

The first record of exceptionally-preserved spiral coprolites from the Tsagan-Tsab Formation (Lower Cretaceous), Tatal, western Mongolia

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Research Article

Keywords: Tsagan-Tsab, amphipolar, IVPP V 27545, Asipenceriformes, ichthyophagous diet

Posted Date: January 15th, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-138265/v1>

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Version of Record: A version of this preprint was published at Scientific Reports on April 12th, 2021. See the published version at <https://doi.org/10.1038/s41598-021-87090-5>.

Abstract

Seven coprolites from the Lower Cretaceous of Tsagan-Tsab formation have been described, thus making this paper a significant contribution to the study of the firstly recorded coprolites from the Mesozoic deposits in Mongolia. The collected coprolites comprised a total of five morphotypes, whereby six of them are considered to be spiral amphipolar and one as rod shape. CT scans have also revealed that all specimens showed various amounts of bony inclusions and fish scales of unknown affinity, hence deducing that the producers may have had a low acid digestive track and were unable to dissolve bone matters. Moreover, SEM-EDS analysis concluded its carnivorous nature. In addition, all coprolites exhibited bony elements of identical morphological structures, which indicated that the producers might have preyed on the same type of organism. Specimen IVPP V 27545 is the only non-spiral coprolite and the smallest compared to the rest and contain plant pollens, an infraorbital bone and clusters of bones of the prey; bioerosional scars are observed on the surface. We suggest that the spiral coprolites were produced by Asipenceriformes with ichthyophagous diet, while the non-spiral rod like coprolite might possibly belong to smaller vertebrate organisms that can't be identified by us in this study.

Introduction

Studies on animal fecal excrement can be traced back to the earliest description by Lister in 1678¹. Duffin² mentioned that the earliest report of vertebrate coprolite could have been written by Edward Lhywd in 1570. Since then, the interest on the subject matter has increased over the years and progressed into the findings of fossilized feces. Coprolite, first termed by Buckland on fossils uncovered by Mary Anning's in Lyme Regis, Dorset, southern England. Buckland identified them as petrified fecal excrement that belongs to ichthyosaurs. Previously, those fossils were thought to be fossilized fir cones due to their similar spiral markings, but later on it was suggested to have belonged to animal origins^{3,4}. Although Buckland successfully referred the coprolites to marine animals, subsequent studies revealed that those spiral coprolites might have belonged to sharks, rather than what he thought was ichthyosaurs, which were commonly found in Lyme Regis^{5,6}.

Coprolite studies are well known over the years, and it has become one of the most important research in the subject of trace fossils and they displayed a wide range of morphological variation, including those that are spiral. According to the definition of Hunt & Lucas⁷, spiral coprolites possess an external appearance of a ribbon, which coils around a long axis, but internally they are formed of piled and spiraling cones. On the other hand, those identified scroll coprolites have a similar structure to a roll sheet of paper. Some of the earliest studies account on spiral valves in extant fishes were conducted by various scientists since 1667^{8,9,10,11,12,13}. As to date, the oldest known spiral coprolites have been recorded from the Soom Shale Lagerstätte of the Upper Ordovician of South Africa¹⁴.

Spiral coprolites were initially differentiated into two distinct morphotypes, the amphipolar and the heteropolar⁵. In later studies, heteropolar edge and knot morphotypes were introduced¹⁵. With that, it was generally agreed upon that spiral coprolites are indeed producer of animals with a complex spiral valve intestine, such as the sharks, rays, lungfishes and maybe ichthyosaurs^{4,16,17,18,19}; and are closely associated to aquatic environment; and generally, rapidly buried.

Notably, the significance of coprolite in the studies of paleontology and its contribution to the understanding of ancient ecosystems has been inevitably recognized in recent years. Coprolites from worldwide Phenerozoic has become one of the important tools in retrieving paleobiological information^{20,21,22,23}. Coprolites did play an important role in preserving the trait of behavior²⁴ and it has been acknowledged that coprolites can provide salient analytical diagnostic on the feeding habits and dietary, prey-predator interactions, digestive physiology, diversity of the biota and

environment in which the organism lived to a certain extent on bacterial residues and DNA fragments^{25,26,27,28,29,30}. This paper describes the biogenic structures, which herein attributed mostly to amphipolar spiral coprolites, found in the Lower Cretaceous of Tsagan-Tsab formation, western Mongolia. Despite the strong morphological structures that tends to support its animal feces origins, our studies have also discussed the coloration, composition of the specimen, surface texture, traces of coprophagous organisms and as well on the inclusions within it. A detailed description of the specimens and subsequent comparison to the anatomical of the intestine features on related extant fishes through past literatures has narrowed down the potential producer of the coprolites, which would possibly belong to Asipenceriformes (sturgeon and paddlefish) (see discussion and interpretations).

Geological settings

Tsagan-Tsab/Tsagaantsav/Tsagantsab formation is part of the Basin of Great lakes and Dornogobi basin, and stretches from northwest to southeast of Mongolia³¹. The exact age for this formation is controversial. According to past literatures^{32,33,34,35,36,37,38}, the Tsagan-Tsab formation could have ranged from late Jurassic to Early Cretaceous, while Graham et al.⁴⁰, reported $40\text{Ar}/39\text{Ar}$ age of 131 ± 1 Ma (Khara Khutul section) and 126 ± 1 Ma (Tsagan Tsav section), thus suggesting a Hauterivian-Barremian age. Krassilov⁴¹ reported a Valanginian to Barremian age from using plant fossils. It is also noted in Hasegawa et al.⁴², that the overall climate during this period is dry due to the presence of reddish beds with calcretes, and possible occurrence of intermittent humid climate due to perennial lacustrine bodies. The Tsagan-Tsab formation is almost 1000 m in thickness, where it is divided into upper and lower part, and consist of basal conglomerate to trough cross-bedded, coarse- to medium-grained sandstone, reddish or greenish shale, and calcretes^{36,42,43}. It mainly consists of alluvial fan to lacustrine deposits⁴² and forms a large shallow lake³¹.

Over the years, Tsagan-Tsab formation has yielded numerous fossil fauna, among some mentioned here but not limited, including insects, mollusca, ostracods, fish, lizards, pterosaurs and indeterminate psittacosaurid, sauropods and theropods^{31,37,39,44,45}.

The specimens were excavated at Tatal, western Mongolia (Fig. 1).

Results

Description

All of the specimens were collected as isolated forms within a close range in the same lacustrine facies. The coprolites can be divided into 4 morphotypes according to their shape and size. None of the spiral coprolites possesses the heteropolar shape.

Morphotype A

Morphology: Incomplete, thyphlosole like, spiral amphipolar coprolites

Referred specimens: IVPP V 27544, IVPP V 27546, and IVPP V 27547

Phase: P1 for IVPP V 27544 and IVPP V 27547

P2 for IVPP V 27546

Descriptions: These three specimens (Fig. 2A-C, H-J and K-N) are up to 47.79 mm in length and can reach a maximum width of 28.34 mm and second width of 25 mm. There are at least three coils which are clearly-developed and wide. Initially IVPP V 27546 (Fig. 2H-J) is thought to be a thyphlosole¹² morphology, but on further examination, we noticed the occurrence of disentanglement at the posterior end. All of their ends are slightly tapered.

Morphotype B

Morphology: Incomplete, medium size, spiral amphipolar coprolites

Referred specimens: IVPP V 27549

Phase: P2

Descriptions: Coils on IVPP V 27549 (Fig. 2S-U) are evidently shown to have the same width in lateral view. Due to their incompleteness, they have an antero-posterior length of more than 49.86 mm. The widest dimension is being measured at 23.8 mm and has a secondary width of 20 mm. It also has one end that has been flattened while the other hand has some damages. There are at least 3 coils in a preserved state.

Morphotype C

Morphology: Complete, kidney like shape, anisopolar, spiral amphipolar coprolites

Referred specimens: IVPP V 27548

Phase: P1

Descriptions: IVPP V 27548 (Fig. 2O-R) is completely preserved without any damage. It has a rough surface with a length of 47.86 mm and a maximum width of 18.61 mm, while its secondary width is 16.59 mm. Coils are clear but not sharply formed. The middle coil is slightly narrow then the end coil. One end is tapered, while the other end is flattened.

Morphotype D

Morphology: Complete, large, anisopolar, spiral amphipolar coprolites

Referred specimens: IVPP V 27550

Phase: P1

Descriptions: IVPP V 27550 (Fig. 2V-Z) is elongated and well preserved with a cross section of a flattened ovoid (Fig. 2Z). It is 94.1 mm long and 30.48 mm in maximum width and 26.87 mm in secondary width. The coprolite has 6 shallow coils that are not sharply separated. One end was slightly broken but the other end has an acute spot. The surface is smooth but has some cracks.

Morphotype E

Morphology: Complete, non-spiral, anisopolar, rod like

Referred specimens: IVPP V 27545

Phase: -

Descriptions: IVPP V 27545 (Fig. 2D-G) is 36.8 mm long, 13 mm in maximum width and 11.52 mm in secondary width. It is a complete coprolite with a rounded cross section. There are visible bone fragments on its surface. One end is slightly tapered than the other end.

Sizes

As from the measurements, all collected coprolites vary in sizes (Table 1). The smallest and complete specimen is IVPP V 27545 (Fig. 2 D-G) and while IVPP V 27550 (2V-Z) is multiple time larger. The maximum length for specimen IVPP V 27544, IVPP V 27546, IVPP V 27547, and IVPP V 27549 are not determined due to their incompleteness.

Surface adhesion and marks

All specimens contained some degree of bone fragments and scales adhered to the coprolite surfaces (Fig. 3). Additionally, all specimens have smooth surfaces with little abrasion. The inner coil lines of specimen IVPP V 27549 adhered with a matrix of red clay with silt (Fig. 2S-U). Only specimen IVPP V 27550 have been seen with concentric cracks (Fig. 2V-Z). Bite marks have also been found on specimen IVPP V 27545, where these traces were short, parallel, shallow and isolated. They have been formed from 3 furrows of roughly 3.8 mm long and 0.3 mm deep (Fig. 4).

