Proceedings of the Geologists' Association 135 (2024) 89–96

Contents lists available at ScienceDirect

Proceedings of the Geologists' Association

journal homepage: www.elsevier.com/locate/pgeola

Coprolites of the ichnogenus *Alococopros* from the Late Cretaceous of Morocco

Christopher J. Duffin [a,b,c,*], David J. Ward [a,b,d]

[a] Science Group, The Natural History Museum, Cromwell Road, London SW7 5BD, UK
[b] Lauer Foundation for Paleontology, Science and Education, Wheaton, IL, USA
[c] 146, Church Hill Road, Cheam, Sutton, Surrey SM3 8NF, UK
[d] Crofton Court, 81 Crofton Lane, Orpington, Kent BR5 1HB, UK

ARTICLE INFO

Article history:
Received 15 August 2023
Received in revised form 24 November 2023
Accepted 28 November 2023
Available online 19 December 2023

Keywords:
Coprolites
Maastrichtian
Late Cretaceous
Khouribga
Morocco

ABSTRACT

A small collection of coprolites (fossilised faeces) is described from the Upper Couche III Bone Bed (latest Maastrichtian) phosphate horizon, approximately 2 m below the K/Pg boundary of Sidi Chennane Quarry in the Ouled Abdoun phosphate basin, Khouribga Province, Morocco. The coprolites have a distinctive morphology that identifies them as belonging in the ichnogenus *Alococopros*. This is the first record of the ichnogenus from the Late Cretaceous of Morocco. The coprolites are assigned to *A. milnei* isp. nov. Inclusions of triturated and polished phosphate debris in some specimens suggest that crocodilians or chelonians may have been the possible producer.

1. Introduction

William Buckland (1784–1856) first identified vertebrate excrement in the fossil record in 1835 and coined the term 'coprolite' to embrace the specimens which he described (Buckland, 1835). These discoveries provided a renewed impetus for investigating ancient ecological interactions. Coprolites contain invaluable insights into aspects of feeding dynamics, behaviours, and even aspects of soft tissue anatomy and physiology of the producing organism that would otherwise remain inaccessible. As our understanding of these tantalising but understudied items has deepened, it has become evident that vertebrate coprolites display a diverse array of forms, prompting the need for a comprehensive and stable ichnotaxonomical framework accompanied by precise descriptive terminology (Hunt and Lucas, 2012, 2021). Furthermore, the potential for employing recurrent morphologies in the geological record for biostratigraphical and biochronological purposes has gained traction (Hunt and Lucas, 2021), whilst the differentiation of various coprofacies within an ichnocoenosis offers potential insights into palaeoecological and palaeoenvironmental reconstruction (Hunt et al., 2018).

With these promising applications in mind, the identification and detailed characterisation of both new and established bromalite ichnotaxa from geographically disparate regions hold increasing significance. The primary objective of this present study is to comprehensively describe a small sample of coprolite specimens originating from the Late Cretaceous (Maastrichtian) period in the Khouribga region of Morocco. One element of the coprofauna of these deposits has already been described as *Struocopros catapitostromata* Duffin and Ward, 2023.

2. Geological setting

The coprolites described here come from the Khouribga area of northeast Morocco (Fig. 1A). Here, the highly fossiliferous deposits are part of the Ouled Abdoun Basin, located to the west of the Atlas Mountains and southeast of Casablanca (Fig. 1). Covering an area of 9000 km^2, this basin is the largest and northernmost of five principal phosphate sedimentary basins which are arranged along a southwest to northeast axis, traversing central Morocco (Fig. 1B). The phosphate deposits hold significant economic importance, as they have been under commercial exploitation since the 1920s. Additionally, they form an integral part of the Mediterranean Tethyan phosphogenic province, which extends from North Africa to the Middle East.

The sedimentary composition of the Ouled Abdoun Basin exhibits remarkable productivity and ranges from Late Cretaceous (Maastrichtian) to the Early Paleogene (basal Lutetian) rocks (Fig. 1C). Indicative of warm, shallow marine deposition at a palaeolatitude approximately 25° North, these phosphate deposits are believed to be linked to offshore nutrient upwelling. They were deposited within one or more gulf-like

* Corresponding author at: Science Group, The Natural History Museum, Cromwell Road, London SW7 5BD, UK.
E-mail address: cduffin@blueyonder.co.uk (C.J. Duffin).

https://doi.org/10.1016/j.pgeola.2023.11.005

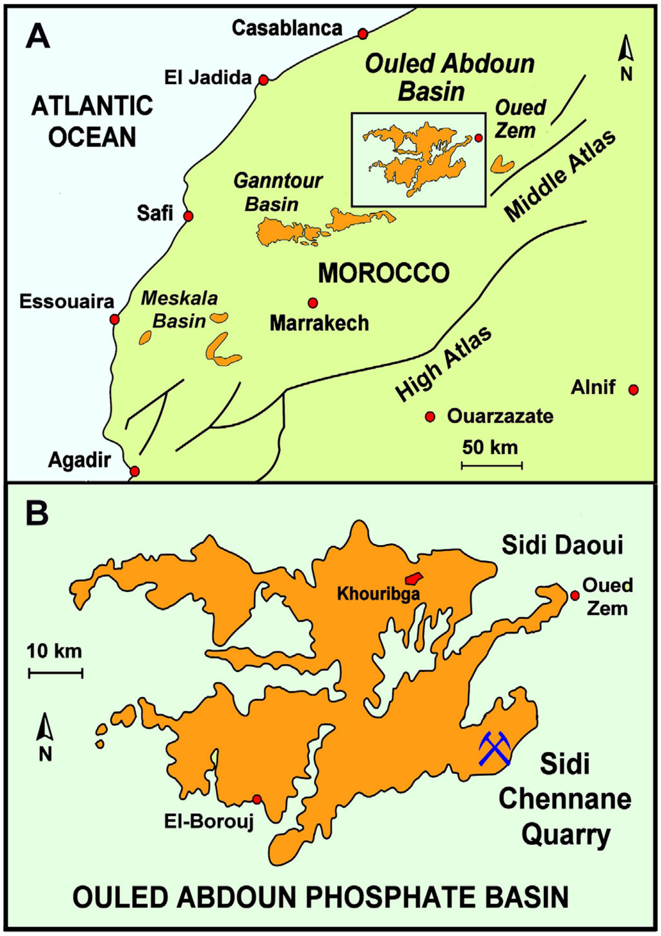

Fig. 1. A: Map of Northern Morocco showing the relative positions of the phosphate deposits. B: Position of the Sidi Chennane Quarry within the Ouled Abdoun Phosphate Basin. The maps are modified from Kocsis et al. (2014) and the phosphate deposits are represented in orange.

structures that opened in a westerly direction into the Atlantic Ocean (Bardet et al., 2015).

