FIRST RECORD OF THE COPROLITE ICHNOGENUS *STRUOCOPROS* FROM THE LATE CRETACEOUS OF MOROCCO

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Abstract—Four spiral coprolites with distinctive morphology are described from the Upper Couche III Bone Bed (latest Maastrichtian) phosphate horizon, approximately 2 m below the KT boundary of Sidi Chennane Quarry, Khouribga Province, Morocco. The spiral coils are relatively coarse, have convex margins and are folded in a "taco-like" stack. These characteristics indicate that the coprolites belong to *Struocopros* Hunt & Lucas, 2023 and they are the first record of the ichnogenus from Africa. The orientation of the coprolites is determined by the presence of a relatively small final coil anteriorly, often with a preserved nubbin indicating the point of fecal mass release. Differences between the Moroccan specimens and those of *Struocopros friedmanae* (the type species recorded from the Cenomanian and Eocene of the USA) include the larger number of coils and the relationships between adjacent coils. The new ichnospecies *Struocopros catapitostromata* is created for the Moroccan material. It is suggested that foreshortening along the antero-posterior axis, elongation along the lateral axis and occasional lateral offset of adjacent coils and declination of coil junctions from the long axis of the coprolite were produced when the fecal ribbon entered a large, non-constraining rectum or cloaca, followed by extrusion through the cloacal sphincter.

INTRODUCTION

The recognition of vertebrate fossilized feces by William Buckland and their naming as coprolites in 1835 (Buckland, 1835) gave new stimulus to the study of ancient ecological relationships (but see Duffin, 2009 for an analysis of the early history of their study). Coprolites held otherwise inaccessible information concerning feeding relationships and behaviors, soft part anatomy and physiology. It has become increasingly apparent that vertebrate coprolites exhibit a wide range of morphologies necessitating the introduction of a utilitarian and stable ichnotaxonomic framework and precise descriptive nomenclature (e.g., Hunt and Lucas, 2012, 2021). It is increasingly obvious that recurrent morphologies in the geological record might permit biostratigraphic and biochronological applications (Hunt and Lucas, 2021) and that the recognition of different coprofacies within an ichnocoenosis could inform paleoecological and paleoenvironmental reconstruction (Hunt et al., 2018). Bearing these potential applications in mind the recognition and description of new and established bromalite ichnotaxa from geographically disparate regions has increasing importance. The purpose of the present paper is to describe some coprolites from the Late Cretaceous (Maastrichtian) of the Khouribga region of Morocco.

Abbreviations: 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 are guaranteed; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico.

GEOLOGICAL SETTING

The fossiliferous deposits of Khouribga are located in the Ouled Abdoun Basin, west of the Atlas Mountains and southeast of Casablanca (Figs 1A, B); at 9000 km^2, this is the largest and northernmost of the five major phosphate sedimentary basins that lie on a southwest-to-northeast trending axis through central Morocco. The phosphates are economically important, having been worked commercially since the 1920s, and are part of the Mediterranean Tethyan phosphogenic province that stretches from North Africa to the Middle East. The sediments of the Ouled Abdoun Basin are highly productive and range stratigraphically from the Late Cretaceous (Maastrichtian) to the Early Paleogene (basal Lutetian) (Fig. 1C). Representing warm, shallow marine deposition at a palaeolatitude of around 25° North, the phosphates are believed to be related to offshore nutrient upwelling and were deposited in one or more gulfs opening westwards into the Atlantic Ocean (Bardet et al., 2015).

In the Sidi Chennane area of the Ouled Abdoun Basin, the Maastrichtian phosphatic series is rather condensed, with a thickness of only 2-5m (Fig. 1C). The lack of invertebrate and floral biostratigraphic markers combined with considerable facies variation means that fossil vertebrates are the main hope for intra- and inter-basinal correlation. As a consequence, a rather informal stratigraphic scheme has emerged for the succession (LeBlanc et al., 2012; Yans et al., 2014; Koksis et al., 2014; Fig. 1B). From the base upwards, the sequence consists of (1) a basal gray phosphatic limestone bone-bed (BBB), (2) soft yellow phosphates referred to as the Lower Couche III (Lower CIII level or LCIII), (3) a discontinuous phosphatic limestone, (4) phosphates that are soft and gray with brown streaks and a bone bed called Upper Couche III (Upper CIII and the UBB), and (5) yellow marls - see Figure 1C.

