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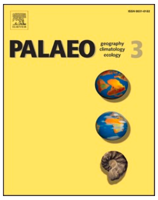

Late Quaternary occurrences of *Zoophycos* in a high sedimentation rate setting on the continental margin off southwestern Taiwan: Implications for trace maker ecology☆

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ABSTRACT

In Quaternary deep marine deposits, the trace-fossil *Zoophycos* is ubiquitous in low sedimentation rate settings (~10 cm ky^{-1}) below about 1000 m water depth. The *Zoophycos*-producer's preference for environments with strong seasonal swings in food flux, and the fact that the material in the trace fossil is both younger and more organic-carbon rich than ambient sediment, indicates that *Zoophycos* represents a cache behaviour, where food is squirreled away during high food fluxes for use during leaner times. The unusual occurrence of *Zoophycos* in a high-sedimentation rate setting (>100 cm ky^{-1}) dominated by homogenite deposition, reported here from the continental margin of Taiwan, therefore raises questions about the ethology and environmental preferences of the producer. Four main hypotheses are tested: (1) opportunistic colonization, (2) event dispersal, (3) response to post-homogenite depositional conditions, and (4) response to climate events. An opportunistic colonization of the homogenite and an event dispersal of *Zoophycos*-producers from upslope locations can effectively be refuted by the fact that *Zoophycos* spreiten are found not only in the upper parts of the homogenites, but also in the lower parts of the overlying hemipelagic sediment. No correlation between the occurrence of *Zoophycos* and known events or rearrangements of the SE Asian climate system could be found, effectively refuting the climate-response hypothesis. Consequently, the *Zoophycos* in the uppermost parts of the homogenites and the lowermost parts of the hemipelagites can best be explained by temporary phases of low sedimentation rates prevailing after the deposition of the homogenites, forming a wide, quasi-horizontal surface in the perched basin limiting the sediment influx to the basin, thus favouring a cache behaviour by the producer.

1. Introduction

A thorough understanding of the environmental parameters and forcings controlling occurrence and distribution of trace fossils is essential for the application of trace fossils in palaeoenvironmental and palaeoclimatic reconstructions.

The trace-fossil *Zoophycos* consists of a helically coiled spreite connected to the sea floor through a vertical shaft that may vary from a few

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cm up to about a meter in length (Wetzel and Werner, 1981; Löwemark and Schäfer, 2003). *Zoophycos* is common in Quaternary marine sediments at water depths deeper than about 1000 m, and is typically tied to areas where sedimentation rates are less than 10 cm ky^{-1} (Wetzel and Werner, 1981; Leuschner et al., 2002; Löwemark and Schäfer, 2003; Löwemark et al., 2006), although *Zoophycos* sometimes occur in settings with up to 20 cm ky^{-1} (Küssner et al., 2018). Often, downcore variations in the abundance of *Zoophycos* are tied to certain stratigraphic intervals that can be correlated over large distances (Wetzel and Werner, 1981; Löwemark and Schäfer, 2003; Rodríguez-Tovar et al., 2011; Küssner et al., 2018). In contrast, the *Zoophycos*-producers appear insensitive to grain-size variations, as spreiten have been found in sediments ranging from fine clays to coarse sediments rich in ice-rafted debris (Löwemark, 2012).

Because the material inside spreiten is younger than surrounding sediment and enriched in organic carbon, the trace-fossil *Zoophycos* has been interpreted to represent a cache behaviour where organic rich detritus is collected at the sea floor and stored deep in the sediment (Löwemark and Schäfer, 2003; Küssner et al., 2018).

We here report the unusual occurrence of *Zoophycos* spreiten in a high-sedimentation rate setting from the accretionary wedge off southwestern Taiwan dominated by event deposits such as turbidites and up-to a few meters-thick homogenites. In this setting, *Zoophycos* was only observed from sediments around the top of the homogenites, suggesting a response to the specific conditions prevailing at the end or directly after the homogenite deposition event. Four possible hypotheses for the occurrence of *Zoophycos* are explored: 1) an opportunistic colonization of the homogenite after the event, 2) colonization of the top of the homogenite by dislocated fauna from upslope areas, or 3) a response to low sedimentation-rate conditions after the displacement and deposition of the homogenite material, 4) the *Zoophycos* intervals correspond to dramatic changes in climate or environment.

