

Zoophycos-like structures associated with dinosaur tracks in a tidal-flat environment: Lower Jurassic (Southern Alps, Italy)

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SUMMARY - *Zoophycos-like structures associated with dinosaur tracks in a tidal-flat environment: Lower Jurassic (Southern Alps, Italy)* - This study reports, for the first time, the occurrence of *Zoophycos*-like structures in the Lower Jurassic of the Italian Alps (Calcarei Grigi Group) through the description of the specimens found in the dinosaur tracksite of Lavini di Marco (Trentino, Southern Alps). The sedimentological features of the layers bearing the *Zoophycos*-like forms can be related to a coastal tidal-flat environment; data in our possession highlight that dinosaurs and the tracemaker of the *Zoophycos*-like structures frequented adjacent environments and possibly the same ones. The occurrence of *Zoophycos*-like structures in peritidal environments possibly represents an important contribution to the evolutionary history of *Zoophycos* in the Eastern Southern Alps.

RIASSUNTO - *Strutture Zoophycos-like associate a orme di dinosauri in ambiente di piana tidale: Giurassico inferiore (Alpi Meridionali, Italia)* - Questo studio documenta per la prima volta la presenza di strutture simili a *Zoophycos* nel Giurassico inferiore delle Alpi italiane (Gruppo dei Calcari Grigi) attraverso la descrizione di esemplari rinvenuti nel sito ad orme di dinosauro dei Lavini di Marco (Trentino, Alpi meridionali). Le caratteristiche sedimentologiche del livello che conserva gli icnofossili *Zoophycos*-like corrispondono a quelle di un ambiente di piana tidale; i dati in nostro possesso mettono in evidenza che i dinosauri e i tracemaker di *Zoophycos*-like popolavano ambienti adiacenti se non il medesimo. La presenza di strutture *Zoophycos*-like in ambiente di tipo peritidale rappresenta un importante contributo alla storia evolutiva di *Zoophycos* nel Sudalpino orientale.

Key words: *Zoophycos*, Lavini di Marco, dinosaurs, ichnology, Eastern Southern Alps

Parole chiave: *Zoophycos*, Lavini di Marco, dinosauri, icnologia, Sudalpino orientale

1. INTRODUCTION

1.1. Geological and geographical setting

The dinosaur tracksite at Lavini di Marco (Southern Alps) is well known for the abundant dinosaurian ichnofauna (Leonardi & Mietto 2000) (Fig. 1). The dinosaur track bearing layers are attributed to the lower part of the Calcarei Grigi Group (Lower Jurassic) (Avanzini *et al.* 1997). More precisely, the trampled layers are included in the “Peritidal unit” of the Monte Zugna Formation, late Hettangian to Sinemurian in age (Masetti *et al.* 1998). This stratigraphical unit corresponds to a coastal tidal-flat environment and is characterized by peritidal shallowing-up metrical cycles: each cycle presents an inferior subtidal bed on which an inter-supratidal layer is superimposed (Masetti *et al.* 1998).

While the dinosaur traces have been the subject of wide study (Lanzinger & Leonardi 1991; Leonardi & Avanzini 1994; Dalla Vecchia 1994; Avanzini *et al.* 1997; Leonardi & Mietto 2000) on the other hand non-dinosaurian ichnology has not been discussed, either for Lavini di Marco or for the basal part of the Calcarei Grigi Group. Monaco & Giannetti (2001,

2002) and Monaco & Garassino (2001) paid attention exclusively to the upper part of the Group (Rotzo Formation).

1.2. Sedimentological setting

The stratigraphical succession of Lavini di Marco is organized in peritidal sequences characterized by the alternation of mainly subtidal beds (bioclastic and peloidal wackestone; oolitic packstone) with layers attributed to an inter-supratidal environment (wackestone and stromatolitic bindstones with desiccation structures and fenestrae) (Fig. 2).

In this study, a basal cycle, corresponding to the layers named in the Lavini di Marco literature (i.e. Avanzini *et al.* 1997) 104, 105 and 106, is described (Fig. 2B). Abundant iron oxides concentrated into veins, laminae or globular bodies, fragments of red carbonated mud, small holes filled with silt and sparry calcite, and chemical transformations are indicative of subaerial exposure of these levels (Avanzini *et al.* 1997).

Layer 104 is constituted of mudstones coarsening upwards to packstone/grainstone, with coated grains and skeletal remains. The depressions present in the upper part of the

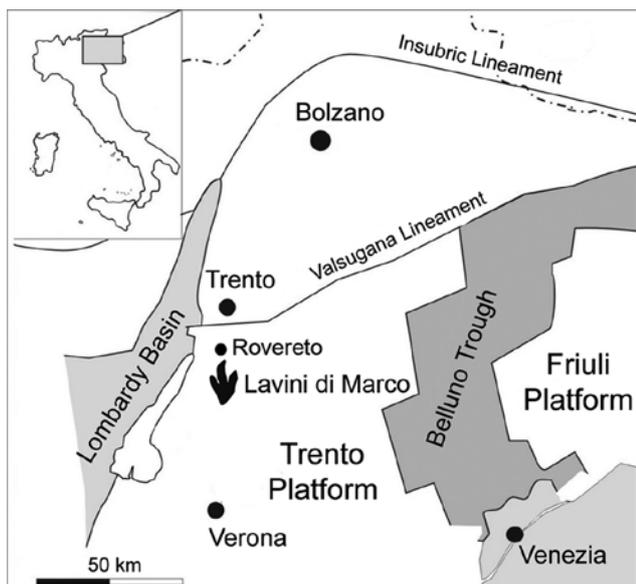


Fig. 1 - Geographic location of the Lavini di Marco ichnosite with an indication of the main Lower Jurassic palaeogeographic domains of the Southern Alps.