MATERIAL AND METHODS

Photographs of the specimens were taken using a Nikon Z6 camera equipped with a 106 mm F2.8 macro lens and a polarizing filter. For illumination, two polarized LED light panels were arranged parallel to each other. To achieve an increased depth of field, stacked digital images were combined using Helicon Focus 8.2.2 software. The coprolite images were isolated using Topaz Mask software and then assembled into plates using JASC Paintshop Pro version 7.00.

Within the Ouled Abdoun basin, there exists an active cottage industry focused on surface collecting from phosphate quarry spoil piles and sieving *in situ* the productive layers to uncover fossil teeth and bones. These findings are sold locally to state-licensed dealers, who typically harden and sort the fossils

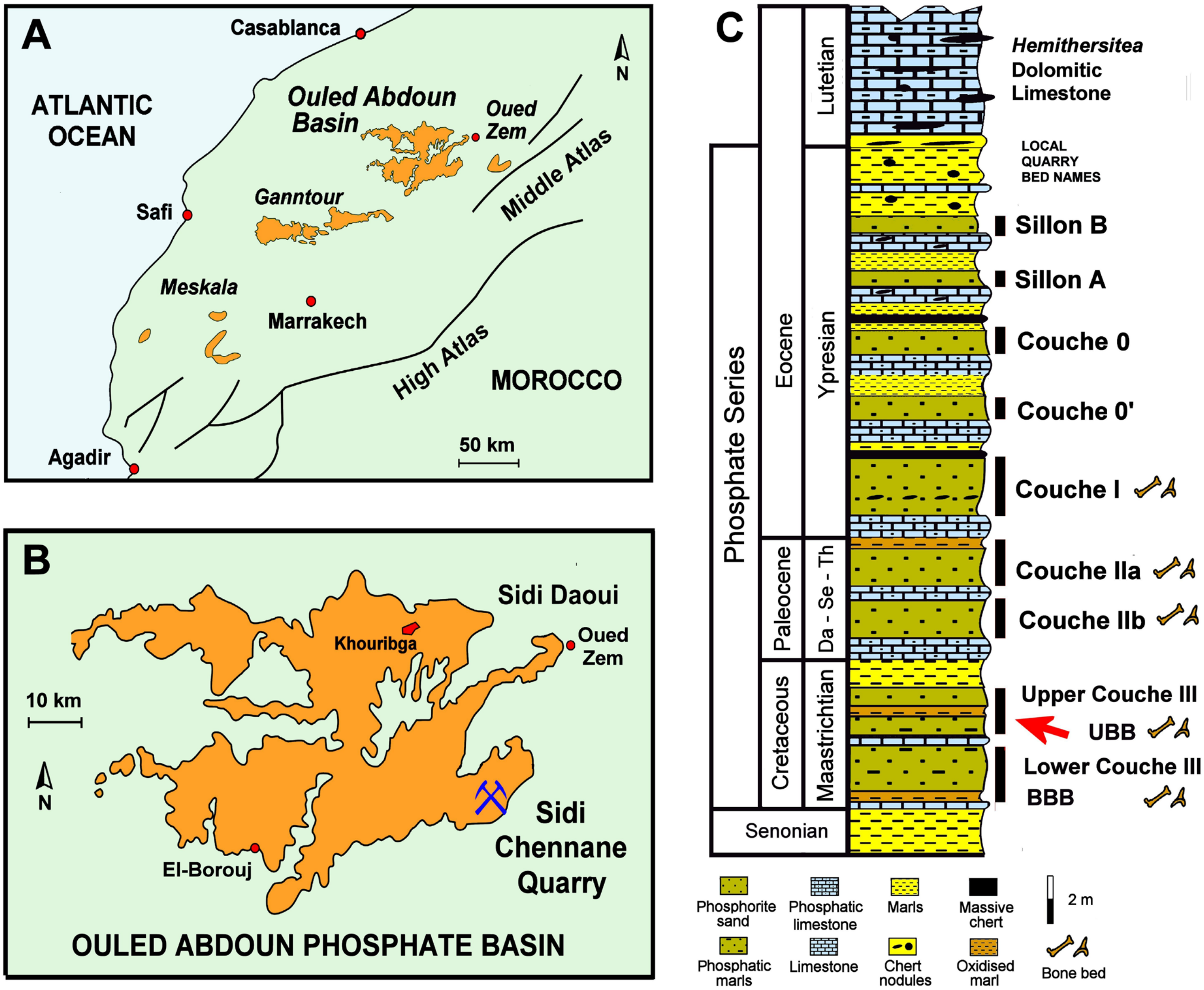

FIGURE 1. **A**. Map of Northern Morocco showing the relative positions of the phosphate deposits. **B**. Position of the Sidi Chennane Quarry within the Ouled Abdoun Phosphate Basin. **C**. Synthetic stratigraphic column for the Sidi Chennane area within the Ouled Abdoun Phosphate Basin indicating the position of the Couche III Upper Bone Bed. The solid vertical bars indicate the levels to which the "Couche" and "Sillon" terms apply. The maps and section were modified after Kocsis et al. (2014) and Yans et al. (2014).

for sale in the wholesale fossil market. The specimens described below represent a part of an informal long-term project aimed at acquiring the rarer non-commercial fossils directly from these dealers.

ICHNOTAXONOMY

