher (2007) and in Jurassic–Cretaceous specimens by Olivero & Gaillard (2007, fig. 38.13) is not represented in the Contessa-Bottaccione sections. In fact, the flat Zoophycos from the Lower Miocene Bisciari Formation follows in time the lobate Zoophycos from the Upper Eocene–Oligocene Scaglia Group (Fig. 7). This seems to be a recurrence of simple shapes. Evolutionary trends proposed by some authors on the basis of material from France (Olivero 2007; Olivero & Gaillard 2007), Turkey (Uchman & Demircan 1999) and New Zealand (Ekdale & Lewis 1991), exhibit changes from the Cretaceous to the Neogene deposits (Zhang et al. 2015b). At Gubbio, the change of sedimentation from pure limestones to marls does not explain alone the high abundance of Zoophycos. Periodic changes of primary sedimentation must be proposed to explain this abundance, such as rhythmical accumulation of phytodetritus, high influx of planktonic food and progressive introduction on the seafloor of volcanoclastic grains that may contribute to a development of bacteria (Kotake 2014). Other peaks of abundance, such as noted immediately below the K–T boundary (Monaco et al. 2015), indicate a sudden change in the sedimentation rate before the impact event at the end of the Cretaceous. In the Apennines, Zoophycos blooms are noted in thin marly levels within the Maiella (L. Passeri, personal communication), and in the Laga flysch units (R. Colacicchi, personal communication; Monaco 1989) before important sedimentary events (G. Ciarapica, personal communication).

The evolutionary trend of the Zoophycos studied and its ichnodensity, therefore, follow the type and rate of the sedimentation, the firmness of the sub-
strate, the tracemaker’s ethological activity, the growth of the organism and the geological context (e.g. rhythmical settling of food and TOC in the seafloor, change of environment). The constructional model of Zoophycos (e.g. downwards or upwards, propagation of the whorls; see Löwemark & Schäfer 2003; Löwemark et al. 2004; Olivero & Gaillard 2007) cannot be solved easily in the studied sections, because of a strong flattening of whorls in marls and high density, which make it difficult to observe complete specimens.

Ethological considerations

The main point emerging from the studied morphotypes is that the ‘major lamellae’ are relicts of the radial, outwards movement of the animal(s). Laminae are always well cemented and with a diameter decidedly greater than a typical lamina; moreover, the internal lamellae are tangential to perpendicular to marginal tube. If these lamellae are ‘deposit-feeding lamella’ (Olivero & Gaillard 2007), or ‘cache food’ for chemosynthesis promoted by high concentration of organic matter on the seafloor (Jumars et al. 1990; Bromley 1991; Löwemark et al. 2004), the J-shaped major ‘lamella’ represents the main burrow hosting the full body of the tracemaker (a sipunculid worm?), permitting its forwards/backwards movement during feeding or cache activity, from the surface to the depth of its burrow, and producing lamella after lamella during processing of muddy soft sediment. According to these two models, after feeding or caching, the worm retreated its body into the same tube — contributing with its mucus and faeces to an early cementation — and protruded forward in a more advanced position to start again produced another lamella parallel to the previous one. As indicated by Petrash et al. (2011), mucous excretions, composed primarily of the glycoprotein mucin, play important roles in the burrow stabilization. Thus, following the previous interpretation, the internal lamellae are well cemented and represent progressive lines of ‘mining’ activity of a worm. This takes some time to spend on mining all the substrate available, without returning to the place already travelled. In this manner, lamellae are parallel and equidistant, or, in the case of lobes, concave towards the apex (Simpson 1970). This produces a cumulative, complex, 3-D structure, which grows in time (see e.g. the model of Dactyloidites ottoi figured in Bromley 1996, fig. 6.7c). This can be an interesting type of growth producing a very complex structure for the presence of thousands of lamellae in different whorls. This seems unlikely for a single worm, though the hypothesis of a one worm, which produced a large structure during its life (D. Olivero, personal communication). It is possible that many worms were active (impossibly at different times) to produce superimposed structures with thousands of lamellae. The very high frequency of flat Zoophycos can be explained by a superimposition of generations of burrowers to cache food on the seafloor depending on the “windfall” of seasonal phytodetritus (Jumars et al. 1990) under a very low sedimentation rate (~0.42 cm/kyr). Moreover, the volcanic ash discovered in sediments studied (Bisciario Formation, Guerrera & Veneri 1989; Amorosi et al. 1994; Guerrera et al. 2015) can trigger the primary production by iron and sulphur minerals and in consequence a higher supply of food to seafloor and proliferation of bacteria on the seafloor (Fig. 2).