Fig. 1 - Localizzazione dell'ichnosito dei Lavini di Marco nell'ambito dei principali domini palaeogeografici delle Alpi Meridionali nel Giurassico inferiore.

layer were filled by laminated mud covered by a crust composed of dolomite, calcite, clays and iron oxides. The topographic characteristics of level 104 are reminiscent of the lateral microkarstification of present day tropical islands. This layer is interpreted (Avanzini *et al.* 1997) as a representative of a subtidal environment, which came rapidly to subaerial exposure when karstification of the tidal flat occurred.

Layers 105 and 106 constitute a decimetre-scale set (Fig. 2).

Level 105 is an alternance of stromatolitic bands, peloidal grey wackestone and reddish mudstone with a thickness that ranges from 15 mm to 100 mm. Its upper part presents mud-cracks with a diameter of 10-30 up to 50 mm. This level shows a vertical alternance of several emersions and drowning with strong environmental changes in a few centimeters of section. The influence of both marine and fresh water is testified respectively by the presence of the marine alga *Thaumatoporella* and the values of the isotopic ratios ($\delta^{18}O$ from -0.5 to 10/00) and by the absence of typical marine organisms (i.e. foraminifers, brachiopods) and microtextures. Diagenetic and sedimentologic features seem to indicate a prevalence of emersion and a possibly distant coastline. Comparison with present carbonate platforms in a tropical humid climate shows that the lenses of fresh water were ephemeral when level 105 formed (Avanzini *et al.* 1997).

Level 106 is 100 to 150 mm thick and presents a high lateral variability. Stromatolites and flat pebbles breccias are common. Level 106 was less exposed to subaerial alteration than level 105. It represents sedimentation in brackish pond ($\delta^{18}O$ from +2 to +40/00), emerged bars and shallow pools intercalated.

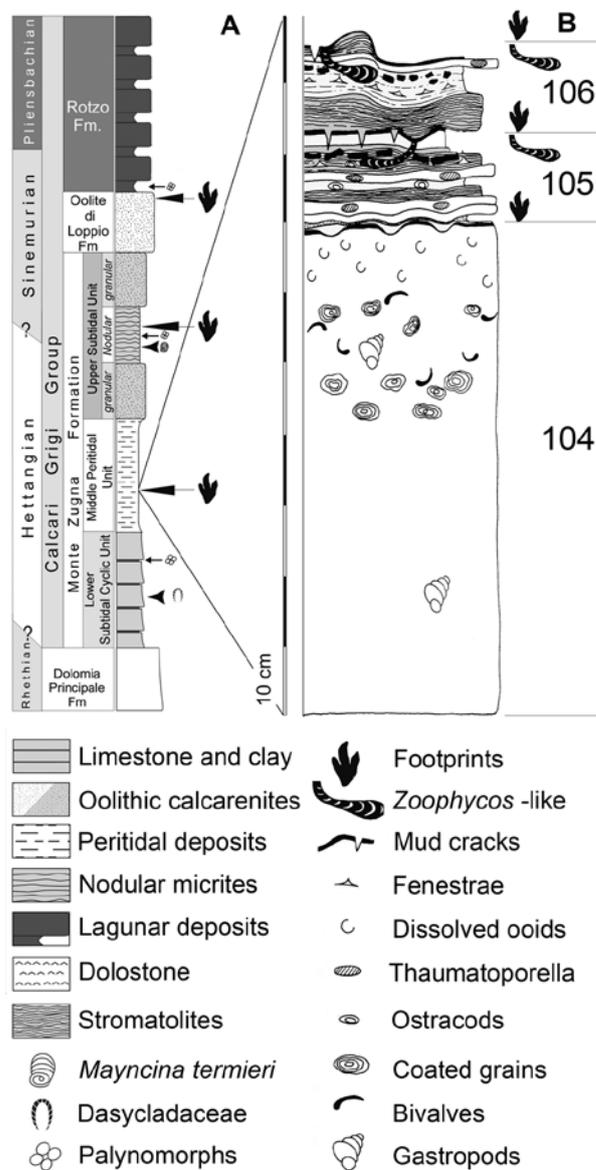


Fig. 2 - Stratigraphical setting. A. Stratigraphy of the Calcarei Grigi Group (from Avanzini *et al.* 2006). B. Detail of the facies cycle considered in the text; *Zoophycos*-like structures have been found in the inter-supratidal dolomitized facies corresponding to layers 105 and 106.

Fig. 2 - Assetto stratigrafico. A. Stratigrafia del Gruppo dei Calcarei grigi (da Avanzini *et al.* 2006). B. Dettaglio della sequenza di base considerata nel testo; le strutture *Zoophycos*-like sono state identificate nelle facies dolomitizzate inter-sopratidali corrispondenti ai livelli 105 e 106.

The whole set consisting of layers 105 and 106 is interpreted (Avanzini *et al.* 1997) as a representative of a complex inter-supratidal environment.