Struocopros Hunt and Lucas, 2023

Type ichnospecies: *Struocopros friedmanae* Hunt & Lucas, 2023 from the Late Cretaceous and Paleogene of North America (Friedman, 2012, fig. 9.5; Dentzen-Dias et al., 2020, fig. 7, 9; Hunt and Lucas, 2023, fig. 1).

Struocopros catapitostromata i.sp. nov. Figs. 2A-L, 3A-L

Holotype: LF 5649 (Figs 2A-F).

Etymology: From the Greek, *catapito* for collapse and *stromata* for layers referring to the possible mechanism for producing the "taco-like" arrangement of the individual coils.

Type locality: Eastern end of Sidi Chennane, 31km south south-east of Khouribga, Khouribga Province, Béni Mellal-Khénifra region, Morocco (Fig. 1A-B). This is a large commercial working quarry complex that 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-T boundary (Late Cretaceous: latest Maastrichtian) (Fig. 1C).

Paratype specimens: LF 5650-5652 (Figs 2G-L, 3A-L).

Diagnosis: Coprolites with three to five coils, an anterior coil with well-preserved lip and nubbin, foreshortened antero-posterior axis and expanded lateral axis, rounded to flattened suboval cross-section and occasionally laterally offset adjacent coils declined at 45° to the coprolite long axis.

Specimens of *S. capitostromata* differ from those of *S. friedmanae* in that the latter may contain inclusions, have thicker individual coils which are fewer in number, and lack the lateral offset and variation in inter-coil junctions shown by the Moroccan ichnospecies.

Description: The holotype (LF 5649; Figs. 2A-F) measures 38.5 mm along the long axis and 18.9 mm across. The anterior