Inclusions

Through CT scans and surface observation, we noticed that all specimens contained bone fragments and scales of varying degrees (Fig. 5). We were unable to identify the bones in detail for specimen IVPP V 27544, IVPP V 27546, IVPP V 27547, IVPP V 27548, IVPP V 27549 and IVPP V 27550, as there were too many of them and also very fragmentary. In contrast, for specimen IVPP V 27545, we noticed a rather complete bone structure such as the ribs and a segment of an infraorbital (Fig. 5H-N). SEM photograph from one random point of specimen IVPP V 27545 yielded result of the existents of pollen grain (Fig. 6C).

Borings

Surface borings of invertebrate burrowing can be seen in 2 spiral coprolites, namely IVPP V 27547 (Fig. 2D-G) and IVPP V 27550 (Fig. 2V-Z). CT scans revealed that the borings of specimen IVPP V 27550 did not intrude internally, and the same for some of IVPP V 27547 as well (Fig. 7). Specimens IVPP V 27546, IVPP V 27547, IVPP V 27548 and IVPP V 27549 are shown to have traces of internal borings (Fig. 5C-F).

EDS Analyses

In this work, regarding Tatal's coprolites, the mineral elements were examined by using EDS and the photos were taken with SEM. Analyses was conducted on 2 morphotypes (A and C) with two sample points on each. All 4 samples showed high peaks of calcium and phosphorus. EDS results of Morphotype A (Fig. 6A-B) and Morphotype C (Fig. 6C-D) gave similar atomic compositions. They were mainly composed of Ca, P and O and small peaks which belong to Nb, Si, C, K, Fe and Al. We have also described a potential pollen structure under SEM image (Fig. 6C). This possible pollen structure in Morphotype C (Fig. 6C) showed different atomic elements from other EDS results, where it contained high peaks of Na and Cl.

Taphonomy inferences

No signs of abrasion were found on all of the coprolites. Coloration of the coprolites varied, thus indicating they were buried in different sedimentary conditions. Through the shape of the coprolites, we can deduce that they have indeed

spent different amounts of time or phases in water bodies before burial (see description). Meanwhile, specimen IVPP V 27550 showed shallow coil deepness, therefore this indicates that it was buried rapidly after excretion.

Discussion And Interpretation

There are several pivotal evidences that corroborate to fecal origins of the Tsagan-Tsab Formation material: (1) basic morphology; (2) general shape and size (3) inclusions of the fecal matter; (4) high calcium and phosphorus content; (5) bioerosional scars; (6) borings and cavities; (7) concentric cracks.

The fundamental puzzle in the studies of coprolite is the difficulty in identifying the potential producer, which can be due to their nature and preservation. Also, that involves the methods used to deduce them with their producer were done by inferring with various forms of relationship based on stratigraphy and geographical relationships, as well as on neoichnology studies^{7,19,46,47}. Such problems similarly arose in our context as well, and the materials were collected from a stratum that is interpreted as lake deposit margins, thus suggesting an amphibious or aquatic producer. The paleoenvironment correlates with the findings of pterosaur fossils such as the *Noriopterus*³⁹ or argued as '*Phobetor*'⁴⁸, the diets of these pterosaurs were dependable on the lake environment^{49,50,51,52}. Among all, and more importantly, is that the shape of the coprolite has to be intact in order to represent the shape of the internal intestine of the producer, whereby, anatomically it can lead to a certain biological aspect and digestive system of the organism. Despite these, there are on-going controversies on the origin of the spiral shaped bromalites, on whether it signify fossilized feces or it was the cololite formed within the colon^{6,17,19,53,54}.

Spiral coprolites are producer of an animal with spiral intestine valves as to increase the surface area of absorption, to slow down food movement in the bowel as to maximize nutrient absorption, and is also a significant strategy in surviving uncertain and harsh environment condition^{24,55,56}. Referring to past literatures, it is generally agreed upon that the spiral shape are the only distinctively coprolite morphology, whereby it has been regarded as true coprolite and can be correctly associated to the source animal, as here to mention to a range of fishes in particular^{6,18,57}. Many primitive bony fishes (except those of teleosts), fresh water sharks (elasmobranches), coelacanth, *Saurichthys*, sturgeons and lungfishes are known to have the spiral valve intestine^{56,58,59,60}. Also, Price⁶¹ suggested that the amphipolar form could have been derived from palaeoniscoids. Additionally, Romer and Parsons⁶² noted that the spiral valves are secondarily lost in teleost and tetrapods, while Chin⁶³ noted a few teleosteans still possess it.

The spiral coprolites collected for this study are all amphipolar in shape. As we know, generally heteropolar spiral coprolite are produced by sharks, which have complex spiral valves⁵⁴. Therefore, we can exclude those in the family of elasmobranches as the potential producers. But it is also noteworthy to mention that, in previous studies, some workers conducted observations on sharks that were kept in tanks, and had not been able to find any spiral fecal pellets. The reasons given were that the sharks' eating habits could have changed due to the tank environment, which might have differed from the natural marine environment. Also, modern day sharks are totally unrelated to the ancient Permian pleuracanth sharks⁶. Despite these, evidence of spiral fecal pellet can still be observed in some of the present-day fishes, such as the African lungfish *Protopterus annectans*, the Australian lungfish *Neoceratodus forsteri*, the long-nosed gar *Lepisosteus osseus* and the spotted gar *Lepisosteus oculatus*^{6,64,65,66}.

In this study, we described 5 morphotypes for all the 7 coprolite specimens. Assigning 5 morphotypes does not assume that the coprofauna are of 5 different types of animals. Considering morphotype A and B are almost similar, we can deduce that at least 4 animals can produce these coprolites. Specimen IVPP V 27550 is remarkably big and its producer should be a massive animal since large animals could produce small excrement, but small animals could not

produce big excrement^{46,57}. Since there are no relevant fossils fauna found in the locality, we were unable to exactly identify the specific producer. However, we do know that 6 of the 7 coprolites are amphipolar spiral in shape, which can be attributed to certain types of fishes. As of these, we can conclude that the coprolites were produced by fishes in different sizes. Specimen IVPP V 27545 differs from the rest by its shape and size, which makes prediction even harder, because it could be produced by either small or big animals.

CT scans revealed that bony inclusions are evident in all of the coprolites (Fig. 5). Except in specimen IVPP V 27545, the bones in the rest of the coprolites are fragmentary. Specially, bones in specimen IVPP V 27545 are rather unaffected by the acidity of the digestive enzyme and these are evident by the presence of clusters of entire bones in the coprolite (Fig. 3A-C), as contrast to the fragmentary bones in the rests of the coprolites. Furthermore, we identified an infraorbital bone of a fish. CT scans revealed that the infraorbital bone has a sensory canal where it branches off at both ends (Fig. 5M-N). With these, we can indicate that the producer of specimen IVPP V 27545 poorly masticated the prey and also has rather low gut digestion for food^{24,47,67,68,69}. Through these results, we can infer the digestive strategies of the producers were in correlation with food intake and digestion process, as discussed in Barrios-de Pedro & Buscalioni⁶⁸. Specimen IVPP V 27545 might belong to the first type of digestive strategy, whereby the producer has limited food processing in the mouth and the food stays in the digestive system for a short period of time. This strategy is regarded to be efficient in conditions where food sources are abundant and the nourishment levels are sufficient⁷⁰. The rest of the coprolites possibly belong to the second digestive strategy, as the bone content are fragmentary. This suggest the producer might have limited mastication with improved digestive assimilation and longer gut time to favor better absorption of nutrients^{47,71,72,73,74}. The third type of digestive strategy does not imply in our study. It is also noteworthy to mention that the quantity of the inclusions is not correlated to the size of the coprolite, rather, it is dependable on the above-mentioned biological variables^{24,75}.

Carnivorous coprolites are normally composed of calcium phosphate and other organic matter, but it is important to be aware that the initial compositions are usually altered during fossilization processes²⁹. Meanwhile, the excretion of herbivores is generally lacking in phosphates and their fossilization are mostly dependable of the mineral enrichment⁷⁶. Through the morphological shape and the density of bone and scale inclusions on the surface through the CT scans as well, we can directly assume that these coprolites are inevitably produced by carnivorous organisms. But we still conducted SEM-EDS tests on 2 coprolite morphotypes (A and C) in order to determine its mineral content and to prove it as a valid coprolite material because we could not compare these materials to any attached locality matrix at the time of this study. The reason was that the specimens were collected 2 decades ago and they were very well-kept in the archives throughout these years. As predicted, all 4 samples gave higher content of Ca and P, thus, there is no doubt that they are fossilized fecal materials. SEM-EDS on specimen IVPP V 27545 (Fig. 6C-D), when randomly pointed to a particular structure yielded unusual results from the rest, where the EDS peaks are composed of Na and Cl. At the same time, the SEM image potentially showed a pollen grain like structure. Hollocher and Hollocher⁷⁷ documented a pollen image using SEM, which brings our potential pollen image (Fig. 6C) dimensionally compatible with their sample. Although specimen IVPP V 27545 is produced by an unidentified carnivorous vertebrate, it is usual for carnivore coprolites to have plant remains within them, and it is known that spores and pollens are exceptionally well preserved within the encasement of calcium phosphate, which inhibits sporopollenin degradation⁷⁸. Various reasons can be inferred for the presence of the pollen in specimen IVPP V 27545, on which it could either be by accident or by preying on an herbivorous animal. It could also be through the adhesion on the excrement when the fecal is still fresh⁷⁹. Pollens are valuable information provider for paleoenvironment reconstruction and as well in understanding the vegetation of a particular era^{78,80,81,82,83}, thus, further palynology analyses are needed for future work.

EDS mineral composition and coprolite coloration can be correlated to a certain degree, in which it could also explain depositional origin²³. Most of the Tatal's coprolites are pink-whitish in color, which is highly associated with the presence of calcium through its carnivorous diets^{84,85,86,87}. The dark colors can also be due to the presence of iron or it could also be due to complete phosphatisation^{19,23}. However, a large part of the colorations is influenced by diagenesis^{23,24}.