Within the Sidi Chennane region of the Ouled Abdoun Basin, the Maastrichtian phosphatic series is relatively condensed, characterised by a thickness ranging from 2 to 5 m. The absence of well-defined invertebrate and floral biostratigraphical markers, combined with notable facies variations, underscores the potential significance of the fossil vertebrate record for both intra-basinal correlation and inter-basinal correlation. An informal stratigraphical framework based on local quarrymen's terminology has evolved to describe the succession (Le Blanc et al., 2012; Yans et al., 2014; Kocsis et al., 2014).

Progressing from the base upwards, the sequence (Fig. 2) comprises:

(1) a basal bone-bed composed of grey phosphatic limestone known as the 'Basal Bone Bed' (BBB)
(2) soft yellow phosphates denoted as the 'Lower CIII Level' (LCIII)
(3) sporadic phosphatic limestone layers
(4) grey phosphates with brown streaks termed the 'Upper CIII Level' (UCIII)
(5) yellow marls.

3. *Alocopros* – history of research

William Buckland introduced a series of names for the coprolites which he described, mainly from the Early Jurassic of the Dorset Coast (U.K.). These early names were seldom used and did not meet the more recently proposed criteria for formal ichnotaxa. Consequently, the recent resurgence of interest in coprolites necessitated the development of an appropriate ichnotaxonomic nomenclature. *Alocopros* is one of the earliest ichnogenera to be created in response to this need (Hunt et al., 2007). It was originally raised for coprolites belonging to two ichnospecies from the Early Triassic to Late Cretaceous of Australia, India and North America (Hunt et al., 2007, p. 88; Suazo et al., 2012, p. 265). *A. triassicus*, the type species, was based on specimens originally described by Case (1922) from the Late Triassic Tecovas Formation (Crosby County, Texas, USA). These coprolites were characterised by often being arcuate in lateral view, sub-rounded in cross-section, and possessing distinctive, thin, regularly spaced longitudinal grooves down the length of the specimen. A second ichnospecies, *A. indicus* from the Late Cretaceous Lameta Formation of India (Matley, 1939), was distinguished from *A. triassicus* on the basis of size — at around 100 mm long, the Indian specimens are more than four times the length of the Triassic material (Hunt et al., 2007, p. 89).

A. triassicus has subsequently been formally identified from the Late Triassic of New Mexico (USA) (Hunt and Lucas, 2015, fig. 11CC–GG), the Early Permian of New Mexico (USA) (Cantrell et al., 2012, fig. 2C–J) the Carnian (Late Triassic) of Morocco (Zouheir et al., 2022) and the Maastrichtian (Late Cretaceous) Kirtland Formation of New Mexico (Suazo et al., 2012, fig. 3E–G).

Further records of striated coprolites not formally designated to an ichnotaxon include specimens from the Triassic of Russia (Ochev, 1974), the Early Triassic of Queensland, Australia (Northwood, 2005 text-figs. B–F), and the Miocene of Venezuela (Dentzien-Dias et al., 2018).

4. Material and methods

Morocco has an increasingly pro-active system of local cottage industries involving the collection of fossils from a wide range of stratigraphical levels. In the Ouled Abdoun Basin, surface collecting from phosphate quarry spoil heaps is permitted, and *in situ* sieving of the productive layers yields a wealth of fossil bones and teeth. These discoveries are sold to local state-licenced dealers who commonly sort the fossils for onwards sale and treat more fragile specimens with hardening agents. The specimens described here were obtained as part of an informal long-term project whose aim was to acquire the rarer, non-commercial fossils directly from these dealers.

The specimens described here were photographed using a Nikon Z6 camera mounted with a 106 mm F2.8 macro lens and a polarising filter. Two polarised LED light panels arranged parallel to each other provided illumination of the specimens. Stacked digital images were combined using the helicon Focus 8.2.2 software in order to produce final images with enhanced depth of field. The Topaz Mask software was then used to isolate the images which were then assembled into plates using JASC Paintshop Pro version 7.00.

The maximum lengths and widths of the coprolites were measured using digital vernier callipers, and the coprolites were examined under ultraviolet as well as ordinary light.

Abbreviation: LF, Lauer Foundation for Paleontology, Science and Education, Wheaton, Illinois, U.S.A. The mission of the Lauer Foundation is to curate its fossil collection providing the scientific community and other museums with permanent access for the purposes of exhibition, study and education. Public access to type and figured specimens, as well as specimens listed or cited in publications together with other scientifically important specimens is guaranteed.

5. Ichnotaxonomy

Alocopros Hunt et al., 2007.