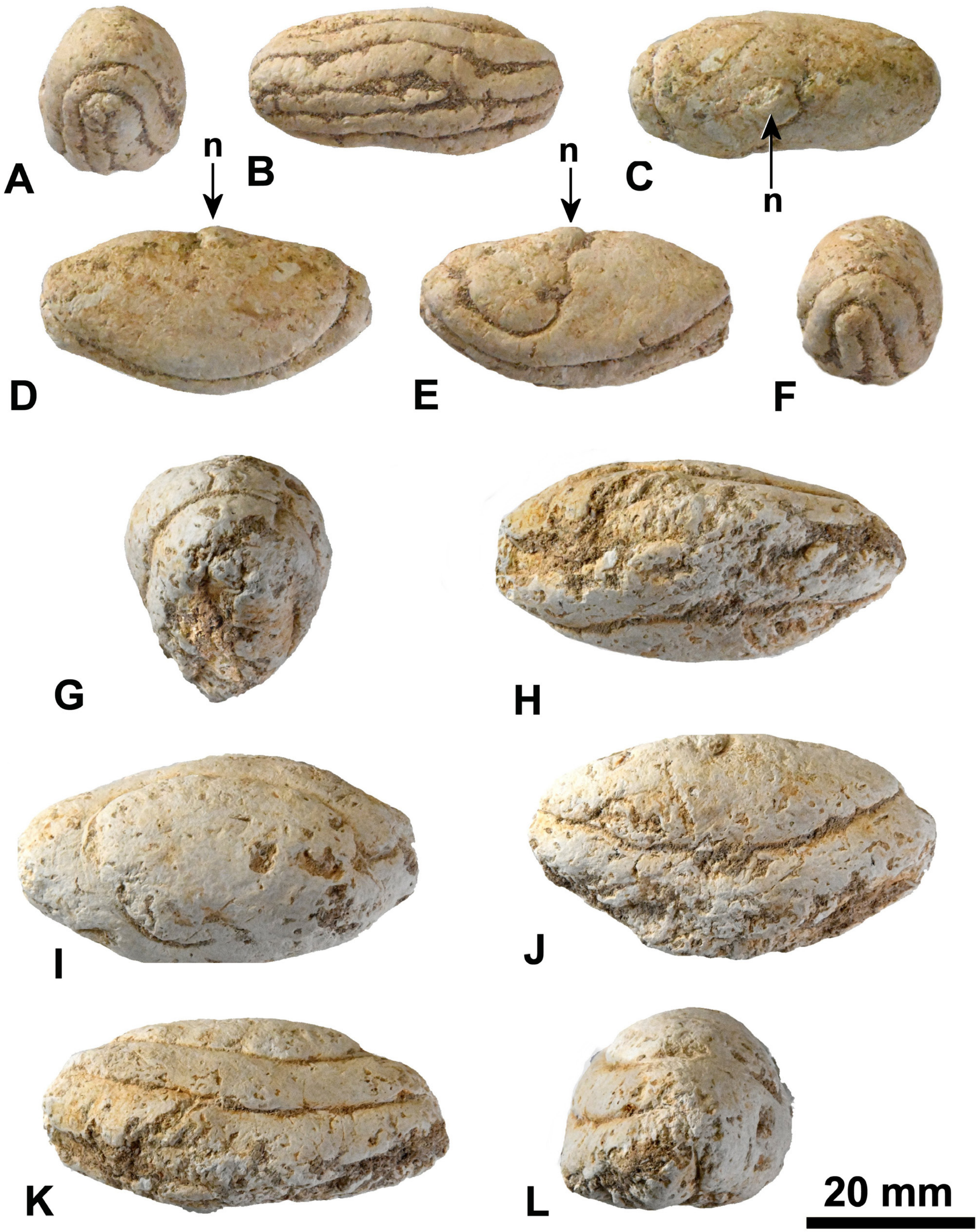

FIGURE 2. Holotype and paratypes of *Struocopros catapitostromata* isp. nov. from Couche III Upper Bone Bed (Late Maastrichtian) of Sidi Chennane Quarry, Ouled Abdoun Phosphate Basin, Morocco. **A-F**. LF 5649**:** Holotype. Coprolite in terminal (**A**), posterior (**B**), anterior (**C**) lateral (D-E) and terminal view (**F**). **K-L**. LF 5650: Paratype. Coprolite in terminal (**A**), posterior (**B**), anterior (**C**) lateral (**D-E**) and terminal view (**F**). All coprolite images are oriented, where possible, according to the convention proposed by Hunt & Lucas 2012, with anterior at the top of the image. The position of the nubbin is indicated by (**n**).