1.3. The trace fossils assemblage

Although the assemblage of trace fossils from Lavini di Marco is in a study stage, we can anticipate that the prevalently subtidal bed 104 bears convex structures ascribed

to *Thalassinoides* at the basis, while the stratum body appears totally bioturbated. On the upper surface, layer 104 shows several dinosaur footprints (mainly theropods) and various locomotion traces constituted by narrow crests or parallel furrows (they are interpreted as produced by gastropods and, doubtfully, by arthropods – cf. *Pterichnus* in Gaillard *et al.* 2005).

The inter- supratidal set (layers 105 and 106) maintains a moderately diversified ichnoassociation. On the lower bed junction of each layer, convex branched structures are commonly found. They are comparable with *Thalassinoides*; on the upper layers junctions very similar traces are found preserved as concave burrows. Abundant footprints of small (i.e. *Grallator*, *Kayentapus*, *Anomoepus*) and large dinosaurs (i.e. *Parabrontopodus*, *Lavinipes*) are common. Several invertebrate trace fossils of the bedset corresponding to layers 105 and 106, have a darker calcareous fill in common. Among the traces highlighted by this peculiar fill, numerous spreite structures are recognized, among which there are structures identifiable with the ichnogenus *Rhizocorallium* and those similar to *Zoophycos*.

2. MORPHOLOGY OF THE ZOOPHYCOS-LIKE SPECIMENS FROM LAVINI DI MARCO

The *Zoophycos*-like structures are concentrated in layers 105 and 106. In planar view, the structures exhibit a spreite with a helicoidal arrangement; the spreite comprises many C- or J-shaped units. Their arrangement typically results in a roughly circular outline shown by the whole structure (Fig. 3A). Some specimens do not fulfill such an outline completely (Fig. 3D, 3F). This fact could be retraced either to preservational or constructional (i.e. the partial development of the structure) mechanisms.

The structures are often highlighted by a filling that is darker than the host rock, analogous to the flat-pebble breccia at times characterizing the top of layers 105 and 106 exposed in dolomitized facies.

The width of the specimens (intended as the distance between the apical point and their external margin) usually varies between 43 and 72 mm. The coiling could be both dextral and sinistral. Locally the trace shows lobate appendages, characterized by a centimetre-scale width; these appendages exhibit a similar development pattern compared to the general coiling of the structure (Fig. 3F). When observed in section the trace consists of a meniscate-like pattern, arranged as an alternation of lamellae, which are light (according to the host sediment) and dark (according to the chromatical/lithological dominance seen in planar view). When it has been possible to determine the contacts between adjacent lamellae clearly, the combined width of a dark and a light one has been measured; the combined width of a dark plus a light lamella is comprised between 0.8 and 1.7 mm. The dark lamellae are often thicker than the light ones, according to an approximate ratio of 1:6. The mean height

of the lamellae, corresponding to a single whorl of the trace, ranges between 1.4 and 4 mm. When the structures are examined in polished slabs, the dark lamellae usually have a homogeneous appearance, even if a structure made up of peloids can sometimes be observed (Fig. 3C). When the traces are observed in thin sections, the dark lamellae show a structure supported by calcite peloids (sometimes of skeletal origin) floating in a matrix that contrasts with the host sediment. On the contrary, light lamellae have textural features that reflect those of the host sediment (Fig. 4B).

The above described structures are reminiscent of the ichnogenus *Zoophycos*.

According to Rodríguez-Tovar & Uchman (2004) (after Frey 1970; Häntzschel 1975; Wetzel & Werner 1981; Fillion & Pickerill 1984) *Zoophycos* is identified as a spreite structure comprising small, more or less U- or J- shaped, protrusive burrows of variable length and orientation, arranged in helicoid spirals with an overall circular, elliptical or lobate outline; a central vertical tunnel or marginal tube may be present.

According to the general morphology of the studied structures it is possible to exclude ichnotaxonomical correspondences with the morphologically similar ichnogenus *Rhizocorallium*, which is represented by oblique or horizontal U-shaped spreite structures (i.e. Fürsich 1974; Häntzschel 1975; Uchman *et al.* 2000; Uchman & Gaździcki 2006). In fact, the spreite of *Rhizocorallium* comprises juxtaposed U-shaped units, while the spreite of the Lavini di Marco structures include C-shaped units coiled helically around a fixed extremity of the “C”. This fact results in differing morphologies: *Rhizocorallium* is commonly represented by tongue-shaped burrows (i.e. Fürsich 1974; Uchman *et al.* 2000), while the Lavini di Marco structures develop a roughly circular outline.

These elements differentiate the above described structures from the ichnogenus *Rhizocorallium*, therefore it is possible to exclude that the here studied structures belong to diagenetically transformed *Rhizocorallium*.

The spreite structures from Lavini di Marco present several diagnostic features analogous with those of the ichnogenus *Zoophycos*. In particular the spreite structure, the helicoidal arrangement and the circular or elliptical outline are common elements of the ichnogenus *Zoophycos* and the Lavini di Marco structures.

Even though the Lavini di Marco spreite structures exhibit a general morphology consistent with the ichnogenus *Zoophycos*, they present considerable differences when they are compared to some representative examples of *Zoophycos* (i.e. Miller & D’Alberto 2001; Bromley & Hanken 2003; Olivero, 2003; Pervesler & Uchman 2004).