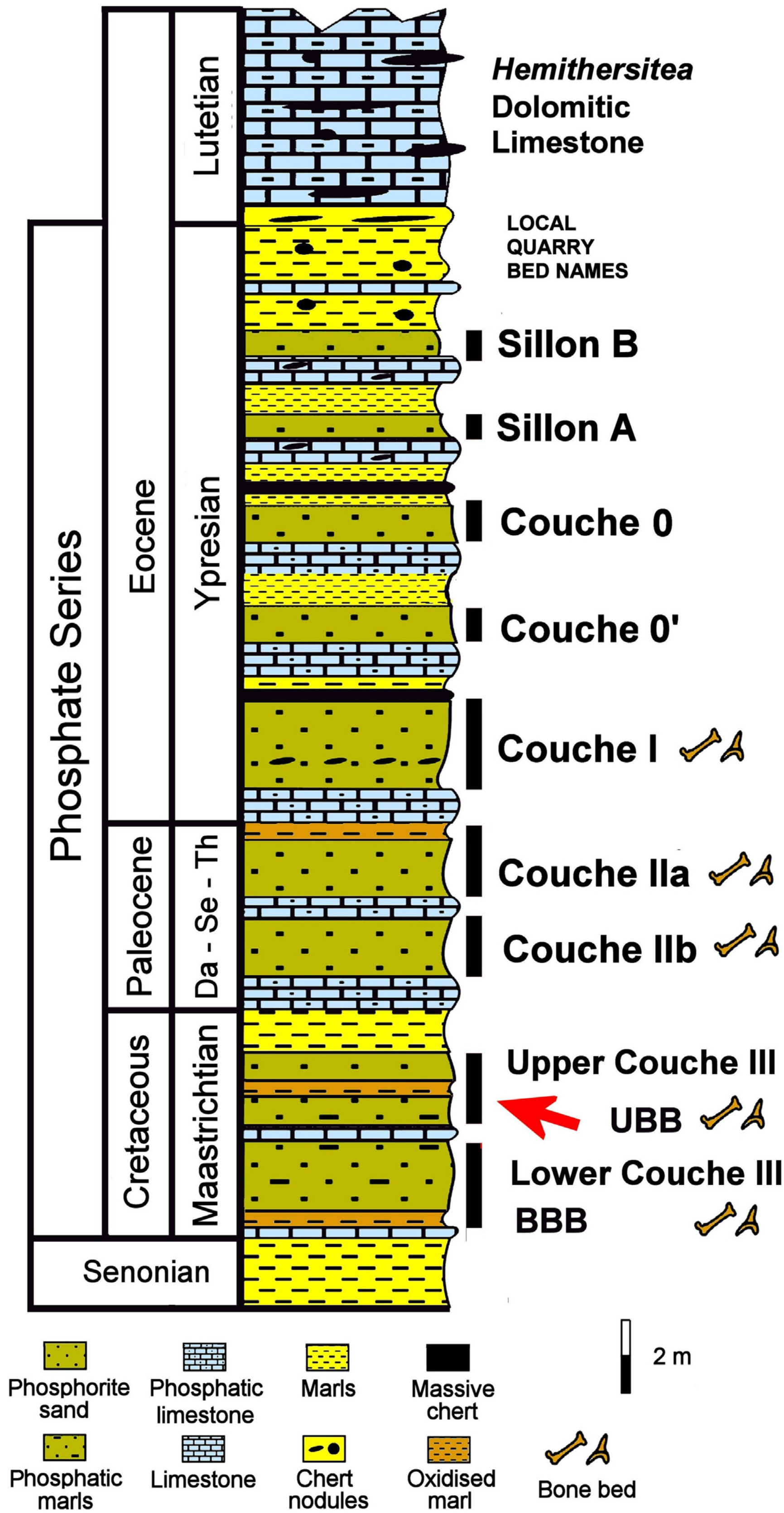

Fig. 2. Synthetic stratigraphical column for the Sidi Chennane area within the Ouled Abdoun Phosphate Basin indicating the position of the Couche III Upper Bone Bed. The solid vertical bars indicate the levels to which the "Couche" and "Sillon" terms apply.
The section is modified after Kocsis et al. (2014) and Yans et al. (2014).

Type ichnospecies: *Alococopros triassicus* Hunt et al., 2007 originally described from the Late Triassic of West Texas (Case, 1922, fig. 33C–D; Hunt et al., 2007 fig. 3A–B).

Referred species: *A. indicus* Hunt et al., 2007 from the Late Cretaceous Lameta Formation of India (Matley, 1939).

Alococopros milnei isp. nov.

Figure 3A–AA.

Holotype: LF 5653, an isolated, complete coprolite (Fig. 3A–F).

Type locality: Eastern end of Sidi Chennane, 31 km south south-east of Khouribga, Khouribga Province, Béni Mellal-Khénifra region, Morocco (Fig. 1A, B). This large commercial working quarry complex stretches about 12 km across from west to east. *Circa* latitude 32° 38′ 31″ N; longitude 006° 38′ 26″ W.

Type horizon: Couche III Upper Bone Bed (UBB), approximately 2 m below the K/Pg boundary (Late Cretaceous: latest Maastrichtian) (Fig. 2).

Referred specimens: 10 isolated coprolites, LF 5654–5663 (Fig. 3G–AA).

Etymology: named in honour of Alan Alexander Milne (1882–1956), creator of the children's fictional anthropomorphic bear character called Winnie-the-Pooh, who first appeared in a collection of stories in 1926. The game of 'Pooh sticks' was first introduced in Milne's book *The House at Pooh Corner* (Milne, 1928). The stick-like nature of some of the Moroccan coprolites and their extrusion in water, together with the commonly used vernacular term for excrement evoked the nomenclatural association.

Diagnosis: Anisopolar coprolites ranging in length from 19 mm to 61 mm with rounded to slightly flattened cross section. Up to three pinch-and-swell structures may be present, dividing the coprolite into segments. Between 11 and 19 parallel longitudinal ridges with intervening troughs radiate from the nubbin and pass down the length of the coprolite, occasionally showing slight sinistral or dextral drift in their trajectories. Longitudinal ridges may be straight or have a zig-zag arrangement. Ridge bifurcation and the presence of intercalary ridges are occasional features. Inclusions are usually absent at the coprolite surface, although some specimens do show polished phosphatic debris measuring approximately 250 μm in diameter embedded over the whole coprolite surface. Sparse angular bone and scale debris may be present internally. The ground mass is usually homogenous and very fine grained, but mild heterogeneity may be present as variations in colour and texture.

Coprolites belonging to *A. milnei* can be distinguished from those of *A. triassicus* and *A. indicus* on the basis of their more rounded cross-section, generally straight shape (as opposed to commonly arcuate), the presence of a well-defined nubbin anteriorly and longitudinal ridges which may show sinistral or dextral drift along the length of the structure. Occasional ridge bifurcation, zig-zag ridge arrangement and intercalary ridges are also confined to *A. milnei*.