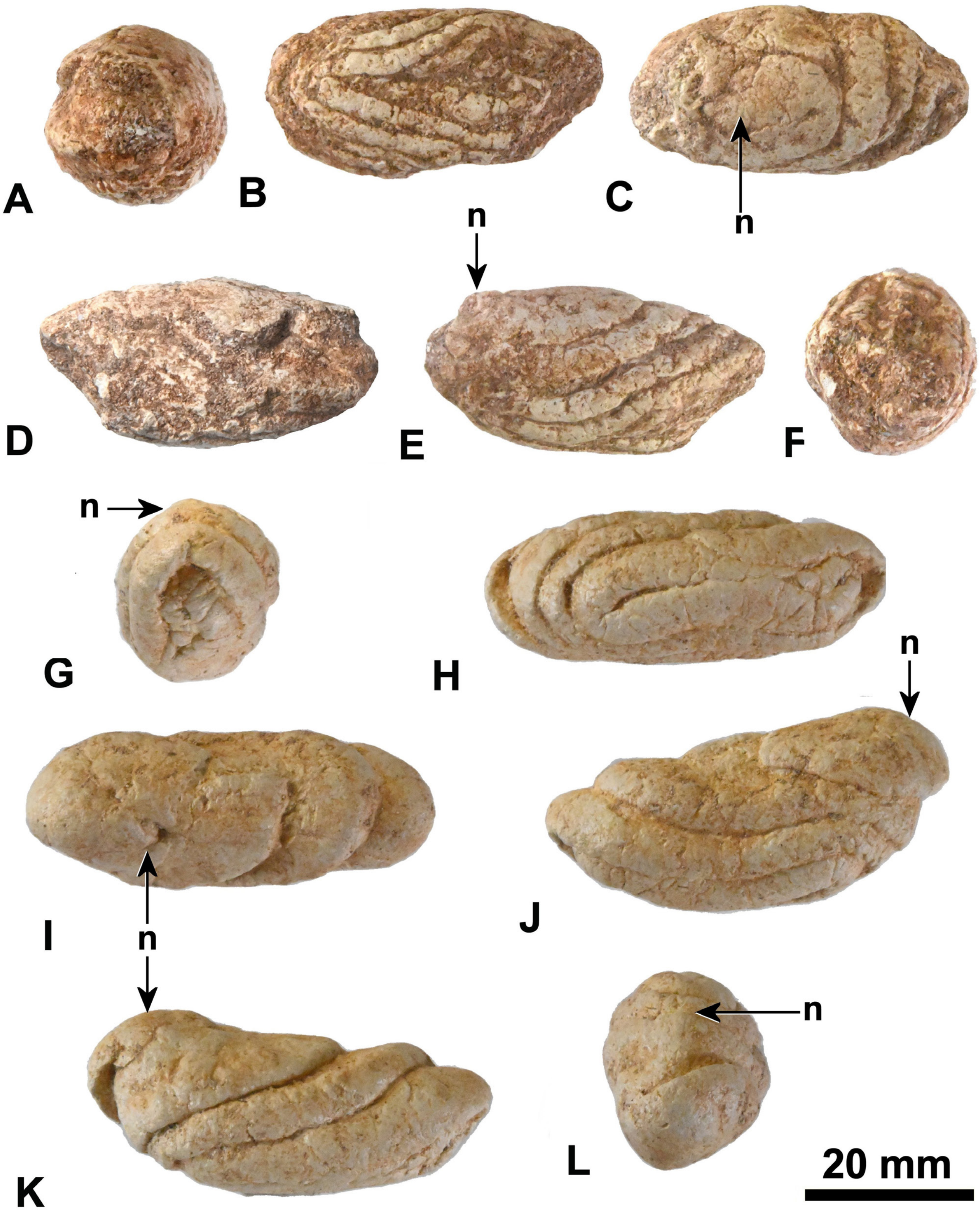

FIGURE 3. Paratypes of *Struocopros catapitostromata* i.sp. nov. from Couche III Upper Bone Bed (Late Maastrichtian) of Sidi Chennane Quarry, Ouled Abdoun Phosphate Basin, Morocco. **A-F**. LF 5652: Paratype. Coprolite in terminal (**A**), posterior (**B**), anterior (**C**) lateral (**D-E**) and terminal view (**F**). **K-L**. LF 5651: Paratype. Coprolite in terminal (**A**), posterior (**B**), anterior (**C**) lateral (**D-E**) and terminal view (**F**). All coprolite images are oriented, where possible, according to the convention proposed by Hunt & Lucas 2012, with anterior at the top of the image. The position of the nubbin is indicated by (**n**).

