全能住宅改造蝦—由東北角番仔澳甲殼類生痕化石探討幼體生物行為

Clues to the Behavior of Juvenile Crustaceans from a Peculiar Trace Fossil (*Ophiomorpha*) at Fanziao

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危機四伏的大海，纖細脆弱的生物只會成為俎上之肉，為了活下去，生物總會發展出一套保命守則。漂浮在茫茫大海中的蝦寶寶究竟要怎麼做，才能避免落入掠食者的腹中呢？近年來研究團隊在臺灣東北角，發現一組具有雙重管壁的生痕化石，似乎和幼蝦的生活行為有所關連……

堅不可摧的建築— *Ophiomorpha* 與泥粒

「凡走過必留下痕跡」，生痕化石保存著過去各種的生物行為，像覓食或移動等等。在這之中，有一種分佈範圍非常廣、辨認度極高、時常被地質學家用來辨識古代環境的生痕化石—*Ophiomorpha*(蝦類掘穴生痕化石)。

Ophiomorpha 是一種多分岔的圓管狀居住構造，管壁外側通常有許多圓球狀突起，內側十分平滑，是最典型的甲殼類生痕化石之一。通常是十足目動物(例如蝦子)為了居住所挖掘的洞穴，而不同個體所製造的通道經常會相連在一起，最後呈現如蟻窩一般的迷宮樣貌(圖1、2)。

Ophiomorpha 表面上凹凸不平的顆粒是其獨有的特徵，稱為「泥粒」(pellet)，一顆顆泥粒佈滿了圓柱狀管壁的表面，構成了凹凸不平的外貌，使這種生痕化石易於辨認。當蝦子、小龍蝦之類的甲殼動物在砂質海床底下鑽洞時，為了避免鬆散的砂子不堪負荷而崩塌，便會用前肢將胸足分泌的黏液與泥砂混合，搓出一顆顆的泥粒堆疊在管壁上，就像我們使用磚塊築牆一樣，可以讓洞穴更為堅固、不易坍塌！

在顯微鏡下可以發現，*Ophiomorpha* 管壁中有許多稜稜角角的顆粒聚集成團，我們稱之為次泥粒(sub-pellet)，它們和其他較小的礦物顆粒及黏液共同組成泥粒。

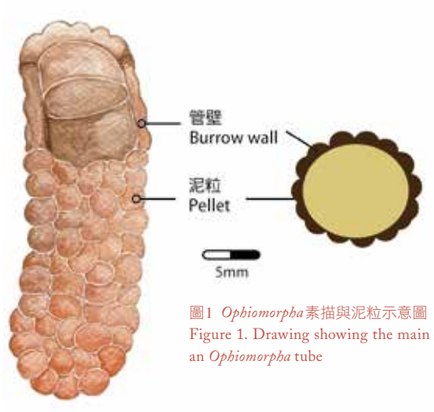

圖1 *Ophiomorpha* 素描與泥粒示意圖
Figure 1. Drawing showing the main parts of an *Ophiomorpha* tube

鑑古知今—生痕化石告訴我們的事

不同形態的生痕化石，反映的生物行為與環境也不相同。在波浪洶湧的濱面環境，海床上鋪滿了豐厚的砂層，部分生物為了躲避強勁的水流，會在海床砂層鑽洞居住。形成 *Ophiomorpha* 的環境多是以淺海為主，但在潟湖、深海的沖積扇或海床上、甚至陸相環境都可以發現其蹤影。從觀察生痕化石及其周圍岩性，地質學家便能解讀岩石形成當時，該地點的古環境(圖3)。

圖2 *Ophiomorpha*，攝於新北市瑞芳象鼻岩
Figure 2. The branching tubes of an *Ophiomorpha* system

In the wild and perilous sea, small creatures can easily become food on larger animals' dinner table. In order to survive, organisms have developed various strategies to avoid or escape from their predators. Recent findings demonstrate how some baby shrimps avoided falling into the belly of a predator. In Miocene sandstones from northeastern Taiwan, researchers recently found something peculiar: vertical shrimp burrows (*Ophiomorpha*) with a miniature tube in the center!