5.1. Description

5.1.1. The holotype

LF 5653 (Fig. 3A–F) measures 45 mm in length with a maximum diameter of 18 mm. The anterior end of the coprolite is indicated by the presence of a distinctive nubbin (Duffin and Ward, 2023) which indicates the point of final extrusion of the faecal mass from the alimentary canal. Roughly cylindrical in shape, the specimen has a round cross-section anteriorly but is flattened towards the posterior end (marking the initial point of exit through the sphincter). The coprolite is anisopolar, *i.e.,* the anterior and posterior ends have different shapes; the anterior end is rounded but a little flattened whilst the posterior end is less rounded (Fig. 3C). A series of 16 longitudinal ridges with intervening grooves radiate from the nubbin (Fig. 3A) and pass down the full length of the specimen (Fig. 3C–F). In anterior view, the trajectory of the ridges and grooves shows a certain amount of sinistral drift (around 12° towards the posterior end of the specimen). Each ridge measures around 3 mm across and has a laterally convex surface. The intervening grooves are around 1 mm deep. In lateral view, the coprolite shows a distinctive pinch-and-swell structure which divides the specimen into three subequal parts, each measuring around 15 mm long (Fig. 3D, F). This morphological characteristic must have been conferred upon the faecal mass as it passed from the ileum to the rectum or cloaca in three separate pulses. The longitudinal system of ridges and grooves can be matched reasonably well as they pass from one section to the next, although each clearly terminates at the pinch (Fig. 3D). The pinch points are more difficult to discern in one lateral view (Fig. 3C), and elsewhere have a diagonal trajectory (Fig. 3D, F). The very fine grained coprolitic ground mass is creamy white and homogenous with no evidence of inclusions at the coprolite surface.

5.1.2. Variation

Variation of the major morphological characteristics in the collection of Moroccan coprolites is presented in Table 1. The maximum length of each coprolite ranges from 19 mm to 61 mm, and the maximum width from 11 mm to 22 mm. All are very slightly flattened laterally (Table 1). In terms of overall shape, most of the coprolites are somewhat cylindrical with straight longitudinal axes. Three specimens have gently curving longitudinal axes (LF 5661–5663; Fig. 3W–AA) giving rise to slightly reniform overall shapes. In around half of the examples (LF 5655–5657, 5661–5663; Fig. 3J–N, W–AA) the central part of the coprolite is the thickest. Most specimens have at least one end broken, but in those for which the shapes of both ends can be judged, the majority are anisopolar (LF 5655, 5656, 5659, 5660–5663; Fig. 3J, K, R, T–V, X). The anterior end can be identified with confidence due to the clear presence of the nubbin in only two of the referred specimens (LF 5657, 5659; Fig. 3L–N, Q–S).

Parallel longitudinal ridges with intervening troughs are a unifying feature in all of the specimens. The ridges have consistently laterally convex outlines and vary in thickness from 1 mm to 5 mm. Some show some, usually minimal sinistral drift (in the order of 10°–12°) in the trajectories of the ridges (LF 5658, 5662, 5663; Fig. 3O, Y–AA). The number of longitudinal ridges varies from at least 11 to possibly 19, and in all cases they are equally spread and radiate from the nubbin or its presumed position at the anterior end of the coprolite (Fig. 3M, Q). In some cases, the preservation of the longitudinal ridge surfaces reveals a series of fine longitudinal striations running the length of those ridges in which they can be discerned (LF 5655, 5656, 5659, 5663). In fewer examples (LF 5662), fine transverse ridges are also visible. The longitudinal ridges are usually straight and follow the long axis of the coprolite. In several examples (*e.g.,* LF 5654, 5655, 5656) the ridges have a zig-zag development for either part or the full length of the ridge (Fig. 3H, I–K). Variation in quality of preservation sometimes makes tracing the paths of individual ridges challenging, but in a few cases the impression is gained that some ridge bifurcation occurs (LF 5655, 56573) although it is not possible to state with confidence in which direction this occurs. In addition, some specimens show the development of occasionally restricted, finer intercalary ridges (*e.g.,* LF 5655).

In most cases, the coprolitic ground mass is devoid of inclusions on the coprolite surface, but one broken specimen (LF 5659) shows occasional, sparse phosphatic inclusions identified as undetermined fish scales in section, unidentified fish teeth and possible spines (Fig. 4A). Consistently very fine grained, the ground mass is generally homogenous, but in some examples, colour and texture variation is visible at the ridge surface (LF 5659, 5661; Fig. 3X). In the case of one specimen (LF 5660), the entire coprolite surface is studded with closely-packed, heavily triturated and polished phosphatic fragments each measuring around 250 μm in diameter (Fig. 4B), plus a single shell fragment measuring 2.7 mm long. The phosphate fragments show occasional imbrication.

The pinch-and-swell structure so clearly visible in the holotype can be discerned in several further specimens (LF 5654, 5660, 5661–5663; Fig. 3G, H, T–V, W–AA) with the coprolite divided into two and three sections.