In particular, the limited size of the Lavini di Marco spreite structures is the most obvious distinguishing element with regard to the most typical occurrences of *Zoophycos*. In fact, several forms of *Zoophycos* present a markedly larger size with respect to the Lavini di Marco spreite structures (see the specimens described by Miller & D’Alberto 2001;

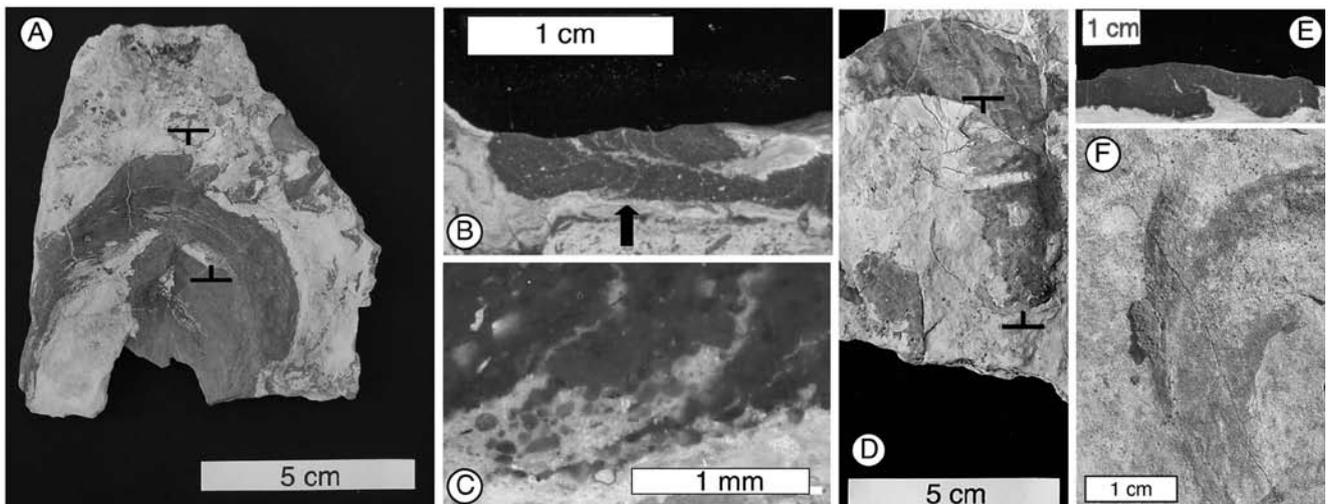


Fig. 3 - *Zoophycos*-like specimens and their cross sections. A. *Zoophycos*-like structure; the superimposed symbols indicate the trace of the section illustrated in figure 3B. B. Polished slab of the specimen illustrated in figure 3A. The arrow points out the area corresponding to figure 3C. C. Detail of the spreite pertaining to the specimen in figures 3A and 3B. D. *Zoophycos*-like structure; the superimposed symbols mark the trace of the section in figure 3E. E. Polished slab of the specimen illustrated at figure 3D. F. *Zoophycos*-like structure, field photograph.

Fig. 3 - *Esemplari Zoophycos-like e loro sezioni oblique. A. Struttura Zoophycos-like; i simboli indicano la traccia della sezione illustrata in figura 3B. B. Sezione lucida del campione illustrato in figura 3A. La freccia indica l'area che corrisponde alla figura 3C. C. Dettaglio dello spreite del campione nelle figure 3A e 3B. D. Zoophycos-like; i simboli sovrapposti marciano la traccia della sezione in figura 3E. E. Sezione lucida del campione illustrato nella figura 3D. F. Struttura Zoophycos-like, fotografia in affioramento*