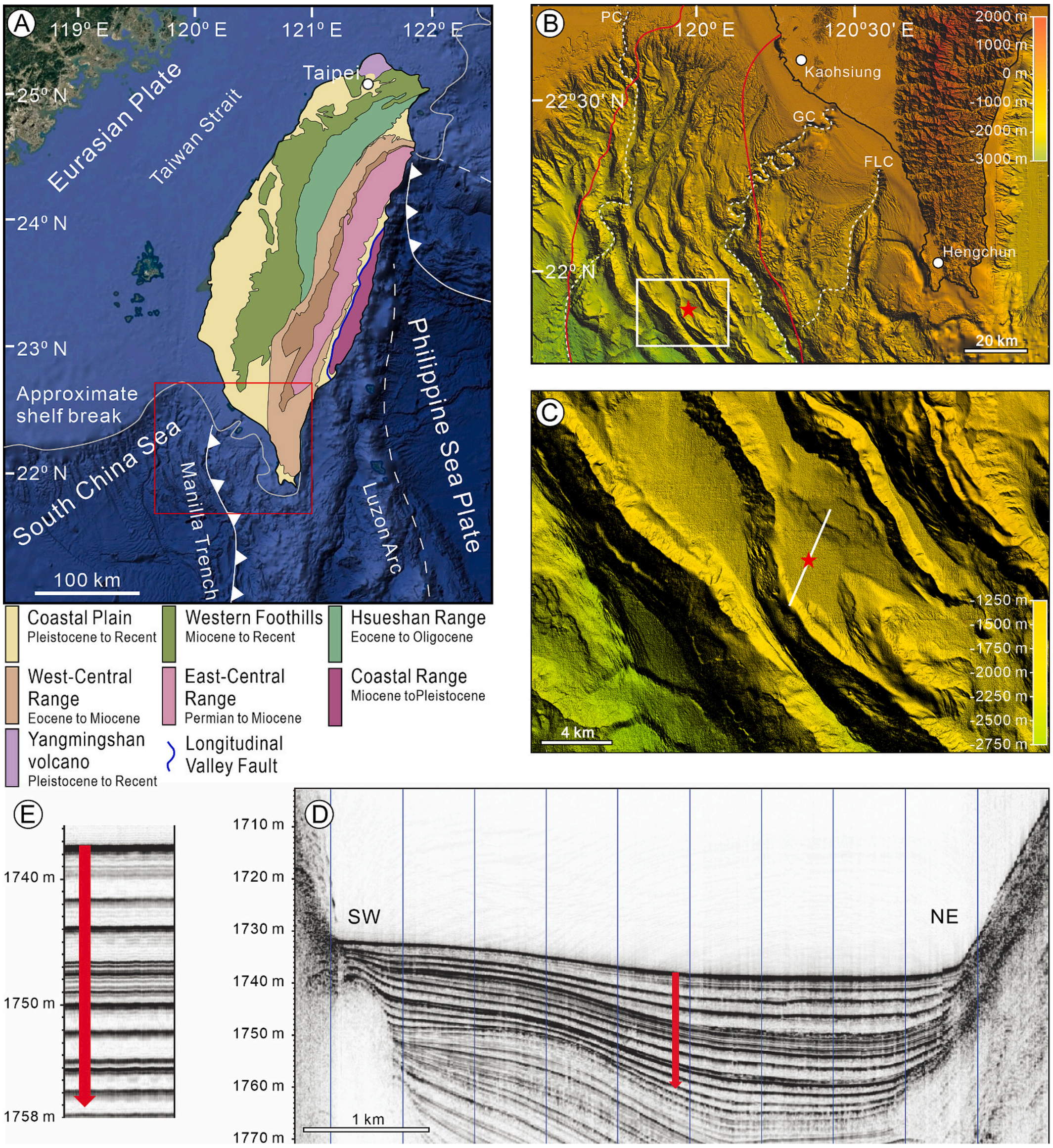

Fig. 1. Study area. A) Tectonic setting of Taiwan at the collisional boundary between the Eurasian Continental plate and the Philippine Sea Plate (after Dashtgard et al., 2020; Lin et al., 2003). Background bathymetry from Google Earth. Red box shows position of bathymetric map of panel B. B) Bathymetry of the continental slope off southwestern Taiwan. Left red line indicates the deformation front, and the right red line indicates splay fault. White dotted lines show three major canyons. PC – Penghu Canyon, GC – Gaoping Canyon, FLC – Fangliao Canyon. White box indicates the study area around the perched basin. Core position marked by red star. C) Detailed bathymetry of the perched basin. The core position marked by red star. White line shows the seismic transect shown in D. D) Seismic transect across the perched basin showing the transparent layers of the homogenites. E) Seismic profile at the coring point. Red arrows in (D) and (E) represent the depth of core penetration in MD18–3548. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2. Geological background

Taiwan is the site of an ongoing oblique collision between the leading edge of the Philippine Sea Plate and the Eurasian continental margin. This collision was initiated further north in the late Miocene and started propagating southward once the oceanic crust was fully consumed and the passive margin entered the subduction (e.g., Ho, 1986; Teng, 1990; Lin et al., 2003). As a result, the accretionary wedge to the west of the Hengchun Peninsula, southernmost Taiwan, is characterized by a number of reverse faults, tectonic ridges and intraslope basins, and frequent seismicity (Fig. 1).

