海沙裡的奇特謎團—螺旋潛跡生痕化石

Zoophycos: The World's Strangest Trace Fossil

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連名字都奇怪：螺旋潛跡生痕化石

「螺旋潛跡」生痕化石可能是世界上最詭異又迷人的生痕化石了。它姿態多樣，最經典的一種當屬呈現巨大螺旋狀向下的形態，且經常可見由中心往外延伸的長葉瓣。辨認這種生痕化石可以觀察到三個重點特色：(一)連接主結構與海床的垂直管，(二)裙擺狀包圍整個結構的邊緣管，(三)邊緣管內呈百葉狀的蹼狀構造(spreite，片狀弧形紋，可能是無脊椎動物來回爬行產生的痕跡，圖1)。儘管不同形態的螺旋潛跡生痕化石出現在地球上的歷史悠久—早至可溯自5億4千萬年前的寒武紀岩石、晚至現今深海沈積物，都可以發現它們的蹤跡；然而卻沒有人知道製造出這種生痕的生物究竟為何。令人玩味的是，這些螺旋潛跡生痕化石的製造者似乎從過去在淺海的生活環境漸漸轉移到了深海……

這是誰的傑作？螺旋潛跡的古怪形態

任何人在野外看到螺旋潛跡生痕化石，第一個浮現的疑問自然就是：「是何種生物製造出這種奇怪的結構？」有追根究柢精神的觀察者或許還要進一步追問：「這樣複雜的結構所為何來？」其實很多問題的答案，我們直接從生痕化石的長相來觀察就可以略知端倪。地質學家常用「截切關係定律」來研判事件的先後關係，意思是後發生的地質事件(如痕跡)會截切先前發生的事件(痕跡)，所以藉此可以得知事件發生的先後順序。生痕化石的研究上，我們也可以利用相同的概念來釐清生痕化石的結構中哪一個部分是先構築的，哪一個部分又是後來才製造的。用截切關係定律觀察螺旋潛跡生痕化石，我們發現它有多種構築方式：有一些似乎是由沈積物深處某定點開始向上旋繞、而另外一些則是往下旋繞，而且越往下越大—這似乎顯示生物的體型也隨著時間變大了。雖然構築方式不同，但它們有一個共同的特徵，那就是「蹼狀構造」的邊緣管在沈積物裡緩慢向外推移的過程中在管內側留下糞球般的粒狀物質(圖2)。想像生物使用類似露天採礦一樣的方式(圖3)，在沈積物裡沿著管壁外壁攝取或過濾砂粒中的養分，然後將糞球排泄物遺留在管壁內側。正因如此這個蹼狀構造代表的行為，幾乎讓早期的研究者斷定這個螺旋潛跡的生痕是一種生物攝取沈積物時產生的攝食構造。

然而，後期的研究卻顯示原先以為是排泄物的組成物質其實來自於海床上；以及現代型態的螺旋潛跡糞球組成成份中也發現含有含量豐富的有機物質—此現象代表生物不只在沈積物裡覓食，也會從海床上攝取更多食物。既然生物一直待在沈積物裡濾食，糞球排泄物中又怎麼會含有從海床上來的成份呢？種種跡象都不符合沈積物攝食生物(deposit feeder)生活在沈積物中濾食該有的特徵。研究學者為此提出了幾個可能的行為模式，設法解釋這個令人困惑的現象：

圖1 (右)*Zoophycos*螺旋潛跡生痕化石的3D圖；(左)螺旋潛跡生痕化石(紐西蘭)。螺旋潛跡生痕化石大小不一，野外觀察到的最大樣本直徑可達到直徑1公尺左右，垂直高度甚至可能超過1公尺。
Figure 1. (Right) 3D reconstruction of the trace fossil *Zoophycos*. (Left) Fossil example of *Zoophycos* from New Zealand. *Zoophycos* vary wildly in size, but the largest observed specimen may reach more than one meter in diameter and have a vertical extent of more than one meter.

