一窺古海洋霸主滄龍—牙齒的奧秘

Unveiling the Secrets of the King of the Paleocean: The Mosasaurs' Mystical Teeth

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睽違14年，電影侏羅紀公園於2015年夏天推出新系列作品—《侏羅紀世界》，一上映就造成全球轟動、不斷刷新各地的票房紀錄。驚險萬分的情節與逼真的特效，滿足各世代的恐龍愛好者，再次掀起一股熱愛恐龍的風潮。影片中各種大型爬蟲類之中，首次出現的「滄龍」其實並非是侏羅紀的生物，而是白堊紀晚期才活躍於地球上。在電影的尾聲，身形龐大的滄龍一口將帝王暴龍咬入水中的那一幕，讓觀眾大開眼界！然而從科學的角度來看，滄龍的牙齒是否能夠在狩獵時，承受如此強大的衝擊而不會損壞？

大洋中稱霸的滄龍家族（Mosasauridae）

滄龍家族外觀上長的像是沒有鱗片的鱷魚，他們生活於晚白堊紀晚期的海洋環境，在世界各地皆有出土化石的資料。從過去對其化石的形態分析—流線型的身體與向前加深的胸腔、似槳的四肢、骨盆缺少陸生動物用以協助行走的骶骨附屬骨，以及不適合陸上行走的尾部等特徵，可以想像滄龍家族其實缺乏在陸地上生活的能力，並已經完全適應水中生活。近年來利用更多新出土的化石，結合古環境資料以及化學分析技術的提升，顛覆過去認為的刻板印象！學者們推測滄龍極有可能為內溫型胎生動物、一出生即具有高超的游泳能力，並能夠適應不同溫度的海洋環境。18世紀中晚期，在荷蘭馬斯垂克地下的採石場中首次發現滄龍化石，但當時人們對於這生物毫不瞭解，直到19世紀經過比較解剖學家居維葉（Georges Cuvier, 1769~1832）研究後才確立了這隻化石屬於一種已滅絕的生物，並由英國地質學家確認滄龍為一個新物種，命名為「霍式滄龍（*Mosasaurus hoffmanni*）」。

滄龍家族體長通常介於3至10公尺之間，化石紀錄最長可達17公尺；然而在電影《侏羅紀世界》當中，為了增加娛樂誇張效果，滄龍身體總長度預估超過幾十公尺。他們首度出現於晚白堊紀的土倫期（9,390萬年前至8,980萬年前），數量在三唐尼期（8,980萬年前至8,630萬年前）到馬斯垂克期（7,210萬年前至6,600萬年前）達到全盛（圖1），成為當時海洋生態系統最頂端的生物，最後與恐龍一同在白堊紀—第三紀滅絕事件消失（圖1）。雖然滄龍的名字裡有龍，但是在生物分類上滄龍並非是恐龍的一員，牠們屬於脊索動物門—蜥形綱—有鱗目，親緣關係上反而接近現今的蜥蜴與蛇。滄龍的祖先原是在陸地生活的蜥蜴，漸漸改變為具有游泳特徵、半水生的中間型生物「崖蜥」，最後演化成現今滄龍家族最原始的生物—達拉斯蜥蜴（*Dallasaurus turneri*）。達拉斯蜥蜴的生存年代約為9,200萬年前，化石出土於美國德州北部，其骨骼特徵顯示牠比中間型的崖蜥屬更能適應水中生活。