end of the coprolite can be distinguished by the presence of a diminutive final coil with a marked lip bearing a small swelling (here termed the nubbin) marking the point of release of the food bolus (Fig. 2E). The short axis of the coprolite is thus the antero-posterior axis, and the long axis is the lateral axis. No inclusions are visible over the coprolite surface. In lateral view it is obvious that three coils with convex margins are present, each around 3.4 mm thick. The junctions between the coils are roughly parallel to the long axis of the coprolite but are arched downwards in the central region. In terminal and posterior views (Fig. 2A, B, F), the folded, "taco-like" arrangement of the coils is clearly visible. The anterior half of the coprolite is wider than the posterior half, and the cross-sectional shape of the specimen is a slightly flattened oval.

Inclusions are absent from each of the three other coprolite specimens. LF 5650 (Fig. 2G-L) is very similar to the holotype, but a little larger, measuring 50.6 mm along the longest axis and 27.8 mm across. The final, anterior-most coil is readily distinguished; a stump of the nubbin is just visible, but considerably worn. As in the holotype, the antero-posterior axis is the shortest and the lateral axis the longest on the specimen. Two coils are present with the "taco-like" arrangement clearly visible in terminal view, and the inter-coil junctions have the same arrangement as in the holotype. The cross section is a slightly flattened oval.

LF 5651 is 47 mm long and 20.2 mm wide (Fig. 3G-L). The oval cross-section is less flattened than in the previous two specimens. The prominent anterior coil with its slightly offset nubbin (Fig. 3J) has a clearly defined lip but is displaced laterally in anterior view. Three coils are present with the characteristic "taco-like" arrangement. The junctions between the coils are somewhat different in this specimen compared to the two described above. Here, they are declined at around 45^{o} to the long axis of the coprolite. Coils 1 and 2 are each laterally offset from the previous coil, but C3 is fully enclosed by the overlap formed by C2 (Fig. 3J).

LF 5652 measures 38 mm long and 19.9 mm wide (Fig. 3A-F). Its' morphology is closest to that of LF 5651. The coprolite cross-section is more rounded than in the other three specimens. In anterior view, the anterior coil can be distinguished clearly, although the nubbin is somewhat eroded. There are at least 4 and possibly 5 further coils present, with their junctions declined from the long axis of the coprolite as in LF 5651. The "taco-like" arrangement of the coils is evident in posterior and terminal views (Fig. A, B, F). As in LF 5651, the coils are laterally offset from more anterior coils (Fig. 3E).

DISCUSSION

The four coprolites described above from the Maastrichtian of Morocco clearly belong in the ichnogenus *Struocopros* Hunt & Lucas, 2023 because they consist of a stack of relatively coarsely spiral coils with convex margins, and which have an internal arrangement that resembles a stacked series of hard tacos (a taco is a discoidal wheat or corn tortilla or pancake that has been folded in half to accommodate a filling).

There are several differences, however, between the material described here and that ascribed to *Struocopros friedmanae* from the Cenomanian Britton Formation of Texas (Friedman 2012; Hunt and Lucas, 2023) and the Eocene Nanjemoy Formation of Virginia, USA. No inclusions are visible on the surfaces of the Moroccan coprolites whereas inclusions may be present in Cretaceous specimens of *S. friedmanae* (e.g. NMMNH P-37769; Hunt and Lucas, 2023), although they are absent from those of the Eocene specimens (Hunt and Lucas, 2023).

In addition to the anterior-most coil which, by convention, is not counted in the overall coil count (Hunt and Lucas, 2012), the Moroccan specimens possess between two and five coils whereas specimens of *S. friedmanae* have only two. At 38 to 50mm along the longest axis, the size range of the specimens attributed here to *S. catapitostromata* is similar to that given for *S. friedmanae* (Hunt and Lucas, 2023). The individual coils are thinner in *S. catapitostromata*.