What is *Zoophycos*?

Zoophycos is probably one of the strangest and most intriguing trace fossils in the world. There are many varieties of *Zoophycos*, but the typical form looks somewhat like a huge corkscrew spiraling down into the sediment. Often, long lobes can be seen extending out from the central parts. The trace fossil generally consists of three main components, a vertical shaft that connected the structure to the seafloor, a marginal tube surrounding the whole structure, and sheet-like structures called "spreiten" which mark previous positions of the marginal tube (Figure 1). Despite the fact that different types of *Zoophycos* have been found in rocks as old as the Cambrian (~540 million years old), and the youngest *Zoophycos* have been found in lose sediment collected in the deep sea today, no one has ever found the animal responsible for the peculiar trace. Interestingly, the producers of these trace fossils seem to have moved from shallow environments in the past to being exclusively found in the deep sea today.

Why was it constructed?

The first question that comes to mind when finding a *Zoophycos* trace fossil in the field is of course "who did this?" What kind of organism could have produced such a strange structure? But more interesting is maybe to consider why some organism built this complex struc-

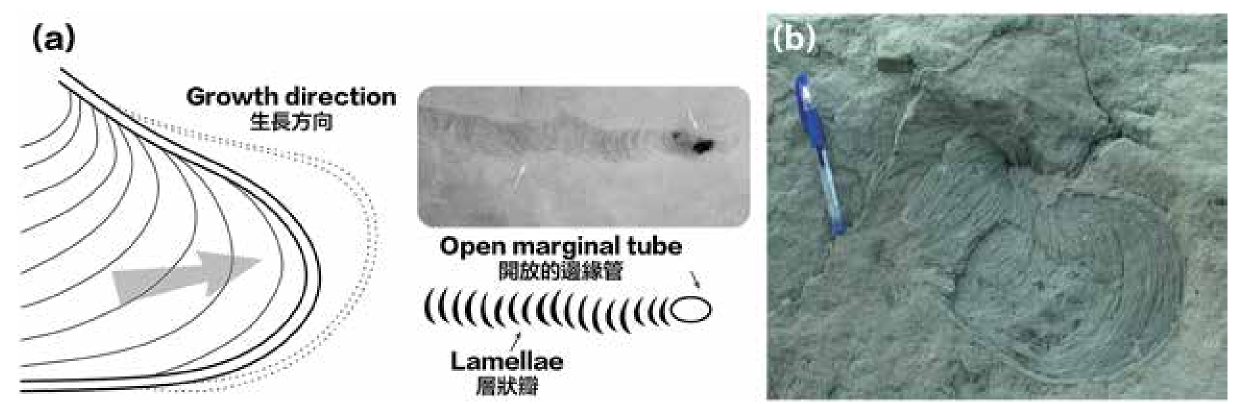


圖2 (a)螺旋潛跡生痕化石的特徵：蹼狀構造。邊緣管在沈積物中推移所留下的痕跡，代表邊緣管先前所在的位置。(b)臺灣的螺旋潛跡生痕化石。(照片提供：游能悌)
Figure 2. Construction of the spreite: (a) The spreite forms between the limbs of the marginal tube through the gradual shifting of the tube through the sediment. The lamellae left behind in the spreite thus represent earlier positions of the marginal tube. (b) Fossil example of *Zoophycos* from Taiwan (provided by Neng-Ti Yu).

- 「碎屑攝食模式」(亦稱「糞坑模式」)：這個模式認為螺旋潛跡生痕製造者並非沈積物攝食生物，牠會到海床上攝食水中沈降下來的有機物質碎屑，然後再到比較深的沈積物中排泄，以確保覓食區的潔淨。螺旋潛跡的生痕可說是精心打造的廁所！
- 「棄渣場模式」：螺旋潛跡生痕製造者確實是沈積物攝食生物，但是會搬運海床上的物質到洞穴中用以支撐管壁防止坍塌。