Traces of burrows are evident on the surface of specimen IVPP V 27547 and IVPP V 27550, but CT scans revealed internal traces burrowing did occur in specimen IVPP V 27546, IVPP V 27547, IVPP V 27548 and IVPP V 27549 (Fig. 5). Since not all possible burrows were dug-in, we gave the term 'pseudo-burrow' on those burrows that were abandoned in the early stages. For example, on all of the burrow traces in specimen IVPP V 27547, only one traces shows burrowing holes, while the rest did not form a hole. While those specimens with internals without any traces on the outer surface, this can be explained by taphonomy processes, whereby the outer surface is covered with sedimentary and non-differentiable. It was reported in Tapanila et al.⁸⁸, that marine bivalves are potential makers of the burrows in coprolites by expanding the diameter of the hole as they dig in, although Milàn, Rasmussen & Bonde⁸⁹, reported a contradictory, where the holes were indeed constant in diameter. In our studies, we couldn't determine if the holes were constantly in diameter or not. Numerous tiny holes were visible on all of the coprolites surface as well within it, and these were most probably caused by gases within the fecal matters. These holes can be called as microvoids or 'degassing holes', which contained gases trapped during digestion^{90,91,92}. Microvoids are quickly filled with water when fecal matter is excreted from the animal body, thus making the fecal becoming heavy and sinking to the lake floor⁹².

A series of three parallel furrows or bioerosional scars were evident on the surface of specimen IVPP V 27545 (Fig. 3). Those lines only occurred once without any repetition on the rest of the surface. The information from these furrows were insufficient to deduce any potential biters, as widely discussed in the work of Godfrey and Palmer⁹³, Godfrey and Smith⁹⁴, Dentzien-Dias et al.⁹⁵, and Collareta et al.⁹⁶. On the other hand, deducing from the dented surface on the bitten marks, we predicted that the marks were most probably made by the biting pressure from fish mandibles, which may indicate coprophagous behavior. The biting could have happened on the lake floor just before sedimentary deposition. Since the bitten marks are on the surface, this probably suggests unintentional scavenging and aborted during food search.

In general, coprolites can be transported from the original place through various modes²¹ and this can be evident by the traces of abrasion^{58,59}. However, in Tatal's coprolites, there were little or almost no marks of abrasion. Yet again, this supports our hypothesis that these coprolites were excrements on shallow waters such as in the lake banks with little turbulence and current, where the fecal matter was dropped *in-situ* after excrement. As seen in past literature^{97,98}, radial and concentric cracks are also evident on the surface of specimen IVPP V 27550, therefore, these indicate that the coprolite was excreted on a very shallow environment where the water body was vastly evaporated and left for subaerial exposure before embedment. This phenomenon caused the coprolite to dehydrate through the cracking, and shrinking occurred in a low magnitude process while retaining its overall shape^{23,46,99}. Previous authors have also discussed that the cracks could possibly be due to syneresis under certain conditions^{23,46,100}.

It has been frequently reported in records that almost all spiral coprolite fossilization from various Phenerozoic ages have occurred in low-energy shallow marine environments⁴⁶. Feces that are being excreted in this humid environment have a higher chance of preservation due to the rapid burial, as well as on the acidity of the water bodies^{5,7,101,102,103}. There are also several crucial factors that are involved in fecal fossilization. Among them, one of the most important criteria includes the content and composition of the fecal matter, and those of carnivorous diets tend to form

coprolites than those who consumed an herbivorous diet¹⁰⁴. As mentioned in Dentzien-Dias et al.¹⁰³, there are three main stages involved in a coprolite taphonomy history, which includes stages before final burial, after the final burial and after exposure. In accordance to this, we introduced the usage of phases to discuss the spiral coprolites morphologies in this study (see material and methods). The phase concept of spiral coprolites disentanglement has been widely discussed in early days by various workers^{6,18,64}. Coprolite specimen IVPP V 27544 and IVPP V 27547 are considered as Phase 1, as the coils are not deep, and this can be explained as during excrement, there's a mucosal membrane covering the surface of the fecal matter and embedment occurring rapidly, thus retaining most of its surface structure. Although there are signs of disentanglement, we predict that the uncoiling on the surface was not by natural processes but has been caused by a breakage after on. Both of these two coprolites could have been large in actual size. Similar explanations can be given to specimens IVPP V 27548 and IVPP V 27550, whereby the coils are shallow, thus classifying them to have occurred in phase one. We classify specimen IVPP V 27546 and IVPP V 27549 as phase 2, in which the spaces between the coils of IVPP V 27546 were slightly separated and in IVPP V 27549 was strongly separated. Both of these specimens could have spent more time in water bodies before burial. Specimen IVPP V 27545 does not provide any external information in regards of phases approach because of its non-spiral morphology. While it is also worthwhile to mention that none of them have spent sufficient time in the water bodies to possess the Phase 3 structure. Through these, we can also conclude that smaller coprolites are much complete while bigger coprolites tend to easily break-off. However, having mentioned that, the preservation of specimen IVPP V 27550 is indeed valuable.

Through the above morphological points, we predict that the amphipolar spiral coprolites could have belonged to groups of either prehistoric lungfishes or Acipenseriformes (sturgeon and paddlefish). Another aim of this work is to portray the existence of possible prey-predation relationships from the collected coprolites. In order to narrow down the identity of the potential producer and possibly the prey, we looked into some related fauna list from past literatures. Geological settings have indicated that the Lower Cretaceous Tsagan-Tsab formation is not only recorded in the area of Tatal, but also in other regions of Mongolia as well³¹. Yondon et al.³¹ reported *Lycoptera middendorffii*, a form of small freshwater Teleost fish from the Eastern Gobi - Tsagan-Tsab formation. Most *Lycoptera* fed on plankton, while some species could have fed on small insects and their larvae¹⁰⁵. Chang and Miao¹⁰⁶, mentioned the name *Lycoptera-Peipiaosteus* Fauna or the "Jehol Fauna", as these assemblages of fishes were not only abundant in the Lower Cretaceous Yixian Formation of northeastern China, but also widely distributed over the region of eastern Siberia, Mongolia, northern China and northern Korea. Several forms, such as those belonging to the Asipenceriformes (sturgeon and paddlefish) were endemic to these areas. It also noteworthy to mention that, the Tsagan-Tsab formations and the Yixian formation were of similar in geological age. As the name indicates, *Lycoptera* and *Peipiaosteus* fauna, which shows a close inter-relationship between these two species. Although there are no fossil records of Asipenceriformes in any of the Tsagan-Tsab formation throughout Mongolia, we can't exclude the possibilities of its existence. This possibility applies as well for the existence of *Lycoptera* in Tatal's Tsagan-Tsab formation, as it was noted that Bon-Chagan is the westernmost locality of *Lycoptera* in Mongolia^{106,107}. In the same context, it is note while to mention the records of *Stichopterus popovi* (Asipenceriformes), from the Aptian lacustrine of Gurvan-Eren Formation of Mongolia, a locality that is close to Tatal^{108,109}. Asipenceriformes are shown to have spiral valves¹¹⁰, and this can further be proven with the work of Capasso⁵⁶ on *Peipiaosteus pani*. Through these interpretations, we can possibly infer that the spiral coprolites in our study might have belonged to Asipenceriformes and Lycopteriformes as the prey, which could further affirm the occurrence of *Peipiaosteus-Lycoptera* inter-relationship (prey-predator) in the Lower Cretaceous of Tsagan-Tsab formation.

Conclusions

This study significantly contributes to the first records of coprolites from the Mesozoic of Mongolia. Specifically, we identified five morphotypes (A, B, C, D, E) from the materials, which were mainly studied on the basis of their morphology descriptions. Morphotype A, B, C, D are composed of amphipolar spiral coprolites, while morphotype E is rod-like. Generally, through the SEM-EDS analyses and CT scans, we can conclude that all the studied coprolites have been produced by carnivorous organisms with ichthyophagous diet. Specimen IVPP V 27545 might be omnivorous consisting of animal and plant diets, as bony fish bones and pollen grain were evident, or it could have eaten prey with herbivorous diet. All coprolites were in different sizes, inferring the producers were of different sized organisms. Additionally, the coloration, desiccation cracks, number of borings, cavities and coils deepness are different indicating that these coprolites are buried under different taphonomy conditions. The producer of morphotype A, B, C, D can be related to *Asipenceriformes*, while for morphotype E, we were unable to specifically link to any vertebrate group at the time of this study. In addition, we predicted that the prey is from the Subdivision of Teleostei. The study also shows that the ecology from where the coprolites were retrieved were once abundant in fish fauna. On a concluding note, a comprehensive future fossils studies and field excavation on the Tsagan-Tsab Formation is necessary to understand its paleoecology and intraspecies relationship.

Materials And Methods

The coprolites from the Tsagan-Tsab formation that are described in this study consist of 7 specimens (IVPP V 27544, IVPP V 27545, IVPP V 27546, IVPP V 27547, IVPP V 27548, IVPP V 27549, IVPP V 27550), in which 3 of them are in complete forms. They were collected *in-situ* by a senior researcher of IVPP (X. Wang) during The Mongol Highland International Dinosaur Project in 1998. All of them came from the same locality, together with other fossil faunas, especially the pterosaurs³⁹. The specimens are currently being housed at the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing.

Terminology. The terminology of this paper follows Hunt & Lucas⁷. Five distinct morphotypes can be distinguished within the collected material. The term spiral coprolite is mainly divided into heteropolar, where the whorls or coils are concentrated at one end of the coprolite; while those of amphipolar, are recognized by the spiral which are spaced along the length of the specimen (see^{5,18,21}). Another category of coprolite in this study can be termed as rod-like or cylindrical elongated (see⁷, Figs. 1 and 6). The term isopolar is referred to coprolite specimens with ends that are identical while anisopolar are for ends that are different in shape⁴⁶. The definition of total length and coil length follows McAllister⁵⁴. The definition of width follows Larkin, Alexander & Lewis⁹² and Halaclar¹¹¹, where two width measurements were taken, one at the widest diameter and another at 90 degree to the first width. The coprolites were measured using the aid of a vernier caliper to the nearest millimeter by eye. Coloration is based on Munsell soil color chart¹¹². Measurements, weight and general characteristics of the 7 specimens are summarized in Table. 1.