Building with recycled materials— *Ophiomorpha* and Pellets

An old Chinese saying goes, "The footprint in the sand shows where you have been". Trace fossils preserve an archive of diverse ancient biological behaviors, such as feeding, hiding, or moving. These precious traces can also help the geologists to identify different paleo-environments.

Ophiomorpha is a widely-distributed group of dwelling burrows characterized by multiple branches and a lining constructed from sandy pellets, generally produced by decapod crustaceans such as shrimps. Tunnels excavated by different individuals may be interconnected, and the final result often resembles a huge maze of winding tunnels. (Figure 1 and 2).

The pellets used to construct the burrow walls are an important characteristic of *Ophiomorpha*. To keep the open burrows from collapsing in the loose, sandy substrate, shrimps use their forelimbs to produce pellets consisting of sediment grains and mucus. The pellets are kneaded into the tunnel walls to enhance the stability and eventually give the external side of the wall a knobby appearance, while the inner side is typically smooth.

Pellets are composed of many little sub-pellets. Under the microscope, sub-pellets usually show a concentric pattern made up by concentrated angular grains.

What can sedimentary rocks tell us?

Different types of trace fossils can reflect specific biological behavior representing an organism's response to its paleoenvironment. To adapt to diverse water depth, salinity, energy and turbidity, distinct communities of organisms colonize different environments, leaving typical sets of trace fossils behind. By observing the assemblage of trace fossils, geologists can translate the information into stories of what happened in the ancient communites that inhabited those environments. For example, in shoreface environments influenced by strong waves, creatures mainly catch organic particles or plankton, and many organisms burrow deeply into the sea bed to resist the strong currents. The occurrence of *Ophiomorpha* usually indicates shallow water environments, although the traces can also be found in lagoons, abyssal fans and even in terrestrial environments (Figure 3)!

樓中樓？—雙層管壁的 *Ophiomorpha*

臺灣東北角的番仔澳地區，保留了距今1千700萬年到1千200萬年前的地層，大量出露的粉砂岩夾薄泥層，顯示了當時環境為易受暴風事件影響的淺海環境。地質學家在此發現了別具型態的 *Ophiomorpha*：這種 *Ophiomorpha* 形狀多呈L型，在直徑約2到3公分的豎管中，包裹著另一根細管子，這根內管會隨著外管延伸，呈雙層管壁的形貌，且內外管壁之間都有沉積物填充（圖4）。外管壁與一般 *Ophiomorpha* 無異，獨特的內管壁則是薄壁、敷有為數不多的小顆粒泥粒。這樣特殊的內管，究竟是怎麼形成的？它是生物製造出來的嗎？還是後來的外力形成的？如果是生物製造的，牠們這麼大費工夫又有什麼特殊目的？

顯微鏡下的發現

為了破解內管壁形成的秘密，我們特別採集具有雙重管壁的L型 *Ophiomorpha*，將其製成岩石薄片放在偏光顯微鏡下觀察，結果發現內管壁及外管壁有著極為相似的特徵。首先，兩管壁的礦物顆粒呈現稜角狀，除了一般造岩礦物如石英、長石之外，更有大量的針鐵礦填充在顆粒之間，形成黑色的基質。針鐵礦的出現顯示形成管壁時的環境為氧化狀態：生長在管壁中的微生物為了獲取能量，會將海水中的二價鐵（Fe^{2+}）氧化成三價鐵（Fe^{3+}），形成針鐵礦（FeOOH）在管壁內的澱積（圖5）。

除了針鐵礦這個發現之外，在內外管壁也都觀察到次泥粒構造，只不過在外管壁上的次泥粒組織較緊密且排列整齊，而內管壁上的次泥粒則排列鬆散。不論是針鐵礦或是次泥粒，都證明了內外管壁皆是由生物所製造，而不是外力（如成岩作用）所造成的。