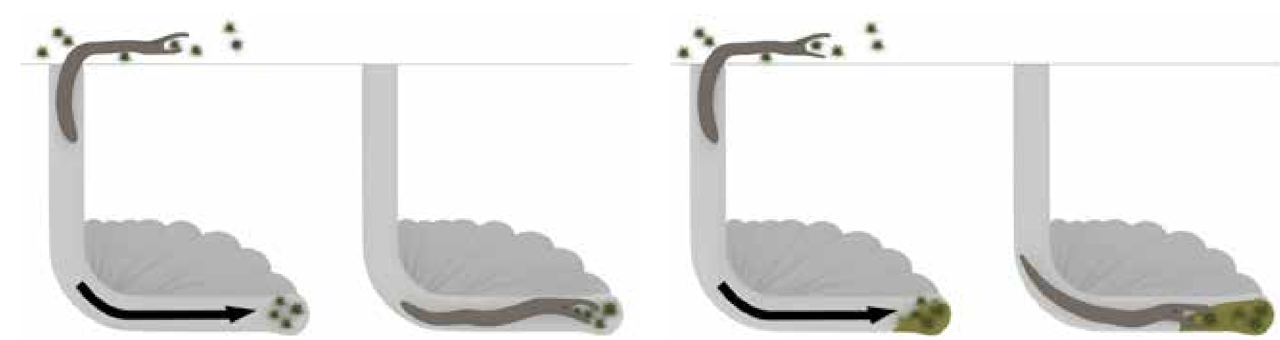
除了上面兩種模式之外，研究學者觀察到有些海洋生物會在沈積物中儲存食物殘渣以備不時之需的行為，有時候甚至讓殘渣長出菌類。而且將食物儲存在沈積物深度較深的地方(甚至達到貧氧帶範圍)的額外好處是食物比較不容易被好氧細菌分解！這種現象啟發了另外兩種模式的概念：


圖3 直升機上拍攝的鑽石露天採礦場(烏達奇納亞，俄國)
Figure 3. The open pit of the Udachnaya Diamond Mine, Russia, from a helicopter. Photographer: Stapanov Alexander (CC BY-SA 3.0).

- 「儲藏室模型」：根據這個行為模式，螺旋潛跡生痕製造者會在食物不虞匱乏的時候在海床上蒐集食物(據推測是在海水表層的藻類大量生長之時)，然後將蒐集到的食物帶到較深的沈積物中儲存以應付糧食供應不足的時期。
- 「園丁模式」：這個模式假設螺旋潛跡生痕製造者一樣在海床上搜集食物然後儲存在沈積物深處，但菌類會在新引入的有機物質(食物)上繁殖生長，因而為生物製造了穩定的微生物食物來源。

上面四種模式皆試著解釋為何在海床下的沈積物中會發現有機含量豐富的成分。而更多的研究發現


(左)「碎屑攝食模式」或「糞坑模式」；(右)「棄渣場模式」。
(Left) Detritus feeding model or cess-pit model, (Right) Refuse dump model


(左)「儲藏室模型」；(右)「園丁模式」。
(Left) Cache model, (Right) Gardening model

ture. From the shape of the trace fossil itself we can draw certain conclusions. By looking at cross-cutting relationships between different components we can see which parts were constructed first, and which parts that must have been constructed later. As it turns out, different types of *Zoophycos* were constructed in slightly different ways. Some seem to have started from a position deep in the sediment and spiraled upwards, while others seem to have been constructed downwards, growing bigger and bigger with depth suggesting that the animal also must have grown larger during its life cycle. A common trait, however, is that the spreiten were formed by the gradual shifting of the marginal tube through the sediment, leaving pelleted material in the shape of a spreite in the sediment (Figure 2). This shifting of the marginal tube through the sediment led early researchers to conclude that the structure must be a feeding trace where the animal ate its way through the sediment much in the same way as modern strip-mines function: material is ingested along the outer wall and secreted as fecal pellets along the inner side of the tube (Figure 3).