In this study, we adapted the coil loosening approach to discuss the period of the excrement in the water bodies from the time of excrement to burial. This biological aspect was noted by some workers in the past. In Dean⁶⁴, Williams⁶ and Jain¹⁸, they observed that these excrements, when deposited in water bodies, tends to uncoil like ribbon like by hourly. In this paper, we noted this process as phases to describe the morphology of the spiral coprolites. With this, we propose 3 phases in order to explain the period of the uncoiling, as explained by the aforementioned authors. Those include: Phase 1 - Early phase of deposition, where all coils remain intact; Phase 2 - Several hours after deposition, which some coils start to disentangle; Phase 3 - After 24 hours, where most coils have already loosened.

Scanning electron microscopy. We conducted the scanning electron microscopy (SEM) coupled with energy-dispersive X-ray spectroscopy (EDS) on two specimens where the samples were easily obtained. For this, a tiny piece of sample

was required by breaking it from the coprolite tip. The specimens were then attached to a stub and coated with gold. The least damaging approach was considered in this process, which explains the reason on why only two samples were considered, and not all seven.

Computed Tomography. A non-destructive technique using Computed Tomography (CT) scanning was used in examining the content and borings in the coprolites as well the production of a 3D model (Supplemental video). Seven specimens of coprolites (IVPP V 27544 to IVPP V 27550) were scanned using the 225 kV micro-computerized tomography (developed by the Institute of High Energy Physics, CAS) at the Key Laboratory of Vertebrate Evolution and Human Origins, CAS. The specimens of IVPP V 27544, IVPP V 27546, IVPP V 27547, IVPP V 27548, IVPP V 27548 and IVPP V 27550 were scanned with beam energy of 160 kV and a flux of 120 μ A at a resolution of 63.00 μ m per pixel, and IVPP V 27545 were scanned with beam energy of 130 kV and a flux of 150 μ A at a resolution of 19.13 μ m per pixel, using a 360° rotation with a step size of 0.5°. A total of 720 projections were reconstructed in a 2048*2048 matrix of 1536 slices using a two-dimensional reconstruction software developed by the Institute of High Energy Physics, CAS. All of the segmentation and the rendering of the CT scanning data were processed by using VG Studio Max 3.0 (Volume Graphics, Heidelberg, Germany).

Photography and drawings. Each specimen was photographed and edited with Adobe Photoshop CS6 to remove backgrounds, and drawings were completed by using Adobe Illustrator CS6.

Abbreviations

CAS Chinese Academy of Sciences

PGI MAS Institute of Paleontology and Geology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia

IVPP Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China

Declarations

Acknowledgements

The authors are profoundly indebted to Dr. X. Wang, who first introduced us to the coprolites, which were respectively collected by him during The Mongol Highland International Dinosaur 1998 Project. Further, Dr. X. Wang has greatly assisted us in understanding the geological settings, from where the coprolites were retrieved. Also, we are grateful to all the members from the IVPP and PGI MAS who has taken part in the 1998 expedition, notably to Dr. Z. Dong. We would like to thank Mr. H. Zang for the magnificent photographs of the specimens and Dr. X. Jin for generously assisting us in the SEM-EDS procedures, followed by Mr. Y. Hou for graciously having the specimens CT scanned. Besides that, we wish to extend our gratitude to Dr. M. Chang and Dr. J Zhang for their valuable points of views during the discussion sessions. Additionally, we appreciate xx for the meticulous proofreading and editing efforts for the manuscript. Lastly, we also want to oblige xx and xx and other anonymous reviewers for their constructive comments and feedbacks on the manuscript.

Funding

Our coprolite study was supported by the Natural Science Foundation of China and the Strategic Priority Research Program of the Chinese Academy of Sciences.

Grant Disclosures

1. Natural Science Foundation of China, Grant No. 41688103.
2. Strategic Priority Research Program of the Chinese Academy of Sciences, Grant No. XDB26000000.

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Contributions

P.R. and K.H. designed the project, performed the specimens descriptive research, performed data collection, wrote the manuscript, prepared the figures. H.C. performed the specimens descriptive research, performed CT reconstruction drawings and figure, and assisted in data collection. All authors contributed to manuscript editing, gave final approval for publication, and are accountable for the contents.

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Conflict of Interest

All authors have no conflict of interest to declare.

References

1. Lister, M. *Letters and divers other mixt discourses in natural philosophy*. York : Printed by J. White for the author (1683).
2. Duffin, C. J. The earliest published records of coprolites. *New Mexico Museum of Natural History and Science Bulletin***57**: 25–28 (2012).

3. Mantell, G. A. *The Fossils of the South Downs Or. Illustrations of the Geology of Sussex*, Lupton Relfe (1822).
4. Buckland, W. On the discovery of coprolites, or fossil faeces, in the Lias at Lyme Regis, and in other formations. *Transactions of the Geological Society of London Series 23*: 223–236 (1829).
5. Neumayer, L. Die Koproolithen des Perms von Texas. *Palaeontographica* (1846-1933) **51(2-3)**: 121-128 (1904).
6. Williams, M. E. *The Origin of Spiral Coprolites. Paleontological Contributions*. The University of Kansas, Paper 59 (1972).
7. Hunt, A. & Lucas, S. Descriptive terminology of coprolites and Recent feces. *New Mexico Museum of Natural History and Science Bulletin 57*: 153-160 (2012).
8. Steno, N. De Anatomie Rajae Epistola. Hafniae. Also published in his De Musculis & Glandulis observationum specimen, etx. Hafniae, 1664.—Maar, 1910, I, No. XVI, pp. 195-207; spiral valve, p. 199 (1664).
9. Perrault, C. Observations qui ont este faites sur un grand Poisson dissequé dans la Bibliotheque du Roy, *le vingt-quatrieme Juin*, 1667, Paris (1667).
10. Müller, J. B. *Vergleichende Anatomie der Myxinoiden*, Deutsche Akademie der Wissenschaften zu. Berlin (1835).
11. Duméril, A. *Histoire naturelle des Poissons ou ichthyologie generale Paris 2vol 1*: 1-720 (1865).
12. Parker, T. J. On the Intestinal Spiral Valve in the genus Raia. *The Transactions of the Zoological Society of London***11(2)**: 49-61 (1880).
13. Gudger, E. W. The history of the discovery (1600-1680) of the spiral valve in the large intestine of Elasmobranchs and a Ganoid. *Journal of the Elisha Mitchell Scientific Society***66(1)**: 53-69 (1950).
14. Aldridge, R. J., Gabbott, S. E., Siveter, L. J. & Theron, J. N. Bromalites from the Soom Shale Lagerstätte (Upper Ordovician) of South Africa: palaeoecological and palaeobiological implications. *Palaeontology***49(4)**: 857-871 DOI 1111/j.1475-4983.2006.00570.x (2006).
15. Dentzien-Dias, P., Figueiredo, A., Horn, B., Cisneros, J. C. & Schultz, C. L. Paleobiology of a unique vertebrate coprolites concentration from Rio do Rasto Formation (Middle/Upper Permian), Paraná Basin, Brazil. *Journal of South American Earth Sciences* **40**: 53-62 (2012).
16. Lea, H. C. On Coprolites: *Philos. Soc., Proc.* **3**: 143 (1843).
17. Frisch, A. Miscellanea palaeontologica 1. *Palaeozoica* 1-23 (1907).
18. Jain, S. L. Spirally coiled coprolites from the Upper Triassic Maleri Formation, India. *Palaeontology* **26**: 813–829 (1983).
19. Duffin, C. J. Coprolites: a brief review with reference to specimens from the Rhaetic Bone Beds of England and South Wales. *Mercian Geologist* **7**: 191-204 (1979).
20. Häntzschel, W., El-Baz, F. & Amstutz, G. C. Coprolites, an annotated bibliography. *Memoirs of the Geological Society of America* **108**: 1–132 (1968).
21. Hunt, A. P., Chin K. & Lockley, M. G. The palaeobiology of vertebrate coprolites, p. 221–240. In S. K. Donovan (ed.) *The Palaeobiology of Trace Fossil*. Wiley, Chichester, U.K. (1994).
22. Eriksson, M. E., Lindgren, J., Chin, K. & Månsby, U. Coprolite morphotypes from the Upper Cretaceous of Sweden: novel views on an ancient ecosystem and implications for coprolite taphonomy. *Lethaia***44**: 455–468 (2011).
23. Krause, J. & Piña, C. Reptilian Coprolites In the Eocene of Central Patagonia, Argentina. *Journal of Paleontology* **86**: 527-538 DOI 10.2307/41480215 (2012).
24. Cueille, M., Green, E., Duffin, C. J., Hildebrandt, C. & Benton, M. J. Fish and crab coprolites from the latest Triassic of the UK: From Buckland to the Mesozoic Marine Revolution. *Geol. Assoc.* DOI 10.1016/j.pgeola.2020.07.011 (2020).