Concerning ethological behaviour, Löwemark et al. (2004) do not accept a ‘deposit-feeding activity’, but proposed a ‘detritus-feeding model’ or much better the ‘cache model’ (see Jumars et al. 1990; Bromley 1991): the surface material was collected by a worm (with jaws in their figure 2) during phases of high food concentration, returning to search the stored material on the seafloor during times of low food flux. This activity agrees with the introduction of organic-rich, nutritional surface sediment. This model is supported by stable isotope analysis, without fundamental variations in δ13Corg between spreites and adjacent host sediment. For these authors, the introduction of a large amount of organic carbon-rich surface material contrasts with a deposit feeding activity alone in modern deep-sea Zoophycos. This model is valid, but in any case needs further analyses, not only for lobate Echinospira-like Zoophycos from the Upper Eocene and Lower Oligocene of the Gubbio area but also for all morphotypes from the Cretaceous to the Miocene (Fig. 7).

Another new observation from Gubbio concerns the number of whorls and external outline of whorls in the specimens studied. About 100% of the Cretaceous–Lower Palaeogene morphotypes show widening of whorls downwards, opposite to the Jurassic morphotypes presented by Olivero & Gaillard (2007) which widen upwards for 95% of them, and downwards only for 5%. The value of proportions clockwise (and counterclockwise), arrangements, is nearly the same as observed by Olivero & Gaillard (2007, fig. 28.6), with a slight dominance of counterclockwise turning compared to clockwise (60% versus 40%).

The contribution of the four morphotypes in the studied Contessa and Bottaccione sections is summarized in Figure 7, which also shows the shape, ichnodensity, ichnocomplexity and dimen-
Conclusions

The study of about 200 Zoophycos specimens, including 90 specimens studied in detail, highlights differences from Upper Cretaceous to Lower Miocene in the Gubbio area sections, which reflects continuous pelagic sedimentation from the Upper Cretaceous to the Lower Miocene, with excellent age control through magneto, bio, chemo and tephrostratigraphy and direct radioisotopic dating. Four morphotypes of Zoophycos recognized here occupy defined stratigraphical position (except in a few cases the co-occurrence of types 1 and 3, and 2 and 4), testifying to different environmental conditions from a carbonate basin plain of the lower Scaglia Group (Scaglia Bianca and Scaglia Rossa formations) to a gentle slope, with an increasing content of clay and fine-grained siliciclastic deposits in the Palaeogene (pre-flysch deposits), perhaps with a change of the seafloor inclination and probably a shallowing due to the progressive development of the Northern Apennines foredeep. The very high ichnodensity (up to hundreds of specimens in a few tens of square metres) indicates calm waters and stable substrates. The progressive increase in clay content from the Upper Eocene in the basin (documented in several papers from the region), e.g. Coccioni et al. (1988) and the high amount of volcaniclastic grains from the Late Eocene (mica beds used for geochronology; Premoli Silva et al. 1988b); culminating in volcaniclastic sediments, also turbidites) in the Lower Miocene Bisciaro Formation (Guerrera et al. 2015) promoted primary production of food, and in consequence, favoured abundance of Zoophycos. The environmental changes probably led to a change in Zoophycos morphology, from a few whorl structures in the Cretaceous–Eocene to many whorled and larger forms in the Eocene–Miocene interval. All the changes need further geochemical analyses (beyond the scope of this paper).

We agree with words of Seilacher (2007): ‘at the moment, there is no simple explanation for all the intricacies of Zoophycos and its evolutionary modifications. The problem will probably stay with us for a while’.

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