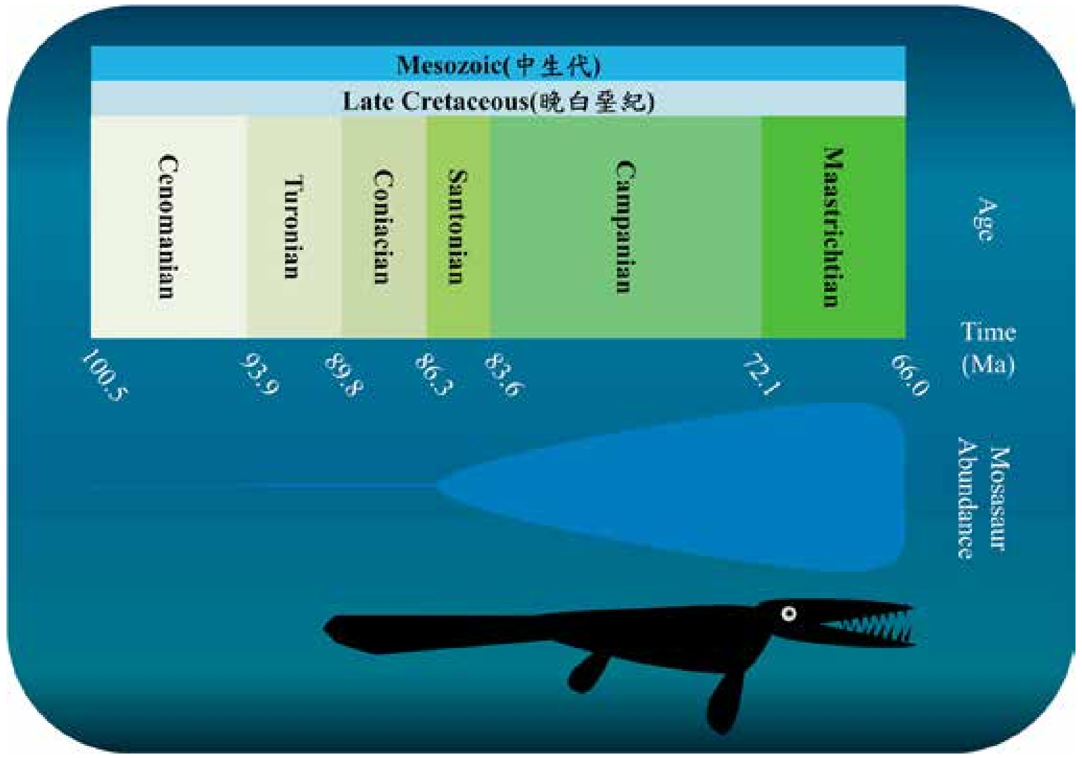

圖1 滄龍家族生存年代表。滄龍家族最早的成員出現於9,200萬年前（土倫期，Turonian），三唐尼期（8,630萬~8,360萬年前，Santonian）開始在數量及物種上明顯增加，最後在白堊紀—第三紀滅絕事件中滅絕消失。

Figure 1. The era of the mosasaur. The first member of the mosasaur group appeared about 92 million years ago during the Turonian age, and thrived in numbers from the Santonian age onward. Finally, all mosasaurs died out in the Cretaceous-Paleogene extinction event.

Jurassic World, the latest film of the Jurassic Park series, was displayed on the big screen in the summer of 2015. Because of its intriguing plot and fantastic special effects, this film caught everyone's eye and broke box-office records all over the world. From a scientific point of view, however, the movie is riddled with inaccuracies. First off, mosasaurs lived during the Cretaceous, making its appearance in a movie called *Jurassic World* anachronistic. Second, judging by the size of the Great White Shark used as bait to trick the mosasaur to jump out of the water, the movie mosasaur is two, if not three, times larger than the largest known mosasaur from the fossil record. Also, the mosasaur's tongue should be forked, as in a lizard or snake. One thing they got right, though, is the shape of mosasaur's teeth. In the final scene, the oversized mosasaur uses its sharp teeth and powerful jaws to bring down the park's latest attraction, the *Indominus rex*. From a scientific viewpoint, how were the teeth that could cut through a monster sized dinosaur constructed?

King of the Cretaceous ocean: Mosasauridae

Mosasaurs, looking somewhat like crocodiles without the heavy scales, inhabited the pelagic environment in the Late Cretaceous, and their fossils are widespread in deposits from this epoch. Based on fossil characteristics, mosasaurs had streamlined and bodies that widened forward, paddle-like limbs, and an asymmetrical tail, but lacked an attachment bone at the pelvis. The mosasaurs were perfectly adapted to the aquatic environment, and they were not mobile on land. New fossils and chemical analyses imply that mosasaurs were endothermal, vivip-

為了瞭解更多這些過去存在過的生物，新化石的出土對古生物學家來說如獲至寶。而摩洛哥出土了兩顆滄龍牙齒，經過專家鑑定之後分別為滄龍家族中滄龍亞科的滄龍屬與圓齒龍屬。我們利用這個機會對這兩顆牙齒的所有細節抽絲剝繭、交叉比對，看看從滄龍的「口中」能說出什麼精采的故事！