25. Poinar H, *et al.* Molecular Coproscopy: Dung and Diet of the Extinct Ground Sloth *Nothrotheriops shastensis*. *Science* (New York, N.Y.). **281**: 402-6. DOI 10.1126/science.281.5375.402 (1998).
26. Hofreiter, M., Sette, D., Poinar, H.N., Kuch, M. & Pääbo, S. Ancient DNA. *Nat Rev Genet***2(5)**: 353-359 DOI 1038/35072071 (2001).
27. Hollocher, T., Chin, K., Hollocher, K. & Kruge, M. Bacterial Residues in Coprolite of Herbivorous Dinosaurs: Role of Bacteria in Mineralization of Feces. *Palaios* **16**: 547-565 DOI 10.2307/3515628 (2001).
28. Jouy-Avantin, F., Debenath, A., Moigne, A. M. & Moné H. A Standardized Method for the Description and the Study of Coprolites. *Journal of Archaeological Science* **30**: 367-372. DOI 10.1006/jasc.2002.0848 (2003).
29. Sharma, N. Fungi in dinosaurian (Isisaurus) coprolites from the Lameta Formation (Maastrichtian) and its reflection on food habit and environment. *Micropaleontology* **51**: 73-82 (2005).
30. Hu, S., Zhang, Q. & Zhou, C. Fossil coprolites from the Middle Triassic Luoping Biota and ecological implication. *Journal of Earth Science***21**: 191-193 DOI 1007/s12583-010-0209-7 (2012).
31. Yondon, K., Badamgarav, D., Yarinpil, A. & Barsbold, R. Cretaceous system in Mongolia and its depositional environments. *Developments in Palaeontology and Stratigraphy* **17**: 49-79 DOI 10.1016/S0920-5446(00)80024-2 (2000).
32. Vasilev, V. G., Grishin, G.L. & Mokshantsev, K. B. *Sovetskaya Geology* **2**: (in Russian) (1959).
33. Martinson, G. G., Sochava, A. V. & Barsbold, R. *AN SSSR* 189-1081. (in Russian) (1969).
34. Shuvalov, V. F. & Trusova, E. K. New data on the stratigraphical position of the late Jurassic and early Cretaceous conchostracans of Mongolia. In *Paleontology and biostratigraphy of Mongolia*, pp. 182–3. *Transactions of the Joint of Soviet–Mongolian Paleontological Expedition 28* (in Russian) (1976).
35. Bakhurina, N. N. A pterodactyl from the Lower Cretaceous of Mongolia. *Palaeontologicheskii Zhurnal***4**: 104–8 (in Russian) (1982).
36. Shuvalov, V. F. *Palaeogeography and historical development of Mongolian lake systems in the Jurassic and Cretaceous*. In *Mesozoic lake basins of Mongolia* (ed. Martinson GG), pp. 18–80. Leningrad: Nauka (in Russian) (1982).
37. Ponomarenko, A. G. Novye setchatokrylye (Insecta: Neuroptera) iz mezozoya Mongolii. *Novye Taksony Iskopaemykh Bespozvonochnykh Mongolii, Sovmestnaya Rossiisko-Mongol'skaya Paleontologicheskaya Ekspeditsiya***41**: 101-111 (1992).
38. Bakhurina, N. N. & Unwin, D. M. A survey of pterosaurs from the Jurassic and Cretaceous of the former Soviet Union and Mongolia. *Historical Biology***10**: 197–245 (1995).
39. Lü, J. *et al.* New material of dsungaripterid pterosaurs (Pterosauria: Pterodactyloidea) from western Mongolia and its palaeoecological implications. *Geological Magazine***146(5)**: 690-700 DOI 10.1017/S0016756809006414 (2009).
40. Graham, S. A. *et al.* Sedimentary record and tectonic implications of late Mesozoic rifting, southeast Mongolia. *Geological Society of America Bulletin***113**: 1560–1579 (2001).
41. Krassilov, V. Early Cretaceous flora of Mongolia. *Palaeontographica B***181**: 1–43 (1982).
42. Hasegawa, H. *et al.* Depositional ages and characteristics of Middle–Upper Jurassic and Lower Cretaceous lacustrine deposits in southeastern Mongolia. *Island Arc***27**: DOI 10.1111/iar.12243 (2018).
43. Samoilov, V. S. & Benjamini, C. Geochemical Features of Dinosaur Remains from the Gobi Desert, South Mongolia. *PALAIOS***11(6)**: 519–531 DOI 10.2307/3515188 (1996).
44. Weishampel, D. B., Dodson, P. & Osmólska, H. *The Dinosauria*. 2nd Edition, 1-880. Berkeley: University of California Press. ISBN 0-520-24209-2 (2004).

45. Barrett P. M., Butler, R. J., Edwards, N. P. & Milner, A. R. Pterosaur distribution in time and space: an atlas in Flugsaurier: Pterosaur papers in honour of Peter Wellnhofer. *Zitteliana B28*: 61-107 (2008).
46. Thulborn, R. A. Morphology, preservation and palaeobiological significance of dinosaur coprolites. *Palaeogeography, Palaeoclimatology, Palaeoecology***83(4)**: 341-366 (1991).
47. Luo M. *et al.* Taphonomy and palaeobiology of early Middle Triassic coprolites from the Luoping biota, southwest China: Implications for reconstruction of fossil food webs. *Palaeogeography, Palaeoclimatology, Palaeoecology* 474 DOI 10.1016/j.palaeo.2016.06.001 (2016).
48. Hone, D. W. E., Jiang, S. & Xu, X. A taxonomic revision of *Noriopteris complicidens* and Asian members of the Dsungaripteridae. Geological Society, London, Special Publications **455(1)**:149–157 DOI 10.1144/SP455.8 (2017).
49. Wellnhofer, P. *The illustrated encyclopaedia of pterosaurs*. London: Salamander Books, 117–121 (1991).
50. Unwin, D. M. *The pterosaurs from deep time*. New York: Pi Press (2005).
51. Witton, M. P. *Pterosaurs: natural history, evolution, anatomy*. Princeton: Princeton University Press (2013).
52. Chen, H. *at all.* New anatomical information on *Dsungaripteris weii* Young, 1964 with focus on the palatal region. PeerJ 8:e8741 DOI 10.7717/peerj.8741(2020).
53. Stewart, J. D. Enterospirae (fossil intestines) from the Upper Cretaceous Niobrara Formation of western Kansas; in Chorn J, Reavis EA, Stewart JD, Whetstone KN, eds., *Fossil fish studies*. The University of Kansas Paleontological Contributions **89**: 9-16 (1978).
54. McAllister, J. A. Reevaluation of the formation of spiral coprolites. The University of Kansas. *Paleontological Contributions***Paper 114**: 12 (1985).
55. Wetherbee, B. M. & Gruber, S. H. Absorption efficacy of the lemon shark *Negaprion brevirostris* at varying rates of energy intake. *Copeia* **1993**: 416-425 (1993).
56. Capasso, L. First direct evidence of the spiral valve intestine of sturgeons in an exceptionally well preserved early Cretaceous fossil. *Bollettino del Museo Civico di Storia Naturale di Verona* 4323–27 (2019).
57. Chin K. *The paleobiological implications of herbivorous dinosaur coprolites: Ichnologic, petrographic, and organic geochemical investigations*. Unpublished Ph.D. Dissertation, University of California, Santa Barbara (1996).
58. Hunt, A. & Lucas, S. The origin of large vertebrate coprolites from the Early Permian of Texas. New Mexico Museum of Natural History and Science **30**: 125-126 (2005).
59. Mancuso, A. C., Marsicano, C. & Palmap, R. Vertebrate coprolites from the Triassic of Argentina (Cuyana Basin): *Ameghiniana* **41**: 347-354 (2004).
60. Argyriau, T., Clauss, M., Maxwell, E. E., Furrer, H. & Sánchez-Villagra, M. R. Exceptional preservation reveals gastrointestinal anatomy and evolution in early actinopterygian fishes. *Scientific Reports***6**:**18758** DOI 10.1038/srep18758 (2016).
61. Price, P. The coprolitic limestone horizon of the Conerbaugh Series in and around Morgantown, *West Virginia: Carnegie Museum, Ann.***17**: 211-254 (1927).
62. Romer, A. S. & Parsons, T. S. *The Vertebrate Body*. Philadelphia, Saunders College Publishing (1986).
63. Chin, K. On the elusive trail of fossil dung in Rosenberg, G.D. and Wolberg, D.L., eds., DinoFest: Proceedings of a Conference for the General Public: Boulder. *The Paleontological Society Special Publication* **7**: 285-294 (1994).
64. Dean, B. Obituary notice of a lungfish. *Popular Science Monthly***63**: 33-39 (1903).
65. Mendoza, R., Aguilera, C., Rodríguez, G., González, M. & Castro, R. Morphophysiological studies on alligator gar (*Atractosteus spatula*) larval development as a basis for their culture and repopulation of their natural habitat. *Biol. Fish.* 12. 133-142. DOI 10.1023/A:1025047914814 (2002).

66. Hassanpour, M. & Joss, J. Anatomy and histology of the spiral valve Intestine in juvenile Australian lungfish, *Neoceratodus forsteri*. *The Open Zoology Journal***2**: 62–85 (2009).
67. Owocki, K. *et al.* Upper Permian vertebrate coprolites from Vyzniki and Gorokhovets, Vyatkian regional stage, Russian platform. *Palaios***27**: 867–877 (2012).
68. Barrios-de Pedro, S. & Buscalioni, A. D. Scrutinizing Barremian coprolite inclusions to record digestive strategies. *Annales Societatis Geologorum Poloniae***88**: 203–221 (2018).
69. Barrios-de Pedro S. Bones of pycnodontiform fishes (Actinopterygii: Pycnodontiformes) in coprolites from the Barremian fossil site of Las Hoyas (Cuenca, Spain), *Journal of Vertebrate Paleontology*. DOI: 10.1080/02724634.2019.1667814 (2019).
70. Cork, S, J. & Kenagy, G. J. Nutritional values of hypogeous fungus for a forest-dwelling ground squirrel. *Ecology* **70**: 577–586 (1989).
71. Diefenbach, C. O. C. Gastric function in Caiman *Crocodylus* (Crocodylia: Reptilia)-I. Rate of gastric digestion and gastric motility as a function of temperature. *Comparative Biochemistry and Physiology***51(A)**: 259–265 (1975).
72. Davenport, J., Grove, D. J., Cannon, J., Ellis, T. R. & Stables, R. Food capture, appetite, digestion rate and efficiency in hatchling and juvenile *Crocodylus porosus*. *Journal of Zoology***200**: 569–592 (1990).
73. Bozinovic, F. Fisiología ecológica de la alimentación y digestión en vertebrados: modelos y teorías. *Revista Chilena de Historia Natural***66**: 375–382 (1993).
74. Stevens, C. E. & Hume, I. D. *Comparative Physiology of Vertebrate Digestive System*, 2nd Edition. Cambridge University Press, Cambridge (1995).
75. Northwood, C. Early Triassic coprolites from Australia and their palaeobiological significance. *Palaeontology***48**: 49-68. <https://doi.org/10.1111/j.1475-4983.2004.00432.x> (2005).
76. Bradley, W. H. Coprolites from the Bridger Formation of Wyoming: their composition and microorganisms. *J. Sc.***244**: 215–239 (1946).
77. Hollocher, K. & Hollocher, T. C. Early processes in the fossilization of terrestrial feces to coprolites, and microstructure preservation. *New Mex. Museum Nat. Hist. Sci. Bull.***57**: 79–92 (2012).
78. Vajda, V., Pesquero, M. D., Villanueva-Amadoz, U., Lehsten, V. & Alcalá, L. Dietary and environmental implications of Early Cretaceous predatory dinosaur coprolites from Teruel, Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 464 DOI 10.1016/j.palaeo.2016.02.036 (2016).
79. Andrews, P., Fernández-Jalvo, Y. 101 uses for fossilized faeces. *Nature***393**: 629–630. DOI <https://doi.org/10.1038/31356> (1998).
80. Scott, L., Fernández-Jalvo, Y., Carrión, J. & Brink, J. Preservation and interpretation of pollen in hyaena coprolites: taphonomic observations from Spain and southern Africa. *Afr* **39**: 83–91 (2003).
81. Prasad, D., Strömberg, C. A. E., Alimohammadian, H. & Sahni, A. Dinosaur coprolites and the early evolution of grasses and grazers. *Science***310 (5751)**: 1177–1180 (2005).
82. Bajdek P, Owocki, K. & Niedźwiedzki, G. Putative dicynodont coprolites from the Upper Triassic of Poland. *Palaeoclimatol. Palaeoecol.***411**: 1–17 (2014).
83. Zatoń, M. *et al.* Coprolites of Late Triassic carnivorous vertebrates from Poland: An integrative approach. *Palaeoclimatol. Palaeoecol.* **430**: 21–46 (2015).
84. Edwards, P. D. Qualitative X-ray diffraction and X-ray fluorescence analysis of some Oligocene coprolites. *Contributions to Geology* University of Wyoming **12**: 25 (1973).
85. Chame, M. Terrestrial mammal feces: a morphometric summary and description. *Memo rias do Instituto Oswaldo Cruz* **98**: 71–94 (2003).