The main difference between specimens of the two species is in the relationships between adjacent coils. In the Moroccan material the inter-coil junctions vary from virtually parallel to the longest axis of the specimen (with a certain amount of sag or posterior arching centrally; Fig. 2E, K) to being declined at around 45^{o} (Fig. 3E, K). Bearing these differences in mind we propose that the Moroccan material be placed in a separate ichnospecies of the ichnogenus *Struocopros*.

The question arises as to how the morphological variation in the relatively small sample of Moroccan coprolites was produced. Hunt and Lucas (2023) remarked how difficult it was to orient the Cenomanian and Eocene coprolites from the USA with respect to the living animal. We believe that we can identify the anterior end of the Moroccan coprolites based upon the presence of the anterior-most coil, aided by the recognition of a nubbin, a small, raised mound where the fecal mass was released from the sphincter. All specimens therefore have a foreshortened antero-posterior axis and an elongated lateral axis, often accompanied by a certain amount of lateral flattening. Some specimens show lateral offset of spiral coils with coil junctions declined at 45^{o} to the coprolite long axis. We suggest that these features were produced as the ribbon of fecal material was extruded from the ileum into a relatively large cloaca or rectum, as briefly intimated by Ward et al. (2020). Being too large to constrain the shape of the fecal mass, as the coprolitic material entered the cloaca or rectum it underwent a certain amount of rotation and collapse. However, the consistent fusiform shape of the coprolites was imposed by subsequent passage through the cloacal sphincter. In some instances, the rotation as the coprolite moved into the cloaca was 90^{o}, resulting in foreshortening along the antero-posterior axis of the coprolite. In others the collapse was at an angle to the coprolite long axis, resulting in lateral offset of adjacent coils and declination of the inter-coil junctions. Further squeezing of the coprolite through the cloacal sphincter resulted in internal folding of the spiral folds to give the "taco-like" appearance characteristic of the genus, and elongation along the lateral axis. We speculate that a larger sample size of coprolites from this horizon might show a range of gradation from the morphotypes described above to an amphipolar form of more regular appearance; this hypothesis must await the collection of a larger number of specimens before it can be tested.

The accompanying fauna comprises crocodilians, mosasaurs, varanoid squamates, chelonians and a wide range of medium to large chondrichthyans, including potentially the earliest myliobatiforms, sclerorhynchids, hexanchids, *Squalicorax* spp., odontaspids (e.g. '*Carcharias*'), *Cretalamna* sp., *Serratolamna* spp., and a wide range of teleosts (see, for example, Arambourg, 1952; LeBlanc et al., 2012). Of these groups, the most likely organisms to have produced the coprolites described here are the medium to large lamniform sharks such as *Squalicorax* and *Serratolamna maroccana* (Arambourg, 1935), rays such as *Schizorhiza stromeri* Weiler, 1930, and myliobatiforms such as *Rhombodus binkhorsti* Dames, 1881.

CONCLUSIONS

A small sample of spiral vertebrate coprolites from the Maastrichtian "Couche III", approximately 2 m below the K-T boundary of Sidi Chennane Quarry near Khouribga in Morocco are described as *Struocopros catapitostromata* isp. nov. The distinctive features of these coprolites are the relatively high number of spiral folds (up to five), foreshortened antero-posterior and lengthened lateral axes, occasional lateral offsetting of adjacent coils and occasional angular declination of the inter-coil junctions to the long axis. The changes in shape were probably brought about by the ribbon of plastic fecal material entering a relatively large rectum or cloaca and then deforming either by compaction along the antero-posterior axis or collapse at an angle. Final extrusion through the cloacal sphincter conferred the "taco-like" folding on the stack of coprolitic coils and elongation along the lateral axis. This is only the third record of the ichnogenus *Struocopros* and the first in the African continent. The most likely producer of the coprolites was one of the medium to large sharks in the diverse chondrichthyan fauna.

ACKNOWLEDGMENTS

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. We would also like to thank Bruce and René Lauer (Lauer Foundation, Illinois, USA) for curating the specimens and providing registration numbers at short notice. The authors are particularly grateful to Adrian Hunt and Spencer Lucas for their prompt and helpful reviews of the manuscript, thereby helping to expedite final publication.

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