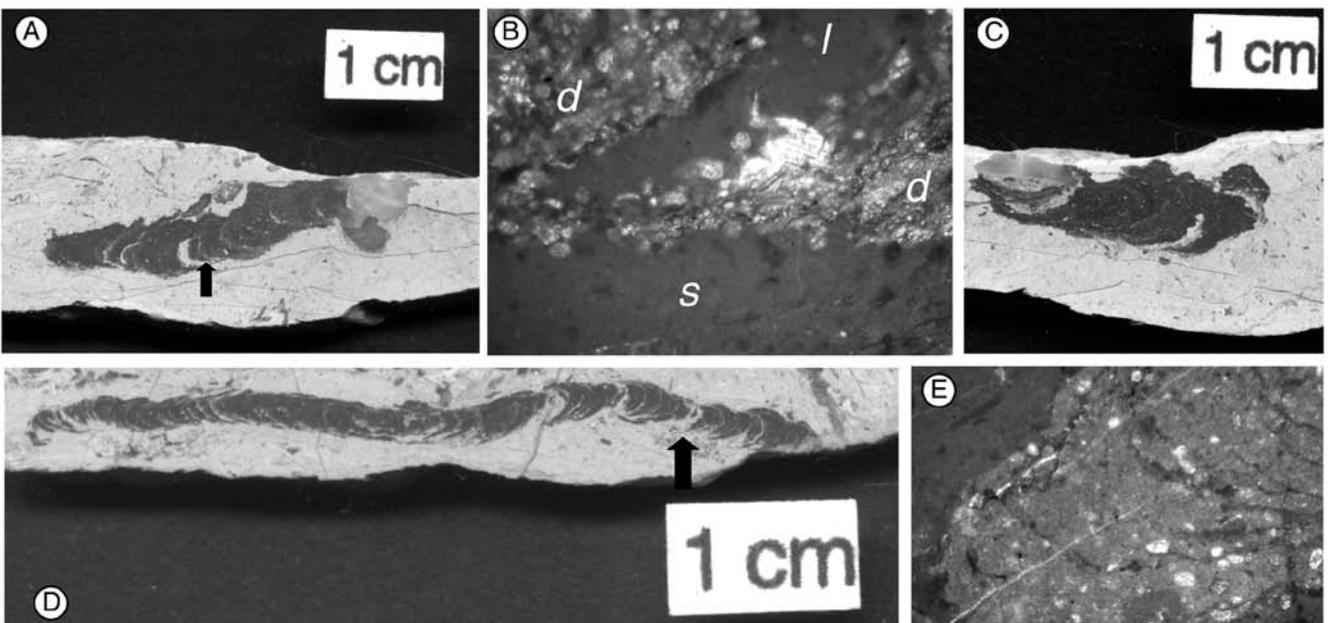


Fig. 4 - *Zoophycos*-like specimens and their cross sections. A. Meniscate structure observed in thin section; the arrows point to the area corresponding to figure 4B. B. Thin section of the structure illustrated in figure 4A (image width: about 2.5 mm; parallel nicols). The superimposed italics mark the spreite constituents (d: dark lamella; l: light lamella) and the sediment not affected by the structure (s: host sediment). C. Spreite examined in polished slab. D. Meniscate structure; the arrow points to the area corresponding to figure 4E. E. Thin section of the specimen at figure 4D (image width: about 2.5 mm; parallel nicols).

Fig. 4 - *Strutture Zoophycos-like e loro sezioni oblique. A. Struttura meniscata osservata in sezione sottile; le frecce indicano l'area che corrisponde alla figura 4B. B. Sezioni sottili della struttura illustrata in figura 4A (ampiezza immagine: circa 2.5 mm; nicols paralleli). Le lettere in corsivo indicano le parti diverse dello spreite (d: lamella scura; l: lamella chiara) e il sedimento non coinvolto dalla struttura (s: sedimento ospite). C. Spreite osservato in sezione lucida. D. La struttura meniscata; la freccia indica l'area che corrisponde alla figura 4E. E. Sezione sottile del campione di figura 4D (ampiezza immagine: circa 2.5 mm; nicols paralleli).*

Bromley & Hanken 2003; Olivero 2003; Pervesler & Uchman 2004). The width of the Lavini di Marco spreite structures recalls *Spirophyton* (i.e. Miller & Johnson 1981; Gaillard *et al.* 1999), a trace fossil morphologically similar to *Zoophycos*. Apart from size, the Lavini di Marco structures are not consistent with the basic morphology of *Spirophyton*, characterized by well-developed vertical growth, a spreite arranged in numerous whorls and an often materialized vertical axis (see Miller & Johnson 1981; Gaillard *et al.* 1999).

As above mentioned, the circular to elliptical outline is one of the common elements shared by the ichnogenus *Zoophycos* and the Lavini di Marco spreite structures. Nevertheless, the spreite structures from Lavini di Marco exhibit a roughly circular outline, sometimes partially developed, while most of the typical *Zoophycos* has a more regular shape and a more complete development of the circular to elliptical geometry (Miller & D'Alberto 2001; Olivero 2003).

For these reasons the spreite structures from Lavini di Marco cannot be assigned with certainty to the ichnogenus *Zoophycos*, even though the affinities between *Zoophycos* and the Lavini di Marco forms are significant.

The caution regarding the identification of the Lavini di Marco forms as *Zoophycos* is also supported by the need of revision proposed for the ichnogenus *Zoophycos* itself (i.e. Gaillard *et al.* 1999; Bromley & Hanken 2003): at present day *Zoophycos* is still a vivid taxonomic problem (see Olivero 2007). In fact, the ichnogenus *Zoophycos* includes a very broad range of morphological characters (see Olivero & Gaillard 1996; Bromley & Hanken 2003; Löwemark & Schäfer 2003; Olivero 2003; Löwemark *et al.* 2004) as testified by the large variety of forms known as *Zoophycos*.

For the above stated reasons the term “*Zoophycos*-like” is used here to indicate the Lavini di Marco spreite structures.

3. CONSTRUCTIONAL AND BEHAVIORAL INTERPRETATION OF THE ZOOPHYCOS-LIKE STRUCTURES AT LAVINI DI MARCO

The pellets characterizing the dark lamellae show rather uniform features as regards dimensional properties, mineralogical composition and roundness; such sorting, together with the quite rigorous geometrical organization of the lamellae, makes a direct biological cause for the fill of the *Zoophycos*-like specimens from Lavini di Marco plausible. Thus, it seems very likely that the dark fill displayed by the *Zoophycos*-like specimens of Lavini di Marco is to be considered as active.

The textural features displayed by the dark fill are comparable with the ones of the dark pebble breccia retraceable at the top of each stratum of the inter- supratidal bed set (layers 105 and 106).

For this reason it could be assumed that the tracemaker has brought darker material from the surface into the deeper part of its burrow.