86. Nobre, P., Carvalho, I., Vasconcellos, F. & Souto, P. Feeding behavior of the Gondwanic Crocodylomorpha *Mariliasuchus amarali* from the Upper Cretaceous Bauru Basin, Brazil. *Gondwana Research***13**: 145 DOI 10.1016/j.gr.2007.08.002 (2008).
87. Pesquero, M.D. *et al.* An exceptionally rich hyaena coprolites concentration in the Late Miocene mammal fossil site of La Roma 2 (Teruel, Spain): palaeological and palaeoenvironmental inferences. *Palaeoclimatol. Palaeoecol.* **311 (1–2)**: 30–37 (2011).
88. Tapanila, L., Roberts, E. M., Bouaré, M. L., Sissoko, F. & O’Leary, M. A. Bivalve borings in phosphatic coprolites and bone, Cretaceous-Paleogene, northeastern Mali. *Palaaios***19**: 565-573 (2004).
89. Milàn, J., Rasmussen, B. W. & Bonde, N. C. Coprolites with prey remains and traces from coprophagous organisms from the Lower Cretaceous (Late Berriasian) Jydegaard Formation of Bornholm, Denmark. *New Mexico Museum of Natural History and Science Bulletin***57**: 235-240 (2012).
90. Guatier, A. Animal life along the prehistoric Nile: the evidence from Saggai I and Geili (Sudan). *Origini* **12**: 50–115 (1983).
91. Horwitz, L. K. & Goldberg, P. A study of Pleistocene and Holocene hyaena coprolites. *Journal of Archaeological Science* **16**: 71–94 (1989).
92. Larkin, N., Alexander, J. & Lewis, M. Using Experimental Studies of Recent Faecal Material to Examine Hyaena Coprolites from the West Runton Freshwater Bed, Norfolk, U.K. *Journal of Archaeological Science.* **27**:19-31 DOI 10.1006/jasc.1999.0437 (2000).
93. Godfrey, S. J. & Palmer, B. T. Gar-bitten coprolite from South Carolina, USA. *Ichnos***22 (2)**: 103–108 (2015). DOI 10.1080/10420940.2015.1030073.
94. Godfrey, S. J. & Smith, J. Shark-bitten vertebrate coprolites from the Miocene of Maryland. *Naturwissenschaften* **97**: 461–467 (2010).
95. Dentzien-Dias, P., Carrillo-Briceño, J. D., Francischini, H. & Sánchez, R. Paleocological and taphonomical aspects of the Late Miocene vertebrate coprolites (Urumaco Formation) of Venezuela. *Palaeogeography, Palaeoclimatology, Palaeoecology***490**: 590–603 DOI 10.1016/j.palaeo.2017.11.048 (2018).
96. Collareta, A., Gemelli, M., Varola, A. & Bianucci, G. Trace fossils on a trace fossil: a vertebrate-bitten vertebrate coprolite from the Miocene of Italy. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen***293**: 117-126. DOI 10.1127/njgpa/2019/0834 (2016).
97. Zangerl, R. E. & Richardson, E. S. The paleoecological history of two Pennsylvanian black shales. *Fieldiana Geological Memoirs* **4**: 1–532 (1963).
98. Ash, S. R. 1978. *Geology, Paleontology and Paleoecology of a Late Triassic lake, Western New Mexico* (Ash S. R.) Coprolites, p. 69–73 (Brigham Young University Geology Studies, 1978).
99. Vogeltanz, R. Austrocknungsstrukturen bei koprolithen. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte***3**: 362–371 (1965).
100. Broughton, P. L., Simpson, F. & Whitaker, S. H. Late Cretaceous coprolites from Western Canada. *Palaeontology* **21**: 443– 453 (1978).
101. Diedrich, C. G. & Felker, H. Middle Eocene shark coprolites from the shallow marine and deltaic coasts of the pre-North Sea Basin in central Europe. *New Mexico Museum of Natural History Bulletin* **57**: 311–318 (2012).
102. Stringer, G. L. & King, L. Late Eocene shark coprolites from the Yazoo Clay in northeastern Louisiana. *New Mexico Museum of Natural History and Science Bulletin* **57**: 275–310(2012).
103. Dentzien-Dias, P., Hunt, A. P., Lucas, S. G., Francischini, H., & Gulotta, M. Coprolites from shallow marine deposits of the Nanjemoy Formation, Lower Eocene of Virginia, USA. *Lethaia*<https://doi.org/10.1111/let.12380> (2020).

104. Chin, K. Analyses of coprolites produced by carnivorous vertebrates. In: Kowalewski, M., Kelley, P.H. (Eds.), The Fossil Record of Predation. *Soc. Spec. Pap 8*: 43–49 (2002).
105. Zhang, J. Y. & Jin, F. In Chen, P, Zhang M, Wang Y. (eds.). The Jehol fossils: the emergence of feathered dinosaurs, beaked birds and flowering plants. *Academic Press*. pp. 69–76. ISBN9780123741738 (2008).
106. Chang, M. M. & Miao, D. S. An overview of Mesozoic fishes in Asia. 535–563. In Arratia G, Tintori A. (eds). *Mesozoic fishes 3 – systematics, paleoenvironments and biodiversity*. Verlag Dr Friedrich Pfeil, München (2004).
107. Sychevskaya EK. Freshwater fishes from the Cretaceous of Siberia and Mongolia. - In: Arratia G & Schultze HP. (org.): *Mesozoic Fishes - Systematics and Fossil Record*. 6-10 July 1997, Buckow, Germany, Abstracts: p. 41 (1997).
108. Jakovlev, Y. N. Acipenseriformes, in Nasekomye v rannemelovykh ekosistemakh zapadnoy Mongolii. *The Joint Soviet-Mongolian Palaeontological Expedition***28**:178-182 (1986).
109. Bemis, W. E., Findeis. E. K. & Grande L. An overview of Acipenseriformes. *Environmental Biology of Fishes***48**: 25–71. DOI <https://doi.org/10.1023/A:1007370213924> (1997).
110. Doroshov, S. I. & Cech, J. J. Physiology of Sturgeon. *Reference Module in Life Sciences* Elsevier (2017).
111. Halaclar, K. *Analysis of Middle Miocene Locality of Afyon-Gebeceler Coprolite Findings*. Master Thesis. Ege University (in Turkish with English abstract) (2015).
112. Munsell Color (Firm). Geological Rock-Color Chart: with Genuine Munsell Color Chips. Grand Rapids (2011).

Tables

Table 1. Biometrical and morphological features of spiral coprolites from Tsagan-Tsab Formation (Lower Cretaceous), Tatal, western Mongolia.

Specimen number	Max. Length (mm)	Max. Width (mm)	Second Width (mm)	Weight (grams)	Phase	Coloration	External features	Internal Features	Morph. Type
IVPP V 27544	46.81	22.38	19.76	25	1	8/1 greenish gray, 2 for gley 8/6 reddish yellow, hue 7.5 yr 3/6 dark red, hue 10 yr	Bone fragments; tiny holes;	Bone fragments	Spiral
IVPP V 27545	36.80	13	11.52	7	-	8/3 pink, hue 7.5 yr 8/1 light bluish gray 2 for gley	Bone fragments; bite marks	Bone fragments	Non-spiral rod like
IVPP V 27546	42.00	24.09	21.56	22	2	8/1 light blush gray, 2 for gley 7/6 reddish yellow, hue 5 yr 5/8 yellowish red, hue 5yr	Bone fragments; tiny holes;	Bone fragments; borings	Spiral
IVPP V 27547	47.79	28.34	25.00	30	1	8/1 light green gray, 1 for gley 8/6 yellow, hue 10 yr 6/8 light red, 2.5 yr	Bone fragments borings	Bone fragments; borings	Spiral
IVPP V 27548	47.86	18.61	16.59	19	1	7/6 reddish yellow hue 5 yr 2.5/3 very dark brown, hue 7.5 yr	Bone fragments	Bone fragments; borings	Spiral
IVPP V 27549	49.86	23.85	20.00	33	2	8/1 light blush	Bone fragments	Bone fragments; borings	Spiral

						grey, 2 for gley			
						8/4 pink, 2.5 yr			
						4/6 red, hue 10 yr			
IVPP V 27550	94.10	30.48	26.87	97	1	8/2 light blush grey, 2 for gley	Bone fragments; borings; cracks	Bone fragments	Spiral
						8/4 pink, 2.5 yr			

Figures



Figure 1

Map showing the location of Tatal, in Mongolia. The coprolites were retrieved from the Tsagan-Tsab formation. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