滄龍吃什麼？—從滄龍的牙齒一窺究竟

科學家馬賽略（Massare）觀察現代海洋獵食者的牙齒特徵，例如尺寸、齒冠形貌、牙齒磨面等，可以建立出牙齒形貌的三相圖：「細且尖銳」、「頂端鈍狀且堅固」和「頂端尖銳且堅固」，而這三種牙齒形貌分別對應到「刺穿」、「壓碎」與「切割」的不同飲食行為。再進一步比對海洋爬蟲類胃中的化石殘骸與其牙齒磨損痕跡，還可以知道他們獵食的對象：細且尖銳的牙齒專於捕捉沒有硬殼的軟體動物、頂端鈍狀且堅固的牙齒適合捕獵具有硬殼的菊石或貝類、而切割功能的牙齒則適合獵食大型魚類或水中爬蟲類（圖2）。這些發現證實了牙齒特徵與獵食對象之間確實存在明顯的關聯。應用在中生代海洋爬蟲類的牙齒上，我們可以利用圓齒龍屬牙齒的形狀來推測，牠們擅長透過壓碎硬殼生物來獲得食物，而且在一些化石證據中也顯示其胃部殘留有雙殼綱生物的碎片；而滄龍屬生物是以利齒切割其他生物，從其胃袋中也可以發現到魚類的頭骨。

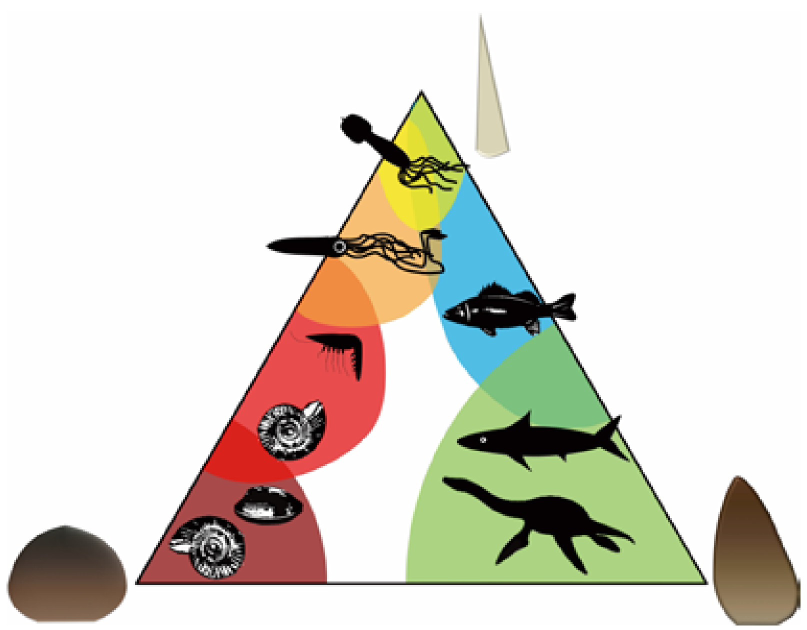

圖2 中生代海洋爬蟲類牙齒外型、功能與獵物關係三角圖。不同顏色代表不同功能與其功能對應到的獵物。深紅色區域牙齒功能為壓碎，主要獵物為菊石和雙殼貝類；鮮紅色區域牙齒功能為咬碎，主要獵物為甲殼類生物與菊石。橘色區域牙齒功能為粉碎，主要獵物為箭石。黃色區域牙齒功能為穿刺，主要獵物為頭足綱的軟體動物。藍色區域牙齒功能為穿刺，主要獵物為魚類。綠色區域牙齒功能為切割，主要獵物為大型魚類與小型海洋爬蟲類（修改自 Massare 1987）。
Figure 2. Triangular diagram of Mesozoic marine reptile teeth, showing the relationships among shape, function and prey preference. Dark red: cutting. Red: crushing. Orange: smashing. Yellow: piercing . Blue: piercing . Green: cutting. (Modified from Massare, 1987)