This fact is partially consistent with the lithologic differences between spreite and surrounding sediments noticed for *Zoophycos* by Simpson (1970), Ekdale & Bromley (1983) and Kotake (1989, 1991). In modern *Zoophycos* similar results are testified by Chamberlain (1975), Ekdale (1977), Wetzel & Werner (1981), Fu & Werner (1994) and Löwemark & Schäfer (2003).

As previously described, some *Zoophycos*-like specimens present a roughly circular outline (Fig. 4A), while some others do not completely fulfil such an outline (Fig. 4D, 4F). The latter forms possibly correspond to the partial development of the whole structure which is represented by the roughly circular forms. According to this interpretation, the spreite was constructed by the consecutive creation of C-shaped burrows departing from a common point and following a sub-parallel arrangement with regard to the burrows previously formed (Fig. 5). As the spreite grew, the new-formed burrows gradually increased their size with respect to the previous ones. Since the individual burrows were connected to a central common point, the growing structure revolved and the helical coiling developed. Probably the central common point corresponded to the lower end of a shaft connecting with the seafloor, even if the presence of such a structure can be only inferred.

The above described model has common elements with the one of Olivero & Gaillard (2007) (one opening at the sea

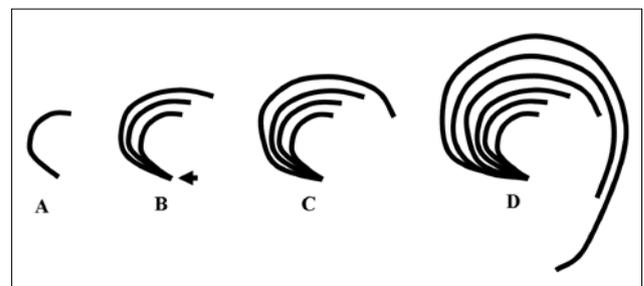


Fig. 5 - Inferred development of the *Zoophycos*-like spreite as seen in planar view: four moments of the spreite construction are schematically represented. A. A C-shaped burrow is constructed. B. New burrows departed from a common point (arrowed) and maintained a sub-parallel arrangement with regard to the burrows previously formed. Possibly the common point corresponded to the lower end of a shaft connecting with the sea-floor. C. Because the individual burrows were connected to a common point, the growing structure tended to revolve. D. The structure gradually increased its size with the development of helical coiling.

Fig. 5 - Ipotesi di sviluppo dello spreite della struttura *Zoophycos*-like in vista planare: sono rappresentati schematicamente quattro momenti della costruzione dello spreite. A. Si costruisce un cunicolo a forme di C. B. Nuovi cunicoli partono da un punto comune (freccia) e mantengono un andamento sub-parallelo rispetto al cunicolo precedentemente. Probabilmente il punto comune corrisponde con la parte terminale di un tubo connesso al fondo marino. C. Dal momento che i tubi individuali sono connessi ad un punto comune, la struttura tende a girare su se stessa mentre cresce. D. La struttura si ingrandisce gradualmente con avvolgimento elicoidale.

floor and lunate initial growth stages), but it is not possible to fully compare the models: the fill of the Lavini di Marco forms is coming from upper levels and the 3D development of the *Zoophycos*-like is not fully deciphered.

In the light of the above mentioned morphological analogies between the *Zoophycos*-like structures and the ichnogenus *Zoophycos* it is conceivable to recall some ethological models proposed for the ichnogenus *Zoophycos* with regards to the *Zoophycos*-like structures.

As stated above, it seems likely that the tracemaker of the *Zoophycos*-like forms has brought material from the surface into the deeper part of its burrow. Such an interpretation would not imply the “traditional” ethological models indicated for the ichnogenus *Zoophycos*, models that are usually traced back to deposit-feeding behaviour (see Seilacher 1967; Wetzel & Werner 1981). According to these assumptions, it is plausible to recall those ethological models proposed for the ichnogenus *Zoophycos* that admit a superficial origin of a part of the *Zoophycos* fill. In fact, we quote Kotake’s model (Kotake 1989; 1991) stating that the tracemaker would be ingesting detritus at the sea floor, then excreting the faecal material derived by this activity downwards. Bromley (1991) proposed some valid ethological models that take into consideration the presence of superficial material inside some *Zoophycos* burrows. As regards the “refuse dump model” cited by Bromley (1991), the tracemaker would be a deposit-feeder: it would convey the sediment from the upper levels to maintain the narrow form of the burrow. The “cache model”, also quoted in Bromley (1991), predicts an ethology of the tracemaker partially similar to Kotake’s model; during times of high food availability the tracemaker would collect surface material to store it in the burrow. During times of low food availability the tracemaker would feed on the stored material. The “gardening model”, cited by Bromley (1991), takes into particular account those *Zoophycos* provided with marginal tubes: the basic ethological scheme is Kotake’s, but the tracemaker could cultivate microbial colonies thanks to the marginal tube.