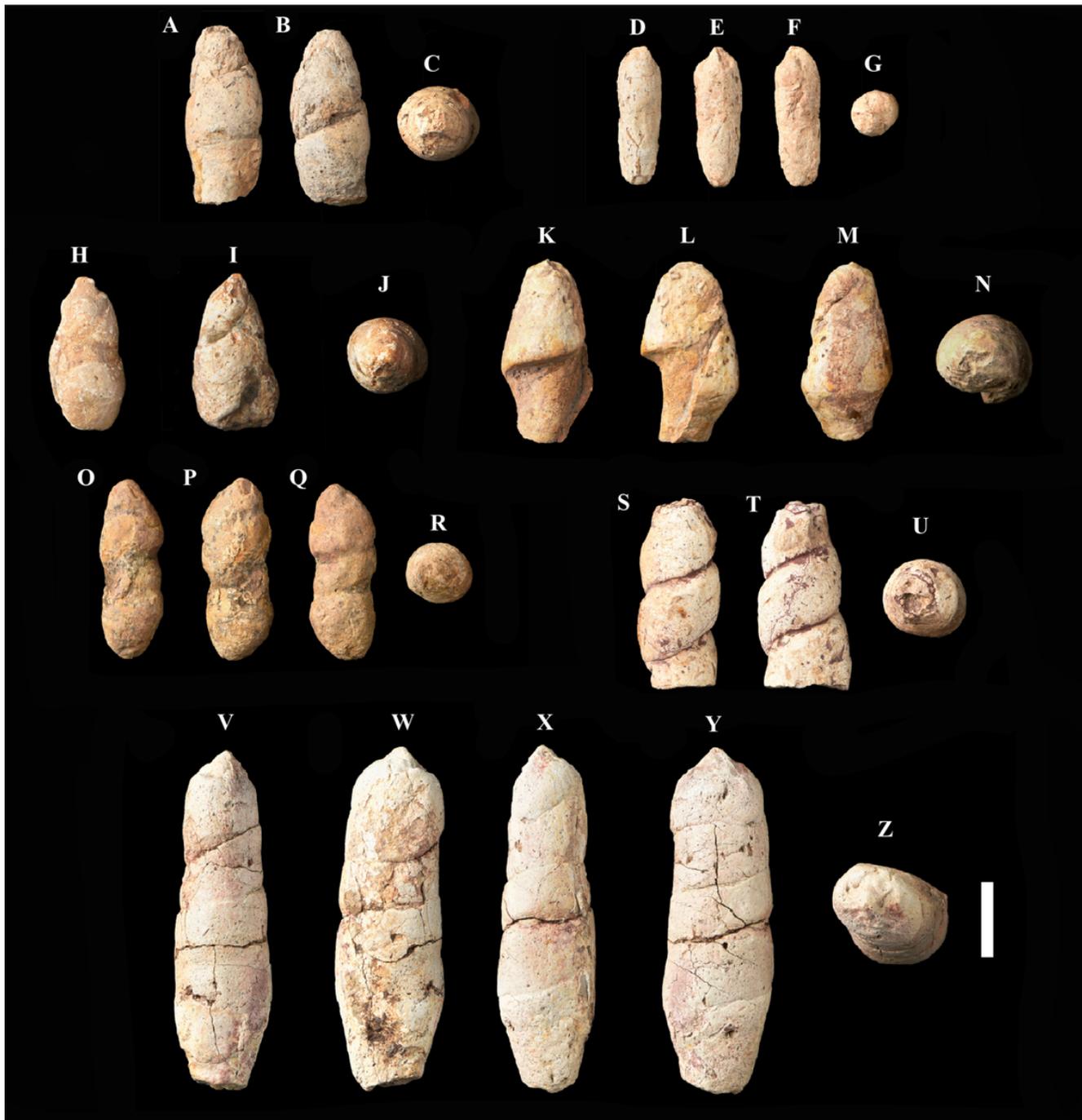


Figure 2

Coprolites from Tatal. (A - B) Specimen IVPP V 27544 in different views. (D-G) Specimen IVPP V 27545 in different views. (H-J) Specimen IVPP V 27546 in different views. (K-N) Specimen IVPP V 27547 in different views. (O-R) Specimen IVPP V 27548 in different views. (S-U) Specimen IVPP V 27549 in different views. (V-Z) Specimen IVPP V 27550 in different views. Scale bar equals 2 cm.

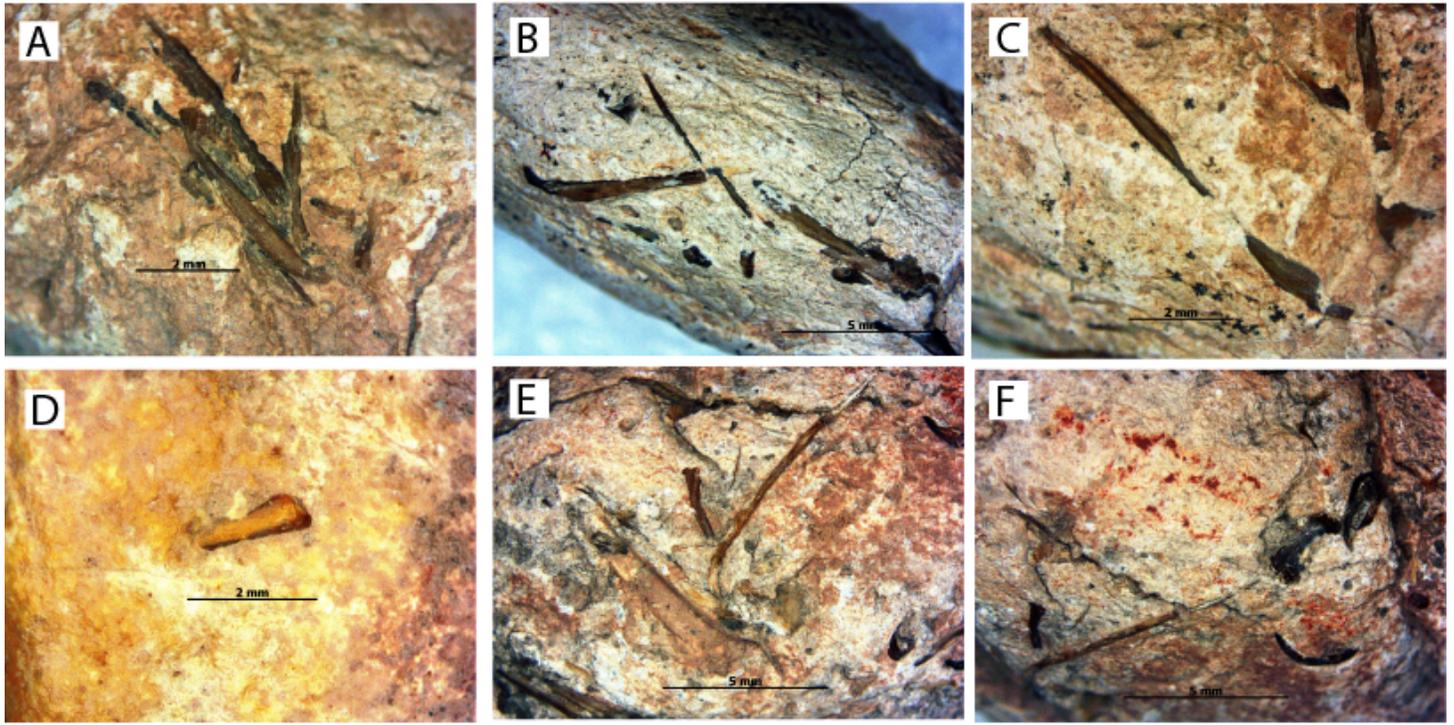


Figure 3

Light microscopy photos of various surface adhesion on the coprolites. Specimen IVPP V 27545 (A-C). Specimen IVPP V 27547 (D). Specimen IVPP V 27544 (E-F). Scale bars as indicated.



Figure 4

Photo showing external surface of specimen IVPP V 27545. One side of the specimen has traces of bioerosional scars. Arrows indicates to the furrows. Scale bar equals 2 cm.