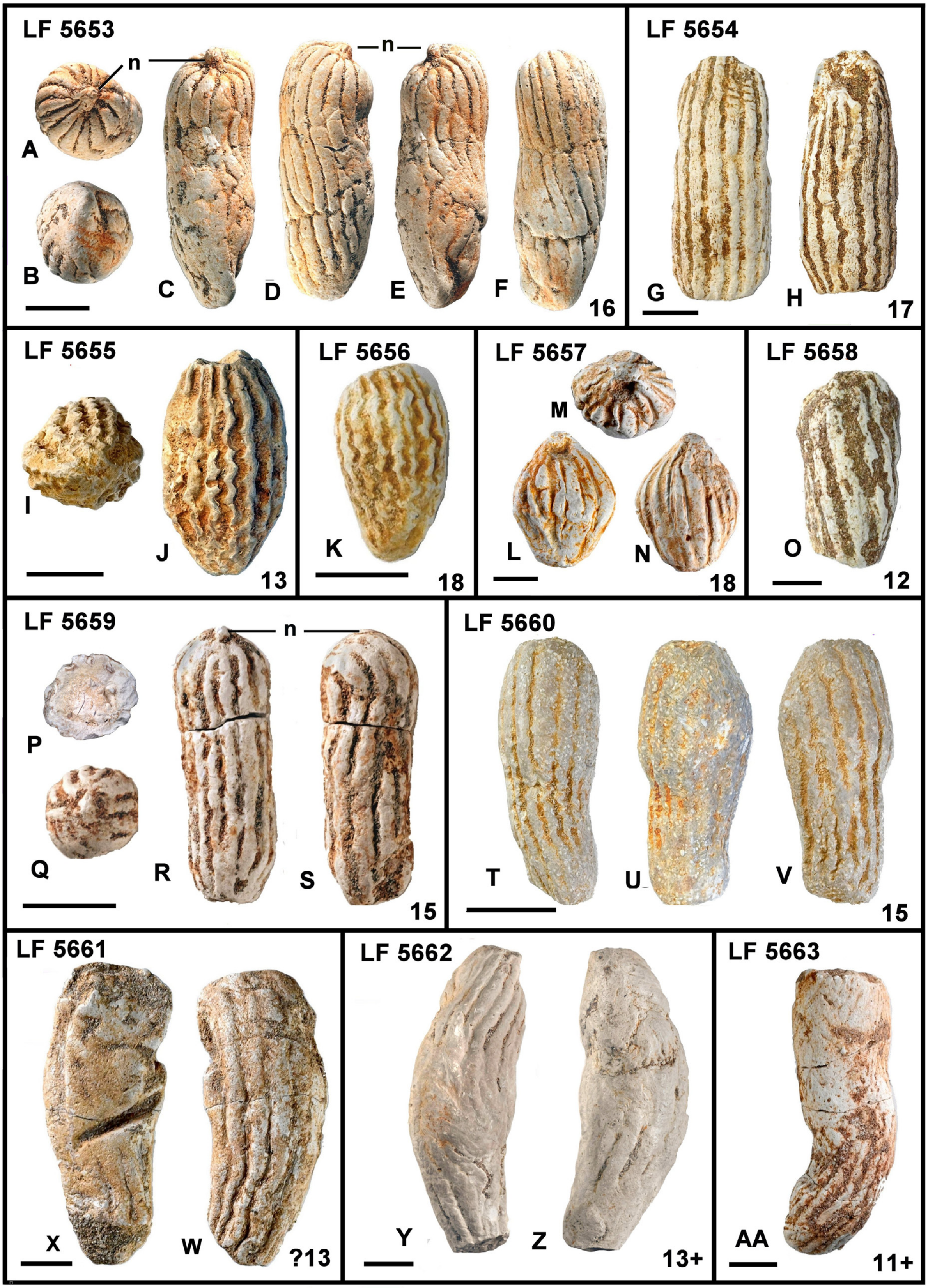

Fig. 3. Specimens of *Alococopros milnei* isp. nov. from Couche III Upper Bone Bed (Late Maastrichtian) of Sidi Chennane Quarry, Ouled Abdoun Phosphate Basin, Morocco. A–F: LF 5653 (holotype); G–H: LF5654; I–J: LF 5655; K: LF 5656; L–N: LF 5657; O: LF 5658; P–S: LF 5659; T–V: LF 5660; W–X: LF 5661; Y–Z: LF 5662; AA: LF, 5663. A, M, Q in anterior view; B, I in terminal view; C–H, J–K, L, N, O, R–AA in lateral view; P in section. The nubbin is indicated by n. The number of longitudinal striations is shown in the bottom right corner of each box. Scale bar = 10 mm throughout.

Table 1
Table to show variation in the major morphological features of coprolites of *Alococopros milnei* isp. nov. from Couche III Upper Bone Bed (Late Maastrichtian) of Sidi Chennane Quarry, Ouled Abdoun Phosphate Basin. LF = Lauer Foundation.

Catalogue number	Shape	Length/mm	Maximum width/mm	Minimum width/mm	Number of ridges	Ridge width/mm	Striation shape	Pinch and swell
LF 5653	Straight	44.4	16.2	14.8	16	2–3	Straight	3
LF 5654	Straight	48.1	18.2	17.5	16	3	Zig-zag	2–3
LF 5655	Straight	36	17.6	15.9	14	2–3	Zig-zag	None
LF 5657	Straight	26.5	19.9	15.9	18	2–4	Straight	None
LF 5658	Straight	33	16.6	15.2	12	3	Straight	None
LF 5656	Straight	19.5	11.2	10.3	19	1	Zig-zag	None
LF 5660	Straight	36.1	13.3	8.7	15	2–3	Zig-zag	1
LF 5659	Straight	36.1	11	10.5	14	2	Straight	None
LF 5661	Curved	49	21.1	15.1	13?	2–5	Straight	2–3
LF 5662	Curved	61	21.4	21.2	13+	3–5	Straight	3
LF 5663	Curved	53.7	20.8	17.5	11+	2–3	Straight	2

6. Comparisons

The presence of clearly delineated longitudinal ridges with intervening grooves indicates that 11 specimens described here from the Late Maastrichtian of Morocco belong in the ichnogenus *Alococopros*. Coprolites of the type species of the genus, *A. triassicus*, were originally characterised as typically measuring around 20 mm in length, less than a quarter the size of specimens of *A. indicus*. *A. triassicus* from the Late Triassic and Early Permian of New Mexico (Hunt and Lucas, 2015; Cantrell et al., 2012) all conform to the size range exhibited by those from the Tecovas Formation (Late Triassic; Hunt et al., 2007; Case, 1922). However, those specimens recorded from the Late Cretaceous of New Mexico (Suazo et al., 2012) are slightly longer (around 38 mm), those from the Carnian of Morocco range from 14 mm to 57 mm long (Zouheir et al., 2022), and specimens from the Late Miocene of Venezuela vary in length from 17 mm to 41 mm (Dentzien-Dias et al., 2018). The Moroccan specimens described here range from 19 mm to 61 mm in length.