體型的大小差異

由前述的觀察可知，不管在結構型態或是礦物組成，內外管壁都有一定的相似性，代表可能是親緣關係相近的甲殼類動物所製造的；而管壁的截面積差異很大，可以推測為體型差異懸殊的不同個體挖

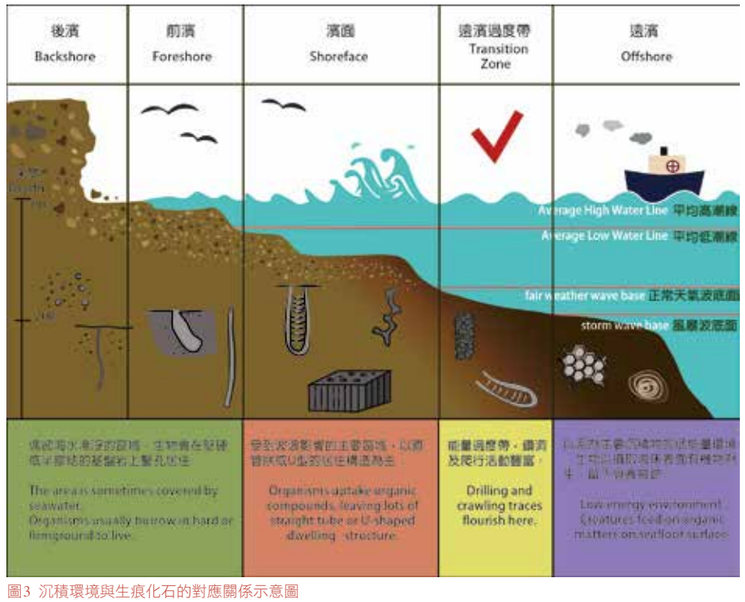

圖3 沉積環境與生痕化石的對應關係示意圖
Figure 3. Sedimentary environment and biological behavior

A room inside a room? The double-tubed *Ophiomorpha*

Our study area in the Fanziao section in northeastern Taiwan belongs to the Nankang Formation, which ranges in age from 17 million to 12 million years ago. From the primary sedimentary structures and trace fossils found in the sandstone, geologists have figured out that this place was a shallow, near shore marine environment, often influenced by storms. In the sections at Fanziao, we found a special kind of *Ophiomorpha* (Figure 4). These tubes are L-shaped and 2-3 cm in diameter. The L-shaped tubes typically contain a small tube running through the center of the larger vertical tube. The walls of these inner tubes are thin but also consist of small pellets. How were these peculiar inner tubes formed? Were they made by animals, or were they produced by non-biologic diagenetic processes in the sediment? If they were made by animals, what was their purpose for building these strange tubes?

圖4 擁有雙層管壁的 *Ophiomorpha* 生痕化石
Figure 4. The double-tubed *Ophiomorpha*

The new discovery under microscope

In order to understand the nature of the inner tubes, we collected double-tubed samples and studied them in thin-sections with a microscope. As it turns out, both the outer and inner tubes have similar features.

First, similar sub-pellets made by shrimp are found in both the outer and inner tubes, meaning that both the outer and inner tubes were produced by the same kind of organisms. However, there are some differences between the sub-pellets in the outer and inner tubes, such as texture and arrangement. In the outer wall, the grains in the sub-pellets are close to each other; while grains in the sub-pellets of the inner walls are more loosely arranged (Figure 5).

Second, in addition to the rock-forming minerals such as quartz and feldspar, we found that a black matrix consisting of goethite fills the space between the mineral grains. The existence of goethite is regarded as evidence of biological alteration of the mucus used by the shrimp to cement their pellets. As a result, we can confirm that both tubes are made by animals.