4. THE CONTRIBUTION OF THE ZOOPHYCOS-LIKE STRUCTURES FROM LAVINI DI MARCO IN THE EVOLUTIONARY HISTORY OF THE ICHNOGENUS ZOOPHYCOS IN THE EASTERN SOUTHERN ALPS

During the geological history of the Eastern Southern Alps, as it has also been observed on a global scale (Bottjer *et al.* 1988), *Zoophycos* has not permanently occupied the same bathymetric range. During the Palaeozoic, *Zoophycos* occupies preferably proximal (but also deep) environments. Venturini (1990) points out its presence in different formations of the Pramollo Group (formerly Auernig Group, Carboniferous *p.p.*), corresponding to palaeoenvironments ranging from lower shoreface to shelf and slope (Venturini 1990). More recent studies (Baucon & Carvalho 2008) signaled estuarine-related *Zoophycos* from the Pramollo Group. *Zoophycos* has al-

so been noted in the Upper Permian Bellerophon Formation of the Southern Alps, occurring in shallow subtidal environments (Twitchett 1999). Until now, in the Triassic of the Eastern Southern Alps, there is no documented occurrence of shallow *Zoophycos*, which is although recognized in proximal environments from neighboring areas (Knaust 2004; “Muschelkalk” deposits; Triassic *p.p.*). Furthermore, recent surveys demonstrated the occurrence of *Zoophycos* within the lagoonal carbonates of the Rotzo Formation (Calcarei Grigi Group, Jurassic *p.p.* – see Fig. 2).

In the Middle Jurassic, the presence of *Zoophycos* is not registered in the Eastern Southern Alps, but it is described in pelagic units of Western Southern Alps (Hinnov & Park 1999; Sogno Formation; Middle Jurassic *p.p.*).

At the Cretaceous-Paleogene transition, *Zoophycos* becomes common in the pelagic formations of the Eastern Southern Alps (i.e. Luciani & Cobianchi 1999; Scaglia Variegata, Cretaceous *p.p.*; Miller 2000; Miller & D’Alberto 2001: Scaglia Rossa, Scaglia Cinerea: Cretaceous *p.p.* - Paleogene). In the Cenozoic of Eastern Southern Alps, *Zoophycos* occurs in turbidite units of relatively deep sea (Tunis & Uchman 1996: Flysch di Calla, Flysch del Grivò, Flysch di Cormons: Palaeocene *p.p.* - Eocene *p.p.*), as it is also observed in the subsequent molassic units of inner-intermediate shelf (Ghibaudo *et al.* 1996: Arenaria glauconitica di Belluno, Upper Oligocene). Occurrence of proximal *Zoophycos* is also recorded in shallow marine sands, in the North Alpine Molasse basin (Miocene; Pervesler & Uchman 2004). Based on these observations, it appears that *Zoophycos* presented a shallowing tendency during the Oligo-Miocene. *Zoophycos* has also been individuated in slope emipelagic muds, in a Plio-Pleistocene core from the Venice area (Massari *et al.* 2004).

The relative exiguity of findings requires an analysis with a more detailed resolution and a specific search of *Zoophycos* across all stratigraphic units of the Eastern Southern Alps. Further studies on the ichnotaxonomical status of the *Zoophycos*-like structures are required to place the Lavini di Marco structures within the mentioned evolutionary history. In particular, it is necessary to verify if the *Zoophycos*-like structures could be definitively assigned to the ichnogenus *Zoophycos*. At present, this is not possible, considering either the need of revision proposed for *Zoophycos* itself (i.e. Gailard *et al.* 1999; Bromley & Hanken 2003) or the morphological discrepancies between the *Zoophycos*-like structures and the typical *Zoophycos* occurrences (i.e. Miller & D’Alberto 2001; Bromley & Hanken 2003; Olivero 2003; Pervesler & Uchman 2004). Nevertheless, there are significant morphological correspondences between the *Zoophycos*-like structures and the ichnogenus *Zoophycos* (as explained above). For these reasons, the *Zoophycos*-like structures could be placed contextually within the evolutionary history of *Zoophycos* in the Eastern Southern Alps.

The contribution of the structures from Lavini di Marco to the reconstruction of the evolutionary trend of *Zoophycos* in the Eastern Southern Alps could result significant. In fact, the *Zoophycos*-like forms found at Lavini di Marco could represent