With annual rainfall well over 2000 mm and frequent typhoons (tropical cyclones), hyperpycnal flows deliver large amounts of sediments eroded from the Taiwan orogen to the ocean, resulting in extensive canyon systems channelling the sediment from the mountain belts to the deep sea (Dadson et al., 2003; Chen et al., 2010). Additionally, turbidity currents can also be triggered by earthquakes, submarine landslides, and tsunamis (Liu et al., 2016; Nayak et al., 2021; Remaud et al., 2024). Consequently, sedimentation on the accretionary wedge is characterized by a number of event beds separated by intervals of lower background sedimentation rates. The abundant event beds result in overall sedimentation rates around 2 m ky^{-1}, and about 50–100 cm ky^{-1} if the event beds are excluded (Pillutla et al., 2025).

Primary productivity and food flux to the sea floor on the accretionary wedge off the Hengchun Peninsula are influenced by the alternating monsoon circulation, the inflow of the Kuroshio Branch, and tropical cyclones resulting in the mixing of surface and intermediate waters (Lo and Lau, 2016; Huang et al., 2020).

3. Material and methods

The Calypso piston core MD18-3548 (21°52.73′N,119°57.17′E, 1752 m) was retrieved by the French research vessel Marion Dufresne II from the accretionary wedge off the Hengchun Peninsula off south-western Taiwan in 2018 (MD 214 EAGER Cruise; Babonneau and Ratzov, 2018). The coring location is situated in a perched basin between the Gaoping and Penghu Canyons and therefore receives little terrigenous sediment from the two canyon systems (Pillutla et al., 2025) (Fig. 1). The core was described, photographed, logged with a Geotek Multi-Sensor Core Logger, and scanned with X-ray Computed Tomography for the detailed assessment of physical and biological sedimentary structures. Trace fossils were identified in 2D sections exported from the CT images following standard methods in the study of X-ray radiographs (cf. Werner, 1967; Wetzel, 1991; Löwemark and Schäfer, 2003; Löwemark et al., 2004b). Grain size and sediment geochemical parameters were analysed at Sediment Analysis Lab of National Central University (SALNCU) (Pillutla et al., 2025). Foraminifera (and a scaphopod shell) from 14 depths in MD18–3548 were used for radiocarbon dating (Pillutla et al., 2025). Variations in trace-fossil content and bioturbation were evaluated from 2D vertical expressions of the CT scanner data. Individual trace fossils and their relative abundance were documented for contiguous 5-cm slices using a semi-quantitative scale from 0 to four, where 0 = No bioturbation, 1 = Few, 2 = Some, 3 = Abundant, and 4 = Dominant. The degree of bioturbation was recorded following the scheme of Droser and Bottjer (1989) and McIlroy (2004). From the trace-fossil data, parameters such as Ethological Ichno Quotient (EIQ: an efficient way to visualize differences between ethological groups, cf. Singh et al., 2023) were calculated.

4. Results

4.1. Sedimentology

Core MD18-3548 consists of four turbidites, six thin silty layers, and seven silty turbidite-homogenite units (hereafter referred to as “homogenites”) intercalated within the hemipelagic background sediment.

The turbidites are thin (1–14 cm) silty graded layers showing parallel lamination and sharp lower boundaries in the CT images. All turbidites are enriched in both broken and complete foraminifera (Pillutla et al., 2025). The upper parts of the turbidites have been reworked by benthic organisms resulting in a gradual transition to overlying hemipelagic sediment. Except for T3, which contains a fairly large *Scolicia*, *Planolites*-like and deformational structures dominate in the reworked upper parts of the turbidites (Fig. 2).

Similar to turbidites, the thin silty layers display parallel lamination and a similar grain size to the turbidites, but the concentrations of broken and well-preserved foraminifera are lower than in the turbidites. Similar to the turbidite layers, the silty layers have been partly destroyed by bioturbation, with trace fossils consisting primarily of *Nereites* and *Planolites*-like traces (Fig. 2).

Both turbidites and thin silty layers are interpreted to be the result of smaller tractional depositional processes (Pillutla et al., 2025).