In terms of overall shape, the bulk of the Maastrichtian Moroccan coprolites is straight, although a few specimens show mild curvature along their length. In the case of *A. triassicus*, most coprolites show a certain amount of curvature; in some cases this is relatively minor (*e.g.,* Northwood, 2005, fig. 2F; Hunt et al., 2007, fig. 3A–B; Case, 1922, fig. C; Cantrell et al., 2012 fig. 2C; Dentzien-Dias et al., 2018, fig. 4B; Zouheir et al., 2022, fig. 4E–F, CC), but in others it is so marked as to give the specimen a reniform or 'cashew nut' shape (*e.g.,* Case, 1922, fig. D; Suazo et al., 2012, fig. 3F, G; Zouheir et al., 2022, fig. 4B–D, G–L, Y–BB). In a few instances, straight coprolites have been assigned to *A. triassicus* (*e.g.,* Cantrell et al., 2012, fig. 2C; Zouheir et al., 2022, fig. 4W).

A nubbin, marking the release point of the faecal mass from the final sphincter, clearly visible in the best specimens of *A. milnei*, is also known in *A. triassicus* (*e.g.,* Cantrell et al., 2012, fig. 2C, D, H; Zouheir et al., 2022, fig. G–L, P–R, U–X). From this point at the anterior end of the coprolite, the longitudinal ridges radiate outwards in terminal view (*e.g.,* Cantrell et al., 2012, fig. 2D, H; Dentzien-Dias et al., 2018, fig. 4C). In *A. milnei*, the coprolites are anisopolar; the anterior end is generally rounded with a sub-circular cross-section whereas the posterior end is more pointed and compressed. Coprolites ascribed to *A. triassicus* include both isopolar and anisopolar forms (*e.g.,* Zouheir et al., 2022).

Previous descriptions of *A. triassicus* note the indicative presence of longitudinal ridges and intervening grooves but there has so far been no attempt to quantify the number of ridges and assess any variation in this feature. Our small sample of coprolites belonging to *A. milnei* and *Alococopros* sp. shows a range of longitudinal ridge numbers from 11 to 21. Furthermore, the number of longitudinal ridges does not seem to be correlated with coprolite size. One of the smallest specimens (LF 5656; Fig. 3K), for example, possesses the highest number of ridges. An additional observation, not recorded for any specimens of *A. triassicus* or *A. indicus*, is the occasional occurrence of ridge bifurcation and the presence of fine intercalary ridges.

In *A. milnei*, the longitudinal ridges often show sinistral trajectorial drift posteriorly. This feature, not recorded in *A. triassicus* or *A. indicus*, presumably records a slight sinistral twist of the faecal mass during expulsion from the body.

The longitudinal ridges and grooves pass along the full length of the coprolite in *A. milnei*, although in some specimens they become increasingly indistinct posteriorly (LF 5662; Fig. 3Y–Z). Full length longitudinal striations are also recorded in the bulk of the specimens assigned to *A. triassicus* where complete specimens are known. The large collection of coprolites referred to *Alococopros* spp. from the Carnian of Morocco is distinctive in showing wide variation in longitudinal ridge development; they may be present on one side only (Morphotypes B4, B5) or short and intermittent (B7; Zouheir et al., 2022). In addition, the striated coprolites from the Arcadian Formation of Australia may be deeply grooved on one side of the specimen, but faint or absent on the other (Northwood, 2005, p. 53).

A certain amount of variation in longitudinal ridge width and groove depth is present in the coprofauna from the Moroccan Cretaceous. Ridge width varies from 1 mm to 5 mm wide, and the intervening grooves vary in depth. Also, detailed examination of the ridge surfaces often shows the presence of numerous fine, superficial, second order longitudinal striations running along the convex ridge crest parallel to the long axis of the ridge, a feature not recorded in other material of *Alococopros* described so far. These fine striations, like the larger scale ridges, must have been conferred on the coprolite surface by the structure of the alimentary canal wall.

The longitudinal ridges have a straight trajectory along the long axis of the coprolite in most specimens of *A. milnei*. In several examples, however, rather than being straight, the ridges show a zig-zag structure. Northwood notes the presence of distorted and wavy ridges in some specimens from the Arcadian Formation of Australia, and conjectures that the feature may have been caused by 'inconsistent pressure on the faecal mass during defaecation or by compaction in the cloaca prior to expulsion' (Northwood, 2005, p. 53). We wonder if variation in the strength of the peristaltic waves might have produced this variable attribute, perhaps even as a consequence of such a minor factor as blood pressure change in the alimentary blood vessels during a single heartbeat.

Most of the coprolites assigned to *Alococopros* possess a homogenous ground mass lacking inclusions at the surface, although phosphatic debris has been identified within one specimen (LF 5659; Fig. 4A) and over the surface of another (LF 5660; Fig. 4B). Microscopic examination of the Miocene Urumaco Formation examples from Venezuela revealed the presence of small undigested plant remains belonging to the Poaceae (grasses) and Eudicotyledoneae (flowering plants) (Dentzien-Dias et al., 2018, p. 593). Specimens of *A. milnei* lack inclusions at the coprolite surface, but occasional shell (?) fragments have been noted in broken specimens.