Size difference

The observations described above, that both tubes have certain similarities in mineral composition and arrangement, indicate that both the outer and inner tubes were produced by crustaceans that had a close genetic relationship. Because it seems highly unlikely that a large shrimp that fit in outer tube could maintain the much smaller inner tube over distances of more than 10 centimeters, the conclusion must be that the outer and inner tubes were made by two individuals of distinctly different sizes. However, the similarities in

掘出來的。況且，過去研究指出甲殼類動物光是維護及強化一般的管壁上，就占了牠們20%的時間，所以一隻蝦子要獨立挖出並維持L型雙重管壁是很困難的，更不用說番仔澳區發現的樣本大多長達10幾公分，要同時保持內外管的完整性，需耗費的氣力不敷成本！

誰是神秘建築師？

藉由詳盡的研究調查與實驗結果，我們可以歸納出雙重管壁的兩大特徵。第一，兩管壁都是以針鐵礦為基質填充，且皆可發現次小球構造，顯示兩管壁都是由生物所築成，且這兩種生物親緣關係接近。第二，雖然兩道管壁顯示是由相近或同樣種類的生物所築成的，但不太可能由同一個建造者獨力完成，且根據管徑尺寸差異可以推測兩管壁的建造者體型差異甚大。

地質學家常說「The present is the key to the past! 現在是通往過去的一把鑰匙！」，過去有些對長臂蝦科及海蛄蝦科的現代生物學研究發現，牠們的幼體在孵化後會進入遠洋浮游，當成長到青少年階段後，這些蝦子會游至近淺海的大陸棚上，進入親代特別準備的洞穴系統尋求庇護。

所以當筆者的研究團隊在番仔澳採到L型雙重的*Ophiomorpha*樣本時，不禁讓人充滿了想像！這些擁有L型雙重管壁的*Ophiomorpha*代表著什麼樣的故事？ 現代甲殼類的行為或許曾在中新世的番仔澳地區上演（圖6）：1千700萬年前，有一批蝦子為牠們將成熟的子代預備好了L型洞穴，做為良好的屏障，在子代結束幼年的浮游期回到陸棚後，由於牠們體型較小且尚未足夠強壯，便進入這些屏障尋求庇護，鑽出口徑和管壁較小的內管。這些幼蝦們在洞內慢慢長大直到完全成熟後，便離開L型內管，在外開拓自己新的洞穴系統，而這些曾經保護牠們的巢穴，保留了父母與自己的痕跡，成為優秀的改造住宅！