All homogenites consist of a silty basal layer overlain by a homogeneous fine-grained interval (Pillutla et al., 2025). In the basal layer, an initial coarsening-upward trend in the lowermost part is replaced by a fining upward trend in the uppermost part of the basal layer. All basal layers display clear planar bedding and most show enhanced abundances of planktonic foraminifera. Two types of boundaries were identified between underlying hemipelagic sediments and the homogenite basal layers: gradual transitions and sharp based boundaries (see Pillutla et al., 2025, for details). On average, the homogenites are approximately 150 cm thick. Of the 100 to 200 cm thick homogenites, the basal silty layers typically make up less than 10 cm, while the rest of the layer is made up of structureless clays. Characteristic for the homogenites is the almost complete absence of bioturbation and trace fossils, except for an opportunistic colonization of the top 10–20 cm (Fig. 2). A high number of pyritized sub-millimetre threads in homogenites H4 and H5 are tentatively assigned to *Trichichnus* or Mycellia (cf. Blanpied and Belaiche, 1981; Wetzel, 1983). Thin pyritized threads such as *Trichichnus* and Mycellia have been attributed to the work of deep-burrowing chemosymbiotic vermiform organisms such as Sipunculids (Weaver and Schultheiss, 1983; Romero-Wetzel, 1987), or bioelectric wires consisting of long, vertically oriented colonies of chemosymbiotic bacteria (Kędzierski et al., 2015). In both cases, the colonization deep inside the substrate happened long after it was deposited, and does not reflect *syn*-sedimentary conditions. The homogenites were interpreted to represent seismogenically triggered remobilization of slope sediments from the sides of the perched basin (Pillutla et al., 2025).

The hemipelagites consist of bioturbated silty clays (D50 ~ 7.8 μm) with bioturbation index typically between 2 and 4, leaving a variable primary bedding still clearly visible in most intervals. *Planolites*-like, and *Nereites*-like traces dominate the hemipelagites, with *Phycosiphon* being abundant in certain intervals. Other deposit feeding or dwelling traces, including *Palaeophycus*, *Scolicia*, and *Thalassinoides*-like traces, occur sparsely (Fig. 2). The hemipelagites were interpreted to represent periods of tectonically relatively stable conditions with minimal input of seismogenically remobilized material, although some of the preserved bedding could represent smaller, largely reworked turbidity-current events (Pillutla et al., 2025).

4.2. Sedimentation rates

Variations in sedimentation rates were calculated from the radiocarbon dates obtained. Overall sedimentation rate for the entire core is about 158 cm ky^{-1}, but if event beds are excluded, an average sedimentation rate for the hemipelagites of around 75 cm ky^{-1} can be calculated, with individual linear sedimentation rates ranging from 38 to 107 cm ky^{-1} (Pillutla et al., 2025). However, given the variable deposition of the hemipelagites, actual sedimentation rates likely varied significantly around these averages.