圓齒龍屬生存於坎帕期晚期至馬斯垂克期，化石分佈於北美洲、西歐、北非與中東地區，生活於熱帶海域（圖3）。從圓齒龍的名字不難想見，牠的牙齒特徵為類似橡樹果實的外觀、球根狀的齒冠、牙齒頂端有小瘤、非常鈍且可觀察到磨損痕跡、齒冠表面有明顯的垂直脊、牙齒高長比接近1，以及牙齒側面與其咬合面形狀不規則等。滄龍屬同樣也是生存於坎帕期至馬斯垂克期，化石分佈於北美洲與西歐一帶，生活於溫暖淺海環境（圖3）。牙齒特徵為尺寸較大、兩側有明顯的隆線、牙齒表面內外不對稱，內部較為平坦且有明顯的刻痕而外部較凸。

arous animals. The first mosasaur to be discovered was found in a limestone quarry near Maastricht in the late 18th century, but at that time the scientists couldn't comprehend what kind of animals the fossils were. It was not until the 19th century the well-known comparative anatomist Georges Cuvier (1769~1832) examined the fossils and confirmed that they belonged to an extinct animal. Later, the English geologist Gideon Mantell established the new species, *Mosasaurus hoffmanni.*

Most mature mosasaurs were 3 to 10 meters long; the record, found in Russia, reaches 17 meters. The mosasaurs first appeared in the late Cretaceous and thrived from 90 to 66 million years ago, when they died out along with the dinosaurs in the Cretaceous–Paleogene mass extinction event (Figure 1). Mosasaurs do not belong to the same groups as dinosaurs, rather, they are relatives of snakes and lizards. The ancestors of mosasaurs were terrestrial lizards that gradually evolved a semiaquatic lifestyle with swimming ability, such as the *Aigalosaurus*. The most ancient mosasaur, *Dallasaurus turneri*, was found in 92 million-year-old strata in northern Texas, and the fossils show that they were more adapted than *Aigalosaurus* to an open marine environment.

Although the skeleton can tell us much about the animals' swimming abilities, it is difficult to draw conclusions about their feeding preferences. Here we demonstrate how detailed studies of animal teeth could give insight into what prey the different mosasaur groups preferred.

What did mosasaurs eat? Evidence from their teeth

Massare (1987) studied the tooth characteristics of modern pelagic predators, focusing on tooth form, shape of the apex, and wear. She found a significant relationship between morphology and function of the teeth. Since tooth morphology of some modern marine animals shows traits similar to that of Mesozoic marine reptiles, she applied this analogy to illustrate the different functions of Mesozoic marine reptiles' teeth in a triangular diagram (Figure 2).

In the diagram, three distinct end members could be identified: at the top a very slender and sharp piercing tooth; at the lower, left a blunt and robust crushing tooth; and at the lower right a sharp, robust cutting tooth. Each end member corresponds to an adaptation to catch certain kinds of prey: creatures with piercing teeth caught soft animals such as squid; creatures with crushing teeth tended to feed on hard-shelled prey such as ammonoids or clams; and creatures with cutting teeth could hunt large prey such as fish or other marine reptiles. According to this hypothesis, *Globidens* were adapted to capture prey through crushing hard-shelled animals, while *Mosasaurus* utilized their strong teeth to cut large fish or small marine reptiles.

Globidens lived in the intertropical ocean, and its fossils are mainly distributed over North America, Western Europe, and North Africa (Figure 3). *Globidens* teeth are acorn-shaped and the ratio of height to width is nearly 1, with a bulbous tooth crown. The teeth are

無所遁形的滄龍牙齒

除了以肉眼直接觀察滄龍的牙齒，我們還可以藉由奈米穿透式X光顯微技術（圖4）的協助，獲得滄龍牙齒內部細微結構的高解析度立體影像。由於牙齒內部主要的微結構位於琺瑯質與象牙質的交界，我們特別針對此區域進行切片，以研究更精密的細部構造。

圓齒龍牙齒齒冠結構分成琺瑯質與牙本質兩層（圖5A左），牙本質中主要是由牙本質小管所組成，從3D影像中可發現其為樹枝狀（圖5C左）。另外從琺瑯質中可以看到一條條細長狀的結構（圖5B左），推測可能為釉叢（enamel tufts），釉叢原本為牙齒中的破裂，從琺瑯質與牙本質交界處向上延伸。形成的原因為當琺瑯質受到壓力或是脫水造成收縮時，在琺瑯質內產生微結構。這類型的微結構傾向使得破裂集中在特定區域，並且從牙本質順著破裂進入的有機物質也有可能填補了裂隙，這些特徵有助於釋放琺瑯質內部的應力，反而強化了牙齒的抵抗能力。與馬賽略建立的模型比較，圓齒龍牙齒外型頂端鈍狀且堅固，適合壓碎較硬或硬殼的生物。因此牙齒易受到垂直咬合面的應力影響，發育數量多的釉叢用於釋放琺瑯質內部的壓力、產生破裂。