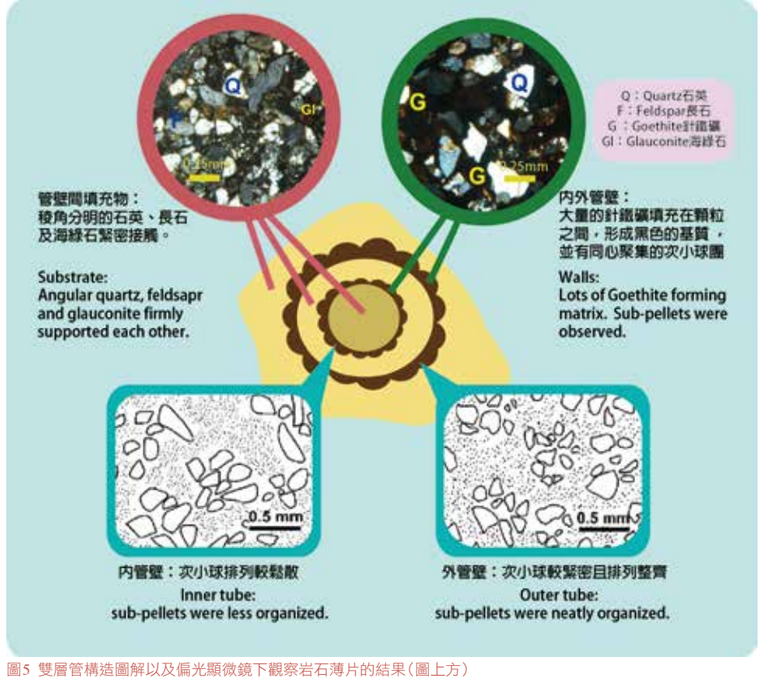

圖5 雙層管構造圖解以及偏光顯微鏡下觀察岩石薄片的結果（圖上方）
Figure 5. Microscopic images of the double tube

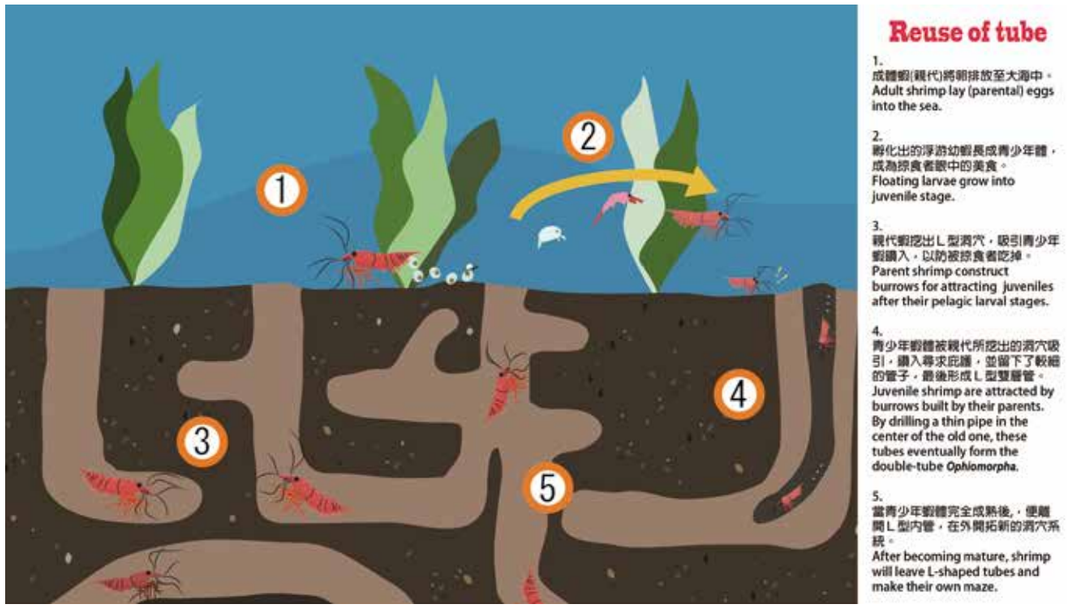

圖6 青少年蝦體的回歸
Figure 6. The life cycle of the shrimp responsible for constructing the L-shaped *Ophiomorpha* tubes with inner tubes.

pellet arrangement and construction suggest that they were excavated by two individuals of the same taxon, but of different size, most likely adults and juveniles.

Who are the mysterious architects?

With these results, we can summarize two main characteristics of the double tubed *Ophiomorpha*. First, both outer and inner tube walls contain goethite and sub-pellets. This indicates that both tubes are the products of shrimps that are close to each other phylogenetically. Second, although the burrowers of both tubes might be similar, or even of same species, they were not the same individuals, because their body sizes were distinctly different. Research has shown that the larvae of some modern shrimp belonging to Palaemonidae and Thalassinoidea have a planktonic stage in the pelagic ocean. After this stage, the larvae swim back to shallow waters where they enter burrow systems prepared by the parental generation.

In light of the present observations on the collected samples in combination with our knowledge of certain modern shrimps' behavior, we use our imagination to explain how these double-tubed *Ophiomorpha* were constructed 17 million years ago, when a group of shrimps built L-shaped burrows to provide a safe way for juvenile shrimps to return (Figure 6). After the young generation was mature enough to build their own burrow system, they connected their burrow to the parents' system and started their new lives as members of the larger maze. The disposable L-shaped tubes were abandoned to become the mysterious traces that we see in the Fanziao section in northeastern Taiwan!