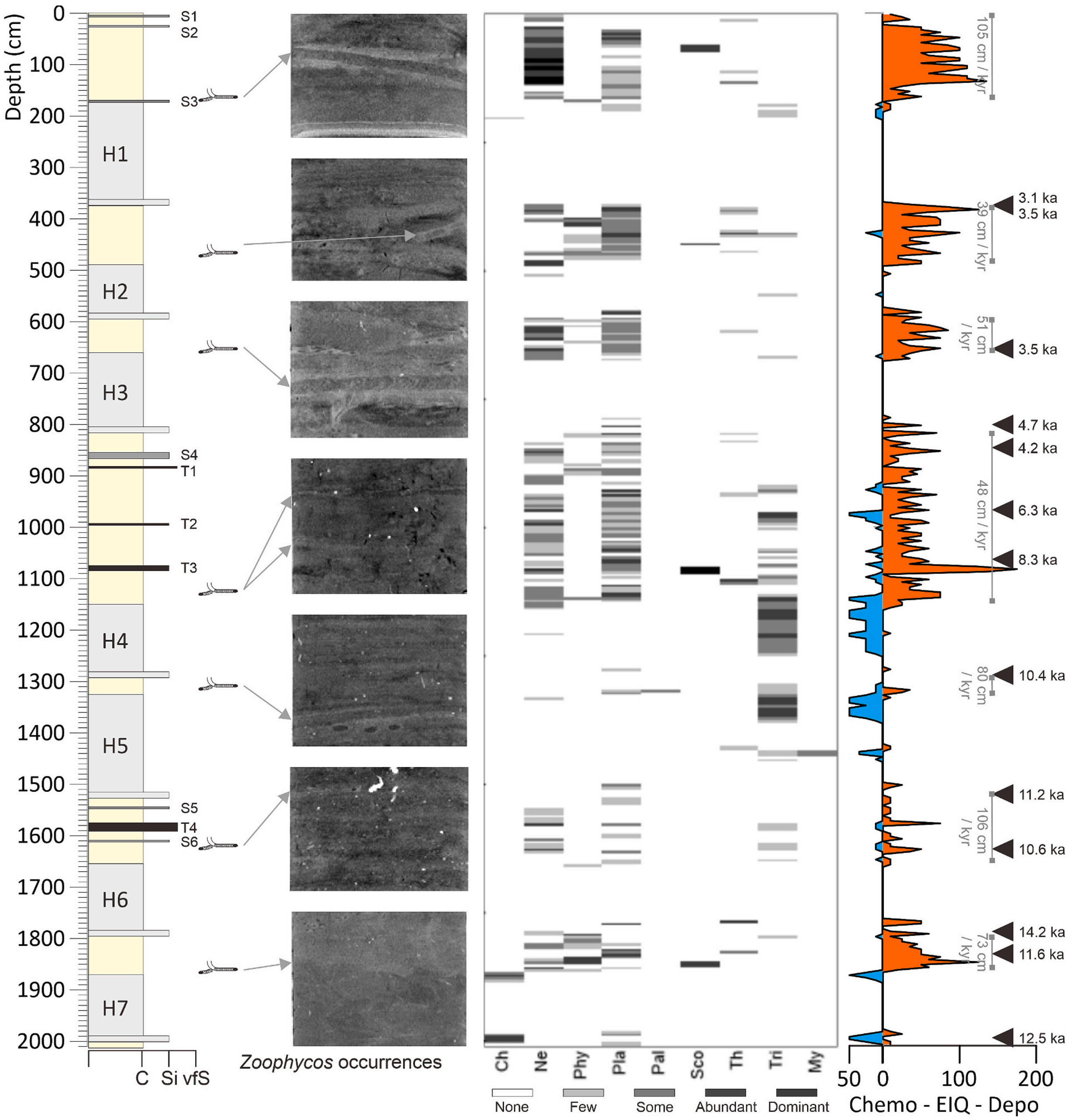

Fig. 2. Stratigraphic columns. Lithologic column of core MD18–3548 showing distribution of hemipelagic sediment (light yellow), homogenites (H1-H7, light grey), turbidites (T1-T4), and silty layers (S1-S6), after Pillutla et al. (2025). CT images (width ca 10 cm) and spreiten symbols indicate intervals with *Zoophycos spreiten. Trace-fossil content: Ch = Chondrites, Ne = Nereites, Phy = Phycosiphon, Pla = Planolites, Pal = Palaeophycus, Sco = Scolicia, Th = Thalassinoides, Tri = Trichichnus, My = Mycellia. EIQ (blue = chemosymbiotic, orange = deposit feeders) calculated following* Singh et al. (2023). Radiocarbon ages in cal kyr B.P. (black triangles) and linear sedimentation rates for hemipelagic intervals (grey bars) from Pillutla et al. (2025). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.3. Trace fossils

The trace-fossil assemblage of the hemipelagic intervals between the homogenites indicates that the core belongs in the *Zoophycos* or *Nereites* ichnofacies (Seilacher, 1967; Buatois and Mángano, 2011). Only rarely can a distinct tiering be observed, such as in the colonization of some of the thicker turbidites, and the bioturbation index rarely exceed 5 (Fig. 2). The relatively low diversity and density in trace fossils are similar to slope settings with rapid sedimentation in the nearby Sulu Sea (Wetzel, 1983). Trace fossils of deposit feeders such as *Nereites* or *Planolites,* and to some extent *Phycosiphon* dominate the hemipelagic intervals, with occasional occurrences of *Scolicia* showing up in silty beds. The prevalence of deposit feeding traces in the hemipelagites is also illustrated by the EIQ (Fig. 2). In contrast, chemosymbiotic traces show distinct maxima in homogenite layers H4 and H5.

While the abundance of *Zoophycos* is generally low, the spreiten are concentrated to the topmost parts of the homogenites and the directly overlying hemipelagites. In H1, H2, and H3, *Zoophycos* spreiten are found inside and just above the top of the homogenite, while in H4 and H5, the spreiten are situated a few cm above the homogenite, although two possible spreiten were also observed inside H4. For H6 and H7, spreiten were observed about 30 cm above the top of the homogenite (Table 1).

Table 1
The occurrence of *Zoophycos* spreiten in relation to the extent of the homogenites in core MD18-3548.

Homogenite	Depth (cm)	*Zoophycos*
H1	173–374	163–186 cm several distinct spreiten
H2	490–594	466–467 cm at least one *Zoophycos* spreite
H3	660–816	655–665 cm at least two *Zoophycos* spreiten
H4	1150–1292	1123 and 1145 cm possible *Zoophycos* spreiten
H5	1325–1525	1310 and 1317 cm, two *Zoophycos* spreiten
H6	1655–1792	1620 cm, possible *Zoophycos* spreite
H7	1870–1999	1849 cm, possible *Zoophycos* spreite