滄龍牙齒齒冠可以分成三層結構（圖5A右）：琺瑯質、象牙質，以及夾在上述兩層中間的球間孔隙（圖5B右）。這層既薄且顆粒狀的結構，在3D影像中為一層網狀結構（圖5C右），此區域質地較軟且生物礦化程度低，這樣的結構看似脆弱，卻反而保護了牙齒免於受到從冠部傳遞至根部的破壞。假設

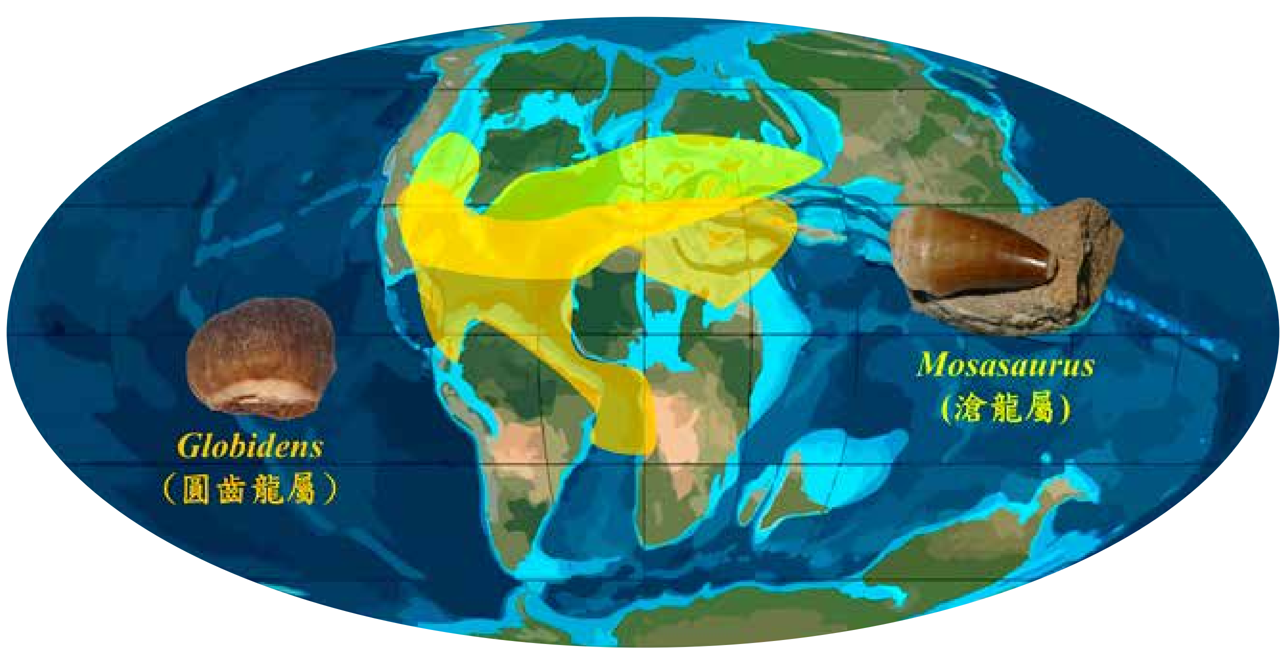

圖3 圓齒龍屬與滄龍屬的活躍區域。圓齒龍屬分布於南北緯20度之間的海域，滄龍屬分布於北緯30至40度之間的溫暖淺海。
Figure 3. The distribution of *Globidens* (orange) and *Mosasaurus* (yellow). *Globidens* lived in the shallow ocean between 20°N and 20°S, while *Mosasaurus* lived in the warm ocean between 30°N and 40°N.

blunt at the tip, with distinct vertical grooves on the crown surface. *Mosasaurus* lived in warm oceans at the same time as *Globidens*, and their fossils have been found mostly in North America and Western Europe (Figure 3). *Mosasaurus* teeth are large, with two significant sharp edges and asymmetrical teeth. The inside surface of teeth is flat while the outside surface is curved.