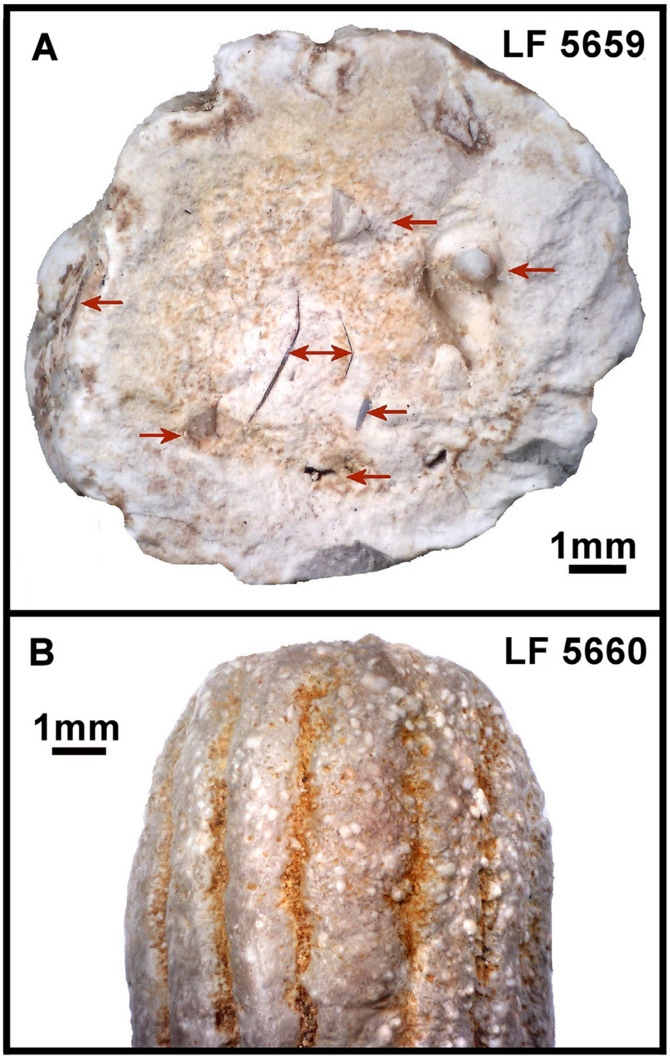

Fig. 4. Inclusions in coprolites of *Alocopros milnei* isp. nov. from Couche III Upper Bone Bed (Late Maastrichtian) of Sidi Chennane Quarry, Ouled Abdoun Phosphate Basin, Morocco. A: Section of LF 5659 showing the presence of isolated scales in section, unidentified fish teeth and possible fish spines (indicated by arrows). B: Surface of LF 5660 showing polished phosphate grains.

7. Potential producers

The ichnogenus *Alococopros* has a long geological range (Late Triassic to Miocene). As with all bromalite ichnogenera it is extremely likely that producers belonged to different animal groups at different points in the stratigraphical column. This is particularly well illustrated in the case of coprolites with longitudinal ridges and grooves.

The presence of a system of longitudinal ridges and grooves on the external surface of these coprolites likely reflects anatomical characteristics of the alimentary canal. Northwood (2005) has presented a useful overview of the suggestions appearing in the literature. In brief, Bradley (1946, p. 217) noted that grooves on the external surfaces of (non-*Alococopros*) coprolites which he examined from the Bridger Formation (Late Eocene) of Wyoming were 'impressed on the feces by muscular pressure', whilst Broughton et al. (1978, p. 450) believed that the range of grooves visible on the surfaces of coprolites from the Late Cretaceous Whitemud Formation of Western Canada was produced by sphincter action. Case (1922, p. 84) pointed to the 'parallel linear folds' or rugae in the distal part of the rectum of amphibians as a potential causative feature, thereby assigning the Tecovas Formation coprolites to production by temnospondyl amphibians. Intestinal rugae were later noted in some extant turtles (Matley, 1939). Dentzien-Dias et al. (2018, fig. 12) have noted the presence of longitudinal ridges and grooves on the curved faeces of extant South American coypu (*Myocaster coypus*), and Young (1964) reported longitudinal striations on the faecal pellet of a Recent crocodile, comparing it with similar structures in a Paleocene example. Note that crocodiles produce very strong stomach acids usually accounting for the complete removal of all identifiable bone remains from their faeces (Milàn, 2012). Furthermore, Milàn (2012, fig. 4B) recorded longitudinal striations on the faecal surface of a scat produced by a living crocodile (*Crocodylus cataphractus*).

Northwood (2005) concluded that the striated coprolites from the Arcadia Formation of Australia were likely produced by proterosuchids and/or prolacertids. *A. triassicus* specimens from the Tecovas Formation of Texas were tentatively assigned to archosauromorph producers (Hunt et al., 2007, p. 88) whilst smaller specimens from the Carnian of Morocco were suggested as being produced by a small temnospondyl or turtle, and the large forms might have been produced by archosauromorphs or temnospondyls such as *Metoposaurus* (Zouheir et al., 2022, p. 16).

The vertebrate fauna accompanying the coprolites in the Couche III Upper Bone Bed at Sidi Chennane includes crocodilians, mosasaurs, varanoid squamates, chelonians, occasional dinosaur remains and a wide range of medium to large chondrichthyans and osteichthyans (Bardet et al., 2017). The sharks can be excluded as potential producers of the striated coprolites as passage of faecal material through their spiral valve normally gives rise to distinctively coiled coprolites. Amongst the other potential producers the crocodilians and especially the chelonians are the most likely candidates.

8. Conclusions

A small sample of distinctively striated coprolites from the Maastrichtian "Couche III", approximately 2 m below the K/Pg boundary of Sidi Chennane Quarry near Khouribga in Morocco is described as *Alococopros milnei* isp. nov. The salient features of these coprolites are their straight to slightly curved shape, the presence of a system of longitudinal ridges and intervening grooves radiating from the anterior nubbin and passing down the full length of the coprolite. Further fine, second order striations are present on the longitudinal ridges. Some examples preserve pinch-and-swell structures dividing the coprolite into segments and representing pauses and pulses in coprolite extrusion. Further examples have the ridges disrupted in a zig-zag pattern whose origin is rather obscure. Possible producers of the coprolites described here include crocodilians and chelonians.

Declaration of competing interest

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

Acknowledgements

DJW would like to thank the fossil dealers in the villages of Sidi Chennane and Ouled Bouali, near Ouled Zem, for providing fascinating and unusual fossils that would otherwise be lost to science. Their hospitality and generosity are very much appreciated. Bruce and René Lauer kindly curated the specimens. Our grateful thanks go to the three reviewers – Drs Adrian Hunt (Everett, USA), Spencer Lucas (Albuquerque, USA) and Jesper Milàn (Faxe, Denmark) – and Caroline Buttler (Cardiff), all of whom made helpful suggestions for the improvement of the manuscript.