5. Discussion

The trace-fossil *Zoophycos* is known in strata from the early Palaeozoic (Alpert, 1977; Sappenfield et al., 2012) to the Recent (Wetzel, 2008). While early *Zoophycos* were found in shallow water environments and likely represent a deposit-feeding behaviour (Gaillard et al., 1999; Kotake, 2014; Zhang et al., 2015a; Zhang et al., 2015b), the modern *Zoophycos* are only found in deep marine settings and most likely represent a cache behaviour (Wetzel and Werner, 1981; Bromley, 1991; Löwemark et al., 2004a) where food collected during episodic high food fluxes is squirreled away for leaner times. On the continental margin off West Africa, Wetzel and Werner (1981) found that *Zoophycos* is largely absent in sediments where the organic carbon content exceeds 2% and where sedimentation rates are higher than 20 cm ky^{-1}. On the accretionary wedge off the Hengchun Peninsula, organic carbon content typically ranges from 0.5 to 1%, and rarely exceeds 2% (Liu et al., 2009; Wang et al., 2016; Zheng et al., 2017), while food flux related to primary productivity show a strong seasonal variability (Wang et al., 2025). Thus, conditions would seem favourable for the *Zoophycos*-producer. However, the extreme sedimentation rates of the homogenites, and the generally high average sedimentation rates of the hemipelagites make the occurrence of *Zoophycos* rather surprising. Below four hypothetical models explaining the recurrent occurrence of *Zoophycos* spreiten in the strata around the top of the homogenites/base of the hemipelagites are explored.

5.1. *Opportunistic colonization*

The opportunistic colonization of event beds is a common phenomenon both in shallow marine environments and the deep sea (e.g., Reineck et al., 1968; Frey and Goldring, 1992). Observations from Eocene muddy turbidites show that the top layers are typically colonized by a suite of deposit-feeding trace fossils such as *Nereites* or *Phycosiphon,* and the chemosymbiotic trace fossil *Chondrites*. This trace-fossil composition is very similar to the composition observed at the tops of the homogenites. *Zoophycos* is typically not considered an opportunistic ichnospecies, but rather represent a climax community (Bromley, 1996), but was recorded as a rare colonizer in the Eocene turbidites (Wetzel and Uchman, 2001). Still, the presence of *Zoophycos* at the top of the homogenites could be interpreted as the result of an opportunistic colonization of a pristine niche on the sea floor.

In the perched basin on the accretionary wedge off SW Taiwan, the colonization window (sensu Bromley, 1996) was likely long enough for the producers of *Zoophycos* to colonize the substrate, even though overall sedimentation rates of the hemipelagic intervals likely were characterized by sedimentation rates too high for *Zoophycos*.

Consequently, if the *Zoophycos* spreiten found around the upper parts of the homogenites were to represent an opportunistic colonization event, we would expect them to be found in topmost layer of the homogenites, and we would expect the development of multiple whorls before the background sedimentation rates of the homogenites made the *Zoophycos* cache-strategy inefficient. As the *Zoophycos* colonization events in core MD18–3548 are characterized by single spreiten and low abundances, their occurrence is most likely not the result of an opportunistic colonization. Even if the return to the high-sedimentation rate conditions of the hemipelagites would mean unfavourable conditions for the *Zoophycos*-producer, the colonization window from the end of homogenite deposition to the onset of normal hemipelagite deposition should have been long enough to allow for the development of multi-whorl *Zoophycos*.

Furthermore, in several cases, the *Zoophycos* spreiten were found several tens of cm above the top of the homogenite, suggesting that the living interval of the producer corresponded to a time period hundreds, or even thousands, of years after the end of homogenite deposition.

In summary, the recurrent occurrence of *Zoophycos* spreiten around the top of the homogenites does not agree with an opportunistic colonization behaviour.

5.2. *Event dispersal*

Turbidity currents may relocate shallow marine benthic faunas into deep-marine settings where some of the displaced organisms exploit their new environment for shorter or longer times (Bigham et al., 2021). For example, Föllmi and Grimm (1990) showed that the producers of shallow-water ichnotaxa such as *Thalassinoides* and *Gyrolithes* were transported to the deep sea where they flourished for a short period of time until they perished because of a lack of oxygen. Another example comes from Miocene deposits in Türkiye, where turbidite fans contain trace fossils typical of shallow water facies, such as *Ophiomorpha* (Uchman and Demírcan, 1999). It is thus conceivable that producers of the trace-fossil *Zoophycos* could have been displaced from upslope environments and relocated to the homogenites in the perched basin. If so, any dislocated *Zoophycos*-producers therefore would have settled at the base of the homogenite, and producers must have been able to migrate through the entire homogenite in order to connect their shaft to the sediment surface. However, the settling of the fine-grained particles of the homogenite is extremely slow and took weeks or even months, while the water above the seafloor remained turbid. The producers thus would have had to remain at the top of the very loose homogenite layer there until the layer consolidated enough for the construction of spreiten. Moreover, it is typically only the shallow-tier burrowers that are relocated (Taylor et al., 2003).