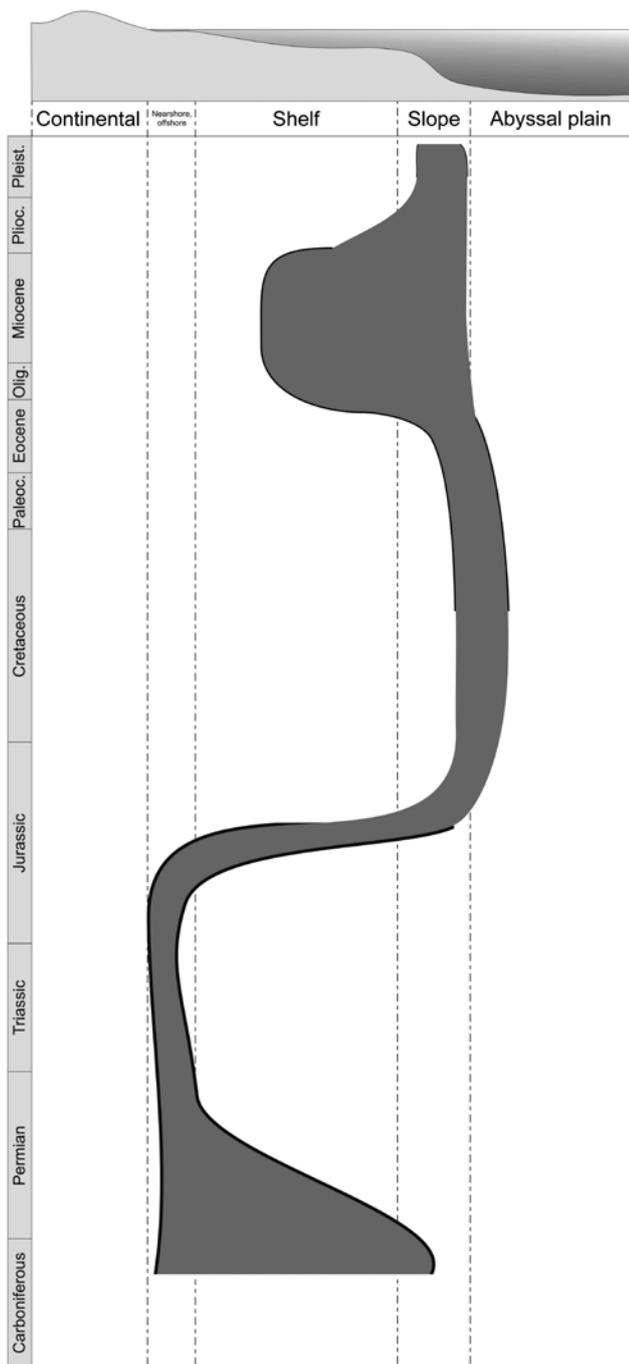


Fig. 6 - Bathymetric pattern of *Zoophycos* in the Eastern Southern Alps. The curve is constructed on the data presented in the previous chapter. The absence of a solid line corresponds to time spans where the occurrence of *Zoophycos* is scarce. During the Paleozoic, *Zoophycos* is present either in shallow or deep environments, whilst during the Mesozoic it is more common in deep settings. This trend is confirmed in the Southern Alps, where the bathymetric shift is often recorded at the Lower-Middle Jurassic boundary. It is also significant to observe a shallowing trend appearing in the Oligo-Miocene.

Fig. 6 - *Pattern batimetrico di Zoophycos nel Sudalpino Orientale. La curva è costruita sui dati presentati nel capitolo precedente. L'assenza di una linea solida corrisponde all'intervallo temporale dove la documentazione è scarsa. Durante il Paleozoico, Zoophycos è presente sia in ambienti poco profondi che profondi, mentre durante il Mesozoico è più comune in ambienti profondi. Questo trend è confermato nelle Alpi Meridionali, dove il cambio di batimetria è spesso registrato al confine Giurassico inferiore-medio. È anche significativo il trend verso bassi fondali in corrispondenza dell'Oligo-Miocene.*

Oliviero (2003) reports similar results in the French Subalpine basin, attesting the shift of *Zoophycos* from shelf to deep basin environments between Toarcian and Bathonian. Bottjer *et al.* (1988) and Knaust (2004) proposed the global occurrences of the ichnogenus, according to a bathymetric shift of *Zoophycos* during the Phanerozoic. Neto de Carvalho & Rodrigues (2003) register similar results for *Zoophycos* in Portugal, confirming a comparable bathymetric tendency while considering the worldwide occurrences of the ichnogenus.

5. CONCLUSIONS

The study of non-dinosaurian trace fossils at Lavini di Marco enhances the already remarkable qualities of the ichnosite, suggesting the possibility of better asserting the palaeoenvironment frequented by dinosaurs. The ethologic interpretation of the *Zoophycos*-like structures from Lavini di Marco would suggest a feasible use of these traces in the stratigraphical study of the ichnosite, especially of the analysis of the spreite lamellae. In fact, part of the material constituting the lamellae of the *Zoophycos*-like specimens would derive from superficial levels, almost entirely obliterated by bioturbation or erosional phenomena. Consequently, the study of the lamellae could highlight variations in the depositional regime, otherwise difficult to notice. The utility of this approach has already been clarified by Savrda (2003) with regards to *Zoophycos*.

At present, it is not clear if the association of *Zoophycos*-like forms and dinosaur footprints pertains to the same ichnocoenosis; yet, it is manifest that the tracemaker of *Zoophycos*-like forms and dinosaurs colonized at least neighbouring peritidal environments, definitively confirming the

the connecting link between the Palaeozoic *Zoophycos* (mostly occurring in shallow environments) and the Cretaceous-Cenozoic forms (inhabiting deeper environments), clearly presenting more analogy with the bathymetric pattern of the shallow Palaeozoic forms. Taking into account the aforementioned bathymetric occurrences of the ichnogenus, the evolutionary trend of *Zoophycos* in the Eastern Southern Alps reveals a gradual displacement from mostly superficial settings (especially in the Palaeozoic) to deep environments (during the Cenozoic). In the Southern Alps, the bathymetric shift of *Zoophycos* probably occurred at the Lower-Middle Jurassic boundary, between Pliensbachian and Bajocian (see Fig. 6).

superficial nature of the *Zoophycos*-like structures found at Lavini di Marco.

The preliminary results of the analysis of the *Zoophycos*-like specimens from Lavini di Marco could also assume a considerable importance in terms of the paleobathymetric trend of *Zoophycos* in the Eastern Southern Alps, placing the shallow Lavini di Marco forms between the Palaeozoic *Zoophycos* forms, mostly superficial, and the deep Tertiary ones.

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