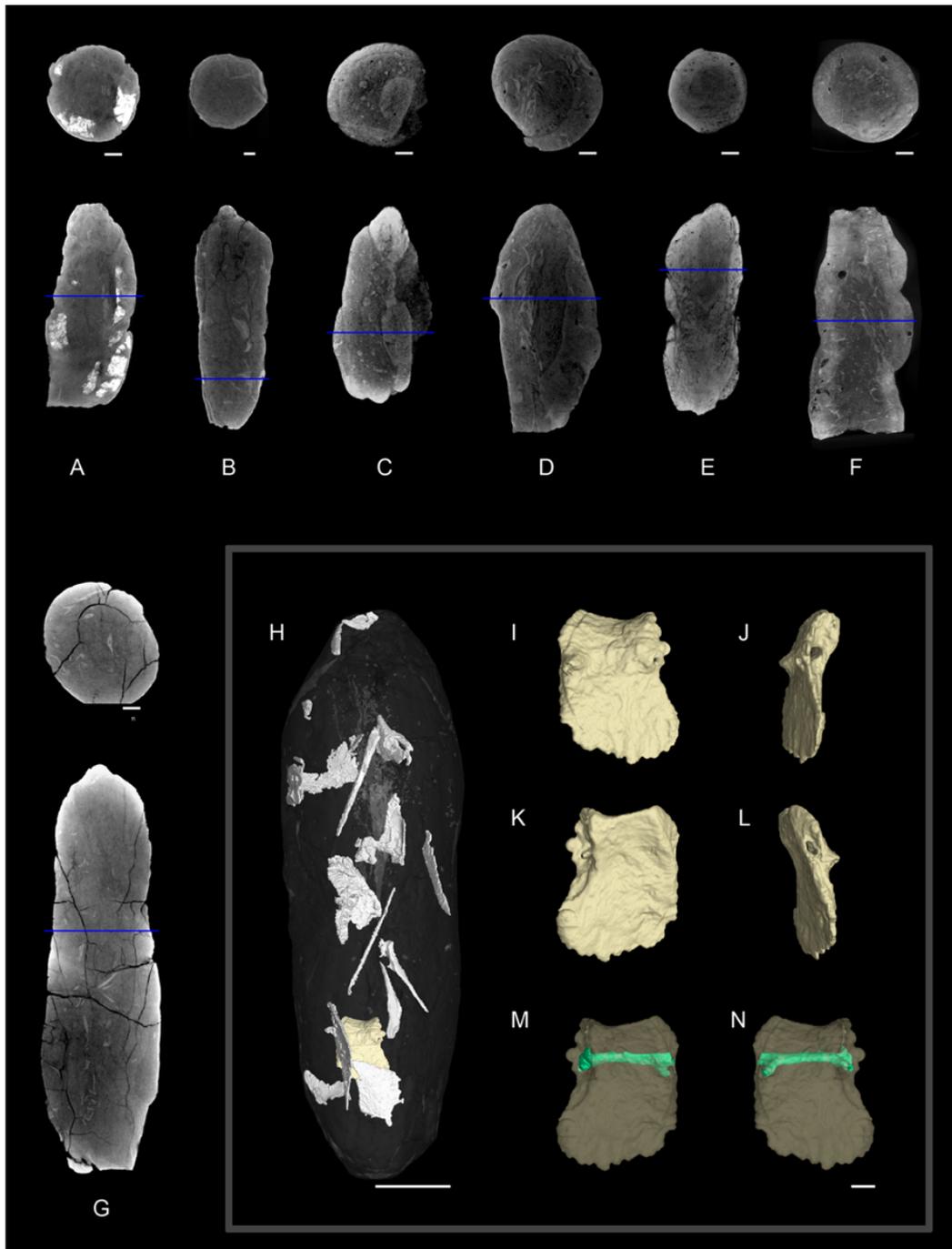


Figure 5

Diagrams showing CT scans of the Tatal's coprolites. (A) to (G), each showing a cross and lateral section of all 7 specimens (in order of the specimen numbers, IVPP V 27544 to IVPP V 27550). Blue line indicates the area where the cross section was made. (H) shows the reconstruction drawing on the bone inclusions in specimen IVPP V 27545. Structure in yellow indicate the infraorbital bone. (I) to (L) indicates the infraorbital bone in different angle. (M) and (N) shows the sensory canal of the infraorbital bone. Scale bars are as following: (A) 3500 μm ; (B) 1500 μm ; (C) 3500 μm ; (D) 3500 μm ; (E) 3500 μm ; (F) 3500 μm ; (G) 3500 μm ; (H) 5000 μm ; (I) to (N) 700 μm .

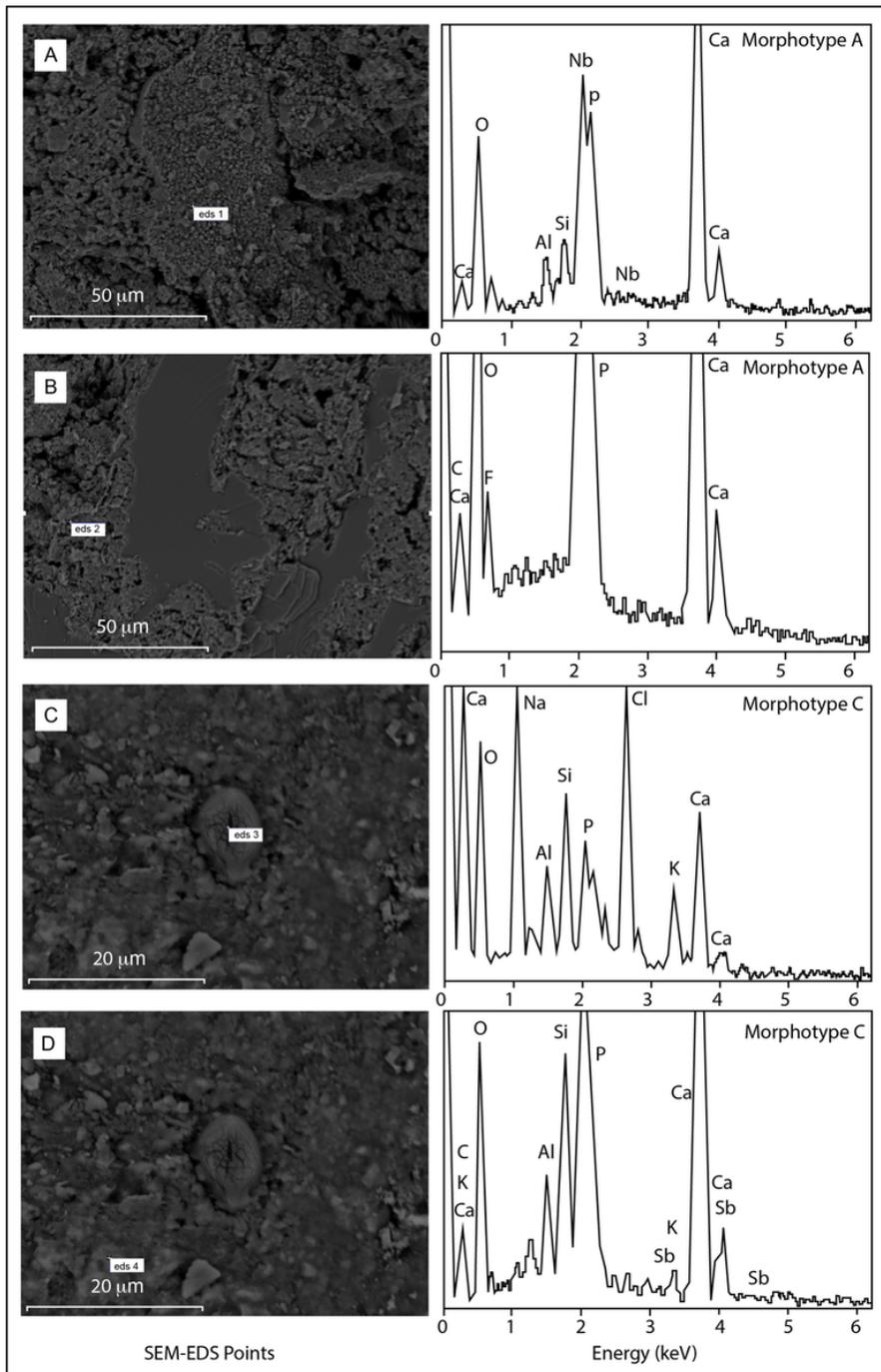


Figure 6

Diagrams showing SEM-EDS analyses results. (A) and (B) belongs to specimen IVPP V 27546, while (C) and (D) to specimen IVPP V 27545.

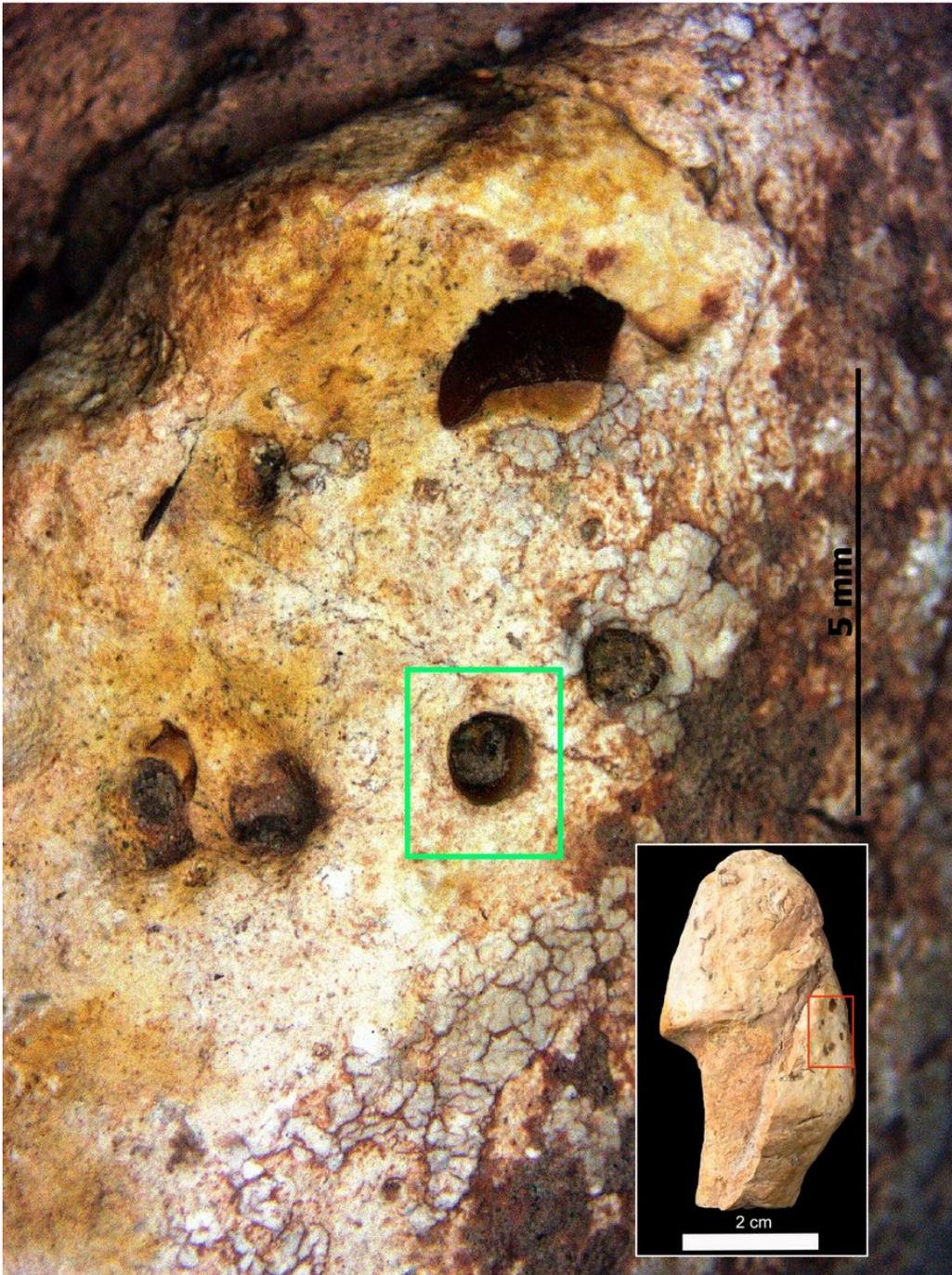


Figure 7

Light microscopy photo of borings on specimen IVPP V 27547. Box in green shows true burrow while the rest are pseudo-borrows. Inset shows the position of the borings on the coprolite. Scales as indicated.

Supplementary Files

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