Later research, however, revealed that the material in the pellets actually must have originated from the seafloor. Furthermore, at least in the modern variety of *Zoophycos*, the fecal pellets contain more organic material, which means more food, than the surrounding sediment. It therefore seems unlikely that the animal should have been a deposit feeder. Several models were proposed to explain the presence of organic rich pellets that apparently stemmed from the seafloor. The "detritus feeding model", sometimes called the "cess-pit model" suggests that the animal fed on organic particles that settled on the seafloor, and that the feces were excreted deep in the sediment to keep the feeding area clean. *Zoophycos* would basically be a very elaborate toilet! Another explanation, the "refuse dump model", suggested that the animal was a deposit feeder after all, but that particles from the seafloor were transported into the burrow system to buttress the cavities against collapse. The observation that some marine animals collect food particles and store them in the sediment for later usage, sometimes after letting bacteria grow on the particles, sparked two more models explaining *Zoophycos*. According to the "cache model", the animal collects food on the seafloor during times of plenty, presumably related to algal blooms in the surface waters, and stores the collected material deep in the sediment where it remains available as a food source to the organism during leaner times. Storing the collected food deep in the sediment also has the advantage of preventing degradation of the food because oxygen levels in the sediment pore waters are usually very low. The related "gardening model" postulates that the material collected on the seafloor is placed deep in the sediment where bacteria grow on the introduced organic material, thereby producing a more readily accessible food source for the animal to return to. The observations that the *Zoophycos* spreiten are often constructed in generally food-poor sediments, contains pellets which are rich in material found on the seafloor, and

螺旋潛跡生痕化石的蹼狀構造中的糞球排泄物裡頭含有在海床上十分富集的物質，且通常是在養分供應不足的沈積物中所構築的，加上整個螺旋潛跡構造所達到的沈積物深度也相當可觀，因此不符合「沈積物攝食生物」(只在沈積物中濾食，不會到海床上覓食)的行為，也與「碎屑攝食/糞坑模式」(沒有理由製造這麼深的糞坑)跟「棄渣場模式」(用海床上蒐集而來更有養分的物質支撐管壁不甚合理)這兩種模式的情境不相容。但卻與「儲藏室模型」與「園丁模式」所表現出的行為與結果相當吻合。特別是現代觀察到的螺旋潛跡生痕化石最有可能就是這兩種行為模式的混合體。

螺旋潛跡中看生物演化的變異

即使我們已知現代的螺旋潛跡生痕化石是生物在海床表面蒐集食物，然後儲存在沈積物深處的行為所製造的結果，如此複雜的行為又是如何演化的呢？被許多研究學者所探討的其中一個假設是，螺旋潛跡生痕化石的演化與海洋環境的大變化有所關聯。當第一個螺旋潛跡生痕化石出現在寒武紀時期，海洋生態系統的發育尚極其簡單，僅有一些生物生活在開闊的大洋裡，其餘大部份的生命活動都集中在淺海區域。那時在海床上見到的大部份生物都是生活在海床的表面，或是只會在沈積物底下幾公分的區域活動。這段期間內，有生痕化石的證據顯示蠕蟲逐漸發展出一種可以很有效率地在沈積物裡攝食的方式，而這樣的攝食方式產生出跟蹼狀構造很相似的外觀。經過一段漫長的時間，海洋生態系統也隨著時間演化地越趨複雜。有一些生物的活動遠離了淺海區域，探索未知開放的海域，同時將豐沛的食物引進了較深的海域。再看看海床上，那些擅於掘穴的獵食者們精進了獵食技巧，沈積物攝食生物只能被迫往更深的沈積物中尋求生機。

之後，時間來到中生代，棲息於開放海域的浮游生物群有了演化上的變異，使得沈降到海床上的有機物數量大增，這樣的優異條件有利於新的生物族群在深海域定殖繁衍；再加上本來的活動方式就像推土機式的沈積物攝食者(例如海膽)強勢的濾食方式，使得螺旋潛跡生痕製造者在淺海區域的生活更為艱困。這些種種因素就像一股無形的浪潮一樣，將生物的活動範圍由淺海往深海推進。不同形態的螺旋潛跡生痕化石，正是反映牠從中生代早期生活的淺海環境逐漸轉移到中生代晚期的深海環境的紀錄。