Scanning and dissecting the mosasaur teeth

Thanks to nano-transmission X-ray microscopy (Figure 4), we could compare high-resolution images of the internal microstructures of two types of mosasaur teeth: *Globidens* and *Mosasaurus*. The microstructures of primary interest to scientists are those of the enamel layers, whose cross sections yield the best information.

The *Globidens* tooth displays a two-layer structure composed of enamel and dentin (Figure 5A left). Within these two layers, two distinct microstructures (dentinal tubules and enamel tufts) can be easily observed (Figure 5B left). The dentinal tubules show up as three-dimensional dendritic structures within the dentin (Figure 5C left), and the enamel tufts are ribbon-like structures extending from the interface between the enamel and dentin. Enamel tufts represent previous cracks at the enamel-dentin boundary, resulting from shrinkage due to dehydration or exposure to pressure. The microcracks are restricted to that particular area and these fissures are healed by the dentin's organic matter. These characteristics not only help to relieve internal stress, but also enhance the tooth's impact tolerance. According to the model of Massare (1987), *Globidens* teeth, with their blunt apex and robust shape, are suited to crush hard-shelled creatures, with the teeth regularly exposed to stresses perpendicular to the top surfaces. Consequently, a higher number of enamel tufts was developed in the enamel to mend cracks and release internal stress.

The *Mosasaurus* tooth, in contrast, displays a distinctly three-layered microstructure (Figure 5A right): enamel, interglobular porous space, and dentin. The interglobular porous space consists of flame-like structures covering the dentin, as seen to the right in figure 5B(right), whereas in three-dimensional photos it demonstrates reticular structures (Figure 5C right). The consistency of interglobular porous space is soft and weakly mineralized; it likely protected the tooth from sudden stress. When the outside stress propagated through the interglobular porous space, this reticular structure would act as a cushion, resisting the stress, and shielding teeth during sudden impacts. However, according to the classification proposed by Massare (1987), the main function of *Mosasaurus* teeth was cutting. It seems unlikely that *Mosasaurus* teeth were exposed to stress that was perpendicular to the top surfaces. The presence of interglobular porous space, therefore, suggests that it acted as an effective shield, not only from perpendicular stresses but also against forces lateral to the top surface of the tooth. If a *Mosasaurus* tooth with its sharp apex were exposed by lateral impacts, enamel or dentin could easily have been damaged. The slight mineralization of the reticular struc-

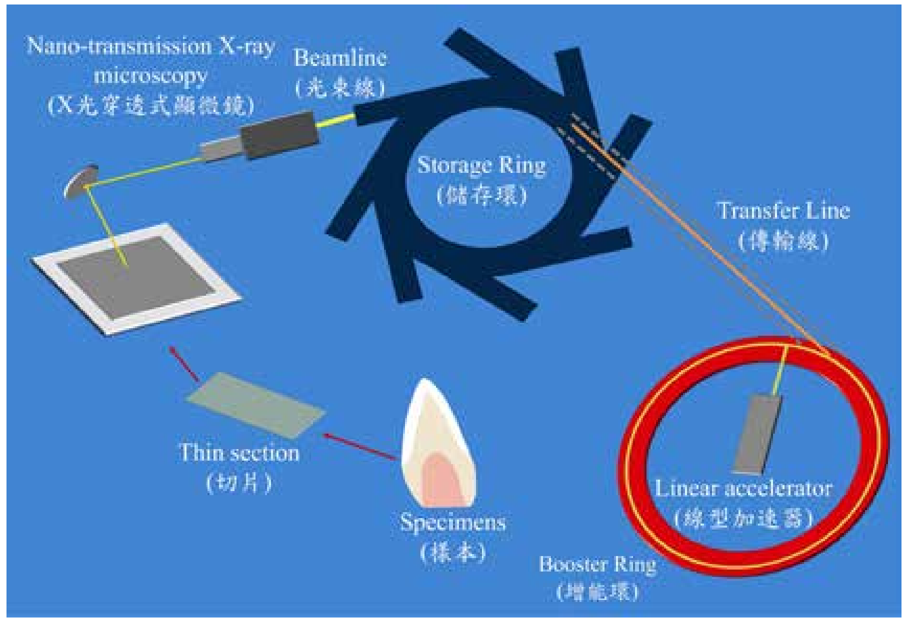

圖4 奈米穿透式X光顯微技術簡化示意圖。電子束由電子槍產生後經線性加速器提升能量，進入增能環後繼續提高能量並且將速度提升至接近光速，經由傳輸線進入儲存環中，儲存環中由磁鐵導引電子不偏離軌道，使得電子束能在偏轉的切線方向放出同步輻射光，最後由光束線進入實驗儀器，剖析樣本的內部物理或是化學結構等。