References

Bardet, N., Houssaye, A., Vincent, P., Suberbiola, X., Amaghzaz, M., Jourani, E., Meslouh, S., 2015. Mosasaurids (Squamata) from the Maastrichtian phosphates of Morocco: biodiversity, palaeobiogeography and palaeoecology based on tooth morphoguilds. Gondwana Research 27, 1068–1078.

Bardet, N., Gheerbrant, E., Noubhani, A., Cappetta, H., Jouvel, S., Bourdon, E., Pereda Suberbiola, X., Jalill, N.-E., Vincent, P., Houssaye, A., Sole, F., Elhoussaini darif, K., Adnet, S., Rage, J.-C., de Lapparent de Broin, F., Sudre, J., Bouya, B., Amaghzaz, M., Meslouh, S., 2017. Les Vertébrés des phosphates crétacés-paléogènes (72,1-47,8 Ma) du Maroc. Mémoire de la Société géologique de France, vol. 180, pp. 351–452.

Bradley, W.H., 1946. Coprolites from the Bridger Formation of Wyoming: their composition and microorganisms. American Journal of Science 244, 215–239.

Broughton, P.L., Simpson, F., Whitaker, S.H., 1978. Late Cretaceous coprolites from Western Canada. Palaeontology 21, 443–453.

Buckland, W., 1835. 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 3 (series 2), 223–238.

Cantrell, A.K., Suazo, T.L., Spielmann, J.A., Lucas, S.G., 2012. Vertebrate coprolites from the Lower Permian (lower Wolfcampian) Gallina Well locality, Joyita Hills, Socorro County, New Mexico. New Mexico Museum of Natural History & Science Bulletin 57, 197–201.

Case, E.C., 1922. New reptiles and stegocephalians from the Upper Triassic of western Texas. Carnegie Institution of Washington, Publication, vol. 321, pp. 1–84.

Dentzien-Dias, P., Carrillo-Briceño, J.D., Francischini, H., Sánchez, R., 2018. Paleoecological and taphonomical aspects of the Late Miocene vertebrate coprolites (Urumaco Formation) of Venezuela. Palaeogeography, Palaeoclimatology, Palaeoecology 490, 590–603.

Duffin, C.J., Ward, D.J., 2023. First record of the coprolite ichnogenus *Struocopros* from the late Cretaceous of Morocco. Fossil Record 9, New Mexico Museum of Natural History and Science Bulletin, vol. 94, pp. 11–16.

Hunt, A.P., Lucas, S.G., 2012. Descriptive terminology of coprolites and recent feces. New Mexico Museum of Natural History & Science Bulletin 57, 153–160.

Hunt, A.P., Lucas, S.G., 2015. Vertebrate trace fossils from New Mexico and their significance. New Mexico Museum of Natural History & Science Bulletin 68, 88–107.

Hunt, A.P., Lucas, S.G., 2021. The ichnology of vertebrate consumption: dentalites, gastroliths and bromalites. New Mexico Museum of Natural History & Science Bulletin 87, 1–216.

Hunt, A.P., Lucas, S.G., Spielmann, J.A., Lerner, A.J., 2007. A review of vertebrate coprolites of the Triassic with descriptions of new Mesozoic ichnotaxa. New Mexico Museum of Natural History & Science Bulletin 41, 88–107.

Hunt, A.P., Lucas, S.G., Klein, H., 2018. Late Triassic nonmarine vertebrate and invertebrate trace fossils and the pattern of the Phanerozoic record of vertebrate trace fossils. In: Tanner, L.H. (Ed.), The Late Triassic World. Springer Verlag, New York, pp. 447–543.

Kocsis, L., Gheerbrant, E., Mouflih, M., Cappetta, H., Yans, J., Amaghzaz, M., 2014. Comprehensive stable isotope investigation of marine biogenic apatite from the late Cretaceous–early Eocene phosphate series of Morocco. Palaeogeography, Palaeoclimatology, Palaeoecology 394, 74–88.

Le Blanc, A.R.H., Cladwell, M.W., Bardet, N., 2012. A new mosasaurine from the Maastrichtian (Upper Cretaceous) phosphates of Morocco and its implications for mosasaurine systematics. Journal of Vertebrate Paleontology 32 (1), 82–104.

Matley, C., 1939. The coprolites of Pijdura, Central Province. Records of the Geological Survey of India, vol. 74, pp. 530–534.

Milàn, J., 2012. Crocodylian scatology — a look into morphology, internal architecture, inter- and intraspecific variation and prey remains in extant crocodylian feces. New Mexico Museum of Natural History & Science Bulletin 57, 65–71.

Milne, A.A., 1928. The House at Pooh Corner. Methuen & Co. Ltd, London.

Northwood, C., 2005. Early Triassic coprolites from Australia and their palaeobiological significance. Palaeontology 48, 49–68.

Ochev, V.G., 1974. Some remarks on coprolites of Triassic vertebrates. Paleontological Journal 1974, 253–255.

Suazo, T.L., Cantrell, A.K., Lucas, S.G., Spielmann, J.A., Hunt, A.P., 2012. Coprolites across the Cretaceous/Tertiary boundary, San Juan Basin, New Mexico. New Mexico Museum of Natural History & Science Bulletin 57, 263–274.

Yans, J., Amaghzaz, M., Bouya, B., Cappetta, H., Iacumin, P., Kocsis, L., Mouflih, M., Selloum, O., Storme, J.-Y., Gheerbrant, E., 2014. First carbon isotope chemostratigraphy of the Ouled Abdoun phosphate Basin, Morocco; implications for dating and evolution of earliest African placental mammals. Gondwana Research 25, 257–269.

Young, C.C., 1964. New fossil crocodiles from China. Vertebrata Palasiatica, vol. 8, pp. 190–208.

Zouheir, T., Hunt, A.P., Hminna, A., Saber, H., Schneider, J.W., Lucas, S.G., 2022. Laurussian-aspect of the coprolite association from the Upper Triassic (Carnian) of the Argana Basin, Morocco. Palaios 38, 1–23.