我們不會感到太意外才是，螺旋潛跡生痕製造者經歷了這麼長久的演化、進入了深海，牠們在沈積物深處構築複雜結構的技巧早已駕輕就熟。或許就是在這段期間，以及處在這樣一種食物的多寡受限於藻類在不同季節大量繁殖而有季節性變化的環境裡，螺旋潛跡生痕製造者發展出在穴室內儲藏食物的行為。螺旋潛跡生痕製造者既能夠未雨綢繆的在食物充足時採集，又能將其儲存在競爭者無法取得之處。如此堅韌的適應力比起其他同樣生活在海床上的生物─不管是淺海或是深海，都具有更多的生存優勢。

然而，俗語說「眼見為憑」，除非我們能親眼看到這種製造螺旋潛跡生痕的神秘生物，或是可以觀察到現代具有類似行為的生痕製造者，來證實這些行為模式假說；否則所有對螺旋潛跡生痕化石形態的詮釋都只是理論性的推測罷了。甚至可以預期的是，未來隨著更多螺旋潛跡生痕化石的出現，或許還會有更多關於這種奇特生痕化石的新假說！

that the whole structure reaches very deep into the sediment does not agree with the deposit feeder, detritus feeding, and the refuse dump models. However, the above mentioned observations agree very well with a cache or gardening behavior, and most likely the modern deep sea *Zoophycos* is the result of the combination of the two behaviors. Below are the conceptual models outlining the four new major behavioral models proposed to explain the construction of *Zoophycos*.

Evolution of behavior

Even if the modern *Zoophycos* trace fossil is the result of an organism collecting material on the surface and storing it deep inside the sediment, how can this kind of complex behavior have evolved?

One hypothesis that has recently been explored by several researchers is that the evolution of *Zoophycos* is coupled to major changes in the oceanic environment. When the first *Zoophycos* appeared in the Cambrian period, the oceanic system was quite simple with few organisms living in the open ocean and most of the activity was focused to the shallow shelf areas. On the seafloor most organisms lived directly on the sediment surface or explored only the topmost few centimeters. During this time, fossil evidence suggests that worms developed an efficient way of deposit feeding that resulted in spreiten like structures. With time the marine system grew more complex, some organisms ventured out into the open ocean, resulting in an increased food flux to deeper environments, and on the seafloor burrowing predators forced the deposit feeders ever deeper into the sediment. Later, during the Mesozoic, evolutionary changes among the plankton groups that inhabited the open ocean led to a strong increase in organic particles that rained down on the seafloor, allowing a colonization of the deep oceans by new groups, and at the same time bulldozing deposit feeders such as sea urchins made life difficult for the producers of *Zoophycos* in the shallower areas. This combined push and pull towards deeper environments is reflected in a transition of *Zoophycos* trace fossils from shallow environments in the early Mesozoic to deep environments in the end of the Mesozoic. Thus, when the *Zoophycos* producing animals entered the deep ocean they were already adapted to constructing complex structures deep in the sediment. An adaptation that became a powerful advantage in an environment where food flux is often limited to food produced during seasonal algal blooms. It was probably during this time that the *Zoophycos* producers incorporated the caching of food deep in their burrows into their behavior. The ability to collect food during seasons of plenty, and store this food resource far out of reach from competitors likely gave the *Zoophycos* producers an edge over other organisms on the deep-seafloor, which is reflected in the almost ubiquitous occurrence in slope and abyssal sediments. However, until we find a fossil producer at the end of the burrow, or can observe their modern counterparts actually constructing a *Zoophycos* burrow, all interpretations remain somewhat speculative and we can expect many new hypotheses about this fascinating trace fossil in the future.