Figure 4. Schematic diagram of nano-transmission X-ray microscopy. Electron beams are produced from an electron gun and promoted through the linear accelerator to the booster ring. After entering the booster ring, the electrons are accelerated almost to the speed of light, after which the electron beams are transferred to the storage ring. Magnets help to keep the electron beams in the circle at high speed and the synchrotron radiation emitted at a tangential angle is transferred through a beamline to the nano-transmission X-ray microscope, where it is used to analyze internal physical characteristics or chemical structures.

滄龍稱霸海洋的秘密

綜合這次的發現，從琺瑯質—牙本質交界向外延伸的釉叢，可作為支持馬賽略模型的有力證據：牙齒依外型分類為壓碎功能者，釉叢數量較多，有助於釋放琺瑯質內的壓力。切割功能的牙齒，由於咬合面不會受到太大的應力破壞，因此琺瑯質內的壓力不會太大，釉叢數量較少。球間牙本質則是與牙齒的外型有關：牙齒外型頂端尖銳者，由於易受到側向或斜側向的撞擊，容易破壞琺瑯質與牙本質，所以在這之間製造出球間孔隙作為撞擊的緩衝墊、強化內部的抵抗能力；而牙齒形貌頂端鈍狀且堅固者，即便受到側向或斜側向的碰撞，也不易破壞牙齒結構，因此不會產生用於緩衝的球間孔隙。

滄龍咬合的力量傳遞至牙根之前先經過網狀結構的球間牙本質，將有助於抵銷應力，並且保護牙齒的牙根免於突然的衝擊。與馬賽略(1987)模型中比較，滄龍牙齒具備切割的功能，應該不至於受到太大應力破壞，這麼一來就與球間牙本質的功能相互牴觸。因此本研究推測球間牙本質不單只有抵抗從冠部方向而來的垂直受力，同時也具有抵抗來自側向力量的能力。滄龍牙齒屬於頂端尖銳而底部堅固的類型，若是牙齒尖端受到側向的受力，容易破壞琺瑯質與牙齒形貌，破壞了牙齒的功能，而這個球間牙本質的結構正發揮了緩衝來自牙齒側向的撞擊、維持牙齒琺瑯質與牙本質不受破壞或損壞的重要角色。

因此，滄龍牙齒是否能夠承受強大的衝擊且不會損壞？牙齒中的「釉叢」可以幫助釋放牙齒內部的壓力，而「球間孔隙」則是作為遭遇咬合衝擊時的緩衝墊。這兩個構造在滄龍的牙齒中扮演了極為重要的角色，使牠們在捕獵時不僅能毫無保留地發揮全部的力量，同時藉由上述的微構造減緩牙齒的壓力、承受強大的衝擊力道。不論是牙齒的外觀形貌或是內部的特殊結構，皆證實了牙齒的外部或內部特徵與獵物之間有顯著的關係。

延伸閱讀與參考文獻 / Further information and references

Massare, J. A. (1987) Tooth morphology and prey preference of Mesozoic marine reptiles. *Journal of Vertebrate Paleontology*, 7, 121-137.

Wang, Chun-Chieh, et al. (2015) Evolution and function of dinosaur teeth at ultramicrostructural level revealed using synchrotron transmission X-ray microscopy. *Scientific reports*, 5, 1-11.

tures would cushion lateral impacts, protect the inside structures and shield both enamel and dentin from the force.

Secrets of the mosasaur empire

In this study, enamel tufts extending from the enamel-dentin junction corroborate the model proposed by Massare (1987). Numerous enamel tufts were observed within the crushing teeth, and their function was evidently to relieve internal stress. Conversely, it seems unlikely that the top surfaces of the cutting teeth were exposed to high perpendicular stresses. Hence, enamel tufts are rarely observed in *Mosasaurus* teeth. On the one hand, enamel and dentin in sharp, pointed teeth could easily have been damaged by lateral impact. Newly evolved interglobular porous space could have acted as a cushion to enhance the tolerance to lateral or perpendicular forces. On the other hand, the structures of *Globidens* teeth, with their bulbous and robust shape, were resistant to lateral or oblique forces. Therefore, it was not necessary to produce a hypomineralized layer in the *Globidens* teeth.