If the *Zoophycos* of the homogenites depended on relocated producers, then *Zoophycos* spreiten would only be expected in the homogenites themselves, and not in the overlying hemipelagites. Furthermore, there is no reason why the colonization should be limited to only one or two whorls, as observed in MD18–3548. In the studied core, *Zoophycos* are found only in intervals from the topmost parts of the homogenites to the lowermost parts of the directly overlying hemipelagites. And, there are no *Zoophycos* observed in relation to the turbidites or silty layers which also brought dislocated material from upslope regions. Consequently, dispersal of *Zoophycos*-producers from upslope regions through density-driven turbidity currents is deemed unlikely.

5.3. *Response to lowered sedimentation rates after homogenite event*

While the general hemipelagic sedimentation rates in the perched basin on the accretionary wedge off the Hengchun Peninsula generally are far too high for the typical development of *Zoophycos* trace fossils, it is conceivable that sedimentation rates directly after the deposition of the homogenite could be substantially lower than the average hemipelagite intervals. As the homogenite settles at the bottom of the perched basin, a wide quasi-horizontal surface develops (Fig. 1E). This wide horizontal plain would initially have limited any sediment input from the continental slope and the sides of the perched basin, resulting in a decrease in the sedimentation rates and food flux in the lower parts of the hemipelagites, creating suitable conditions for the *Zoophycos*-producer. In Quaternary deep-marine settings, *Zoophycos* is typically tied to regions with moderate sedimentation rates (10–20 cm ky^{-1}) and strong seasonally alternating fluxes in food to the sea floor (Wetzel and

Werner, 1981; Löwemark and Schäfer, 2003; Rodríguez-Tovar et al., 2011; Küssner et al., 2018). While direct measurements of the flux of organic material to the perched basin are not available, the waters west of the Hengchun Peninsula are characterized distinct differences in chlorophyll *a* (Wang et al., 2025), an indicator for the surface primary production (Fig. 3). Consequently, conditions on the sea floor directly after the deposition of the homogenite layer should be suitable for the colonization of the substrate by the *Zoophycos*-producers. The position of the observed *Zoophycos* spreiten thus agree with a response to low sedimentation rates in the lower parts of the hemipelagites, directly overlying the homogenites. The *Zoophycos*-producer penetrated deep into the homogenites from a colonization surface in the lower portion of the hemipelagite during a colonization window when sedimentation rates and food flux were favourable for a cache behaviour, but unsuitable for competing organisms such as bulldozing deposit feeders. Based on the distance between *Zoophycos* spreiten and the boundary between homogenite top and hemipelagite base (a few tens of cm) and the sedimentation rates of the hemipelagites (>30 cm ky^{-1}; Pillutla et al., 2025), the duration of this colonization window likely only was a few hundreds to a thousand years. Moreover, the disappearance of *Zoophycos* in the upper parts of the hemipelagites could be interpreted as a response to gradually increasing sedimentation rates as influx of sediments from the sides of the perched basin increases over time.

5.4. Climate induced colonization by the Zoophycos-producer

Finally, it is possible that the intervals with *Zoophycos* spreiten correspond to climatic events leading to a dramatic reorganization of oceanographic parameters such as primary production or ocean currents influencing sedimentation rates. For example, seasonal current direction in the Taiwan Strait have been shown to intermittently reverse due to the passing of frontal systems (Chuang, 1986), and the passage of tropical cyclones have been shown to strongly influence primary productivity through mixing and influx of nutrients (Shiah et al., 2000; Ko et al., 2016; Tseng et al., 2020). However, comparing the distribution of the *Zoophycos* intervals with variations in insolation and known major climate events such as the 4.2 ka and 8.2 ka events show no correlation (Fig. 4). The short bursts in *Zoophycos*-producer activity do not indicate a relationship with long-term climate change, and the stratigraphic positions of the *Zoophycos* spreiten do not correspond to any known climate events. We therefore refute this hypothesis.

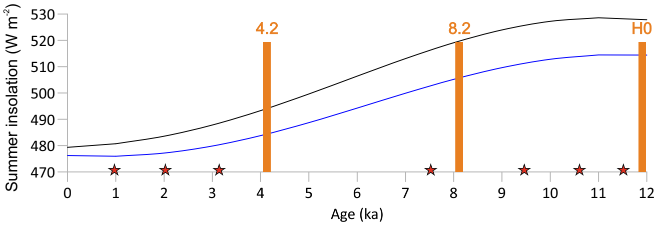

Fig. 4. *Zoophycos vs climate parameters. Distribution of Zoophycos spreiten in relation to climate parameters from the South China Sea. Black curve = summer insolation at 65° N. Blue curve = summer insolation at 30° N. Cold events at 4.2 ka, 8.2 ka, and Heinrich Event Zero marked by orange bars. Occurrences of Zoophycos spreiten are marked by red stars. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)*

6. Conclusions

From the observations of the recurrent occurrence of *Zoophycos* spreiten in a high-sedimentation rate setting dominated by homogenites on the continental slope off SW Taiwan, several conclusions can be drawn.