Based on the position of enamel tufts and interglobular porous space in the teeth, it is likely that these structures help to release internal stress and enhance the strength of the teeth. The result in this study confirms that there are relationships among tooth internal structures, external characteristics and prey preference.

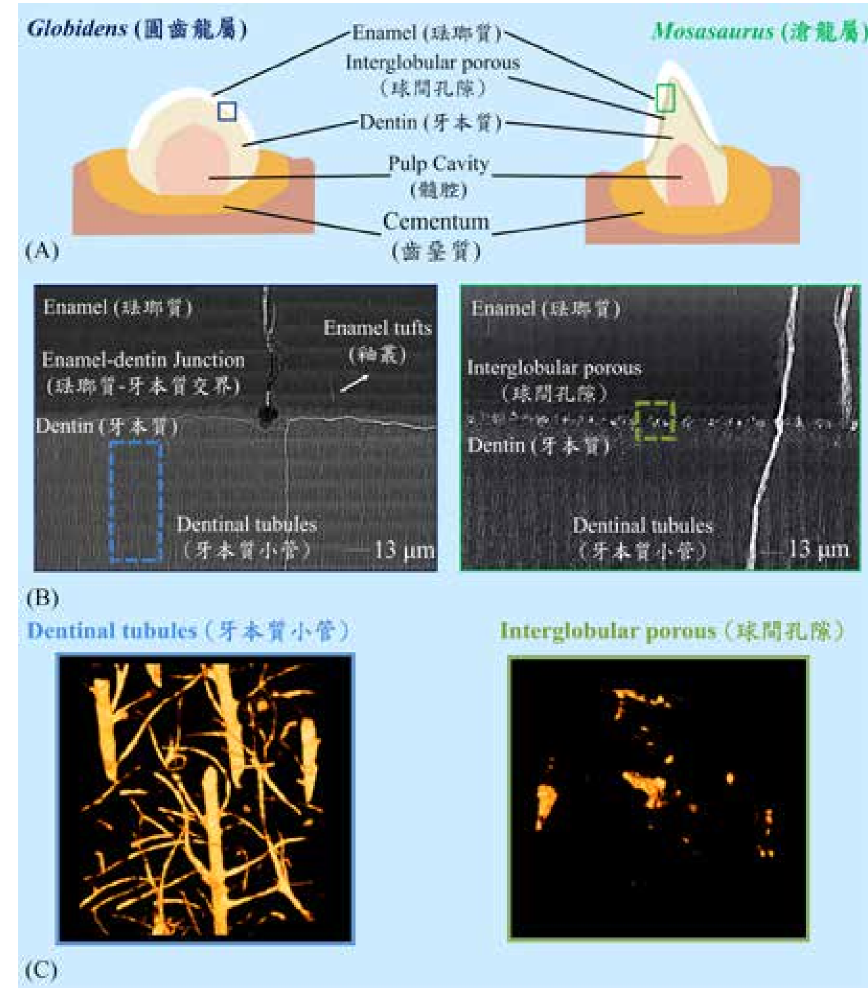

圖5 (A)圓齒龍屬與滄龍屬牙齒剖面簡圖，圓齒龍屬與滄龍屬的牙齒結構最大的差別在於滄龍屬內有球間孔隙。(B)圓齒龍屬與滄龍屬牙冠剖面X光影像圖，圓齒龍屬牙冠可分成兩層結構(琺瑯質與牙本質)，滄龍屬牙冠可分成三層結構(琺瑯質、球間孔隙與牙本質)。(C)牙本質小管與球間孔隙立體結構影像，牙本質小管為樹枝狀結構，而球間孔隙為網狀結構。

Figure 5. (A) Schematic sections comparing the teeth of *Globidens* and *Mosasaurus*. The most significant difference in microstructures between *Globidens* and *Mosasaurus* is that interglobular porous space was only observed in the *Mosasaurus* tooth. (B) X-ray microscope images of *Globidens* and *Mosasaurus*. The *Globidens* tooth display three layers: enamel, interglobular porous space, and dentin, while the *Mosasaurus* tooth displays a two-layer structure composed of enamel and dentin. (C) High-resolution images of dentinal tubules and interglobular porous space. Dentinal tubules are dendritic structures and interglobular porous space are web-like structures.