Zoophycos spreiten were only observed in the topmost part of the homogenites and directly overlying hemipelagites.

No *Zoophycos* were observed in relation to turbidites. Together with the fact that several spreiten are situated well above the tops of the homogenites, this renders the opportunistic colonization model, and the model invoking colonization by displaced fauna from upslope unlikely.

The time intervals with *Zoophycos* activity do not correspond to any major climatic events or reorganizations of the oceanographic system in the South China Sea. A climatic control of the occurrence of *Zoophycos* is therefore refuted.

We therefore propose that the most likely explanation for the unusual occurrence of *Zoophycos* in a generally high-sedimentation rate setting lies in conditions created by the deposition of the homogenites. After homogenite deposition, the perched basin is characterized by a quasi-horizontal surface, effectively limiting sediment transport from the slopes surrounding the basin, leading to an interval of relatively lower sedimentation rates in the parts of the hemipelagites directly above the tops of the homogenites, allowing for a brief period of *Zoophycos* colonization. Consequently, conditions just after homogenite deposition likely corresponded to the low-sedimentation rate conditions in areas with strong alternations in food-flux observed in Quaternary

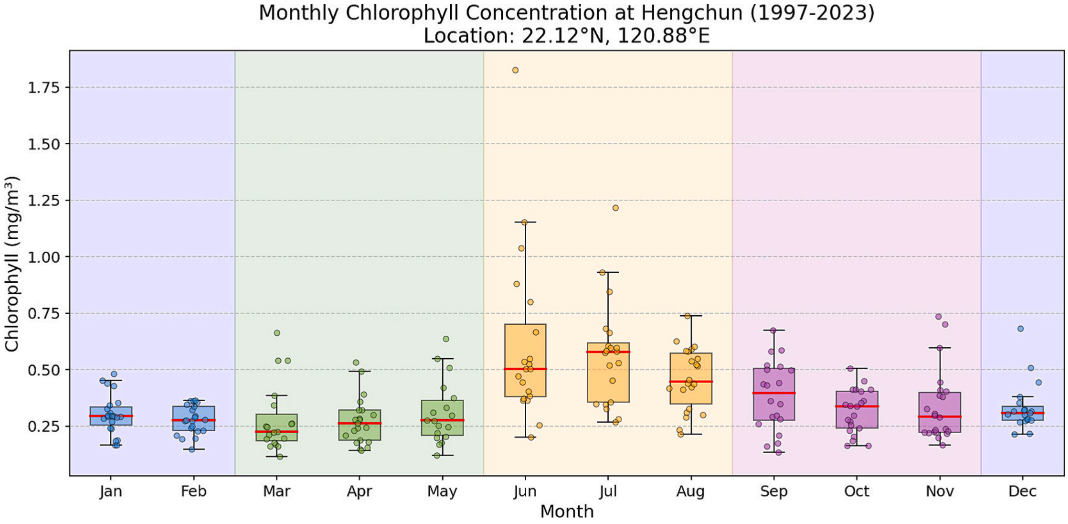

Fig. 3. Seasonal variations in chlorophyll at the coring site off Hengchun Peninsula, Taiwan. Seasonal variations in chlorophyll concentration (25 km resolution) as an indicator for primary productivity for the southern Taiwan Strait and the region west of the Hengchun Peninsula. Data are retrieved from GlobColour case 1 waters, funded by the European Space Agency (Maritorena and Siegel, 2005). The climatology represents an average over the period 1997–2023.

cores from many other regions around the world (Leuschner et al., 2002; Löwemark and Schäfer, 2003; Rodríguez-Tovar et al., 2011; Löwemark, 2012; Küssner et al., 2018).

A better understanding of the sedimentary processes and climatic conditions that govern the stratigraphic distribution of trace fossils in core is of fundamental importance for our usage of trace fossils in palaeoenvironmental reconstructions.

CRediT authorship contribution statement

Ludvig Löwemark: Writing – original draft, Methodology, Conceptualization. **Radha Krishna Pillutla:** Writing – review & editing, Visualization, Data curation. **Andrew Tien-Shun Lin:** Writing – review & editing, Investigation, Data curation. **Jen-Chu Yeh:** Writing – review & editing, Investigation. **Gueorgui Ratzov:** Writing – review & editing, Investigation. **Nathalie Babonneau:** Writing – review & editing, Investigation. **Shu-Kun Hsu:** Writing – review & editing, Investigation. **Chih-Chieh Su:** Writing – review & editing, Investigation. **Serge Lallemand:** Writing – review & editing, Investigation. **Wan-Ling Tseng:** Writing – review & editing, Visualization, Software.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2026.113681.

Data availability

The authors confirm that all data necessary for supporting the scientific findings of this paper have been provided.

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