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Accurately assign fossil droppings to vertebrate spiral intestine types: case of the coprolites from the Kem-Kem beds (Morocco; Cretaceous)

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Abstract

The Kem Kem Geological Group (Morocco) is renowned for its emblematic mid-Cretaceous vertebrate fauna and the high abundance of predators represented among its fossil assemblage. In such predators-dominated context, analysing associated fossil faeces may yield valuable insight on the trophic interactions and biotic dynamics existing at that time in this ecosystem. Here, we analysed the first reported Kem Kem coproassemblage (ca. 200, relatively large, coprolites) in order to assess how their external and internal morphological features allow separating groups assignable to different vertebrate producers. Recognising a majority of spiral-shaped coprolites, we first produce a phylogeny with robust ancestral character state reconstruction for the evolution of the spiral intestine among vertebrates based on our review of the fossil and modern occurrences of this organ. Applying microtomography and thin-sectioning to the dataset, we compare the relevance of different morphological features of the faeces to differentiate among producing taxa, depending on if they are externally or internally observed. Finally, we use faeces size, and inclusions content, to achieve discriminating between producers, providing a relevant framework to enable producer assignation. Our results reveal that both tetrapod and non-tetrapod faeces were similarly deposited and preserved at burial and deposit, but that it was mostly four different types of non-tetrapod producers (with funnel-type spiral guts and one another with a scroll-type spiral gut representing an extinct convergence) which were the most prompt to deposit faeces in the system. Globally, in the sample locality, spiral and non-spiral types were produced by intestine of comparable diameters. The assemblage reveals that external features can be indicative of interspecific differences of the

producers, but that equivalent internally measured features are more efficient at indicating groups of producers. The absence of specific types of valves in the assemblage corresponding to likely abundant taxa (e.g. holosteans) could evidence some ancestral state of the spiral valve in the mid-Cretaceous, relative to its inferred evolution among vertebrates.

Keywords: faeces, spiral valve, Albian–Cenomanian, producer, funnel, scroll.

Introduction

The Kem Kem Geological Group (Drâa-Tafilalet region, Morocco) is renowned for its emblematic vertebrate fauna and the unusual high abundance of predators represented among its fossil assemblage (e.g. Cavin et al. 2015a, b, Myhrvold et al. 2022, Benyoucef et al. 2022, Lacerda et al. 2024). The formation consists of series of continental deposits dominated by an ancient fluvial system which was flowing South to North (Ibrahim et al. 2020). For the first time, a large collection of vertebrate coprolites (187 specimens of fossil faeces) from this formation was assembled, originating from the locality of Aferdou N'Chaft (Taouz, **Fig. 1A**). This collection includes large specimens reaching 13 cm and 9 cm in length and width. In this predators-dominated context, coprolite analysis may yield new insights onto the recognition of coprolites producers and fossil faeces, opening a new trophic interactions and broader biotic dynamics within the Kem Kem ecosystem.

Among fossil faeces (described in Buckland 1829), a key distinction exists: faeces derived from a spiral intestine — characterized by axial internal walls in part of the digestive tract organized in helix — and those lacking such structures. These two intestinal morphologies reflect very different digestive strategies. The non-spiral intestine of tetrapods is a long tube folded upon itself, such that when extended, it exceeds the animal's body length (Leigh et al. 2021). In contrast, the spiral intestine (also called spiral valve) is relatively straight and shorter, with an internally invaginated structure that increases food transit time through the digestive tract, thereby enhancing digestion efficiency (Leigh et al. 2021). Both strategies ultimately aim to increase absorption surface area and digestive efficiency. Spiral intestines are found today in all non-teleost actinopterygians, non-tetrapod sarcopterygians, chondrichthyans, and lampreys (McAllister 1985).

Based on parsimony, the spiral valve is acknowledged as a symplesiomorphy of gnathostomes, while the non-spiral intestine of tetrapods and teleosts represent morphological

convergences (e.g. McAllister 1985, Sanketi et al. 2025). Based on the fossil record now, it is hypothesized that the earliest spiral valves appeared in Paleozoic agnathans (McAllister 1985, Aldridge et al. 2006), notably based on isolated, scroll-shaped spiral coprolites presumed to have been produced by these animals (Gilmore 1992). The spiral intestine was reported for in a later placoderm (*Bothriolepis*; Denison 1941), corresponding to the oldest direct evidence of this feature in gnathostomes. Over the Paleozoic, an homoplastic spiral midgut is also reported outside of vertebrates, notably in eurypterids (Waterston et al. 1985, Braddy et al. 1995). Cololites (infilled colon portions found fossilized) showing spirals were reported in fossils of the chondrichthyans *Cladoselache* (Woodward 1917), and *Cladodus* (Claypole and Wright 1893), as well as in the actinopterygian *Saurichthys* (Argyriou et al. 2016) which revealed new insights on the organisation of whorls.

Spiral coprolites divide in amphipolar and heteropolar distribution of spirals (Neumayer, 1904) which are often assigned either to faeces of non-tetrapod sarcopterygians or non-teleostean actinopterygians when amphipolar; or to chondrichthyans when heteropolar (e.g. in Eriksson et al. 2011, Anagnostakis 2013, Dridi 2018). However, the link between this distinction and differences in valve shape is not that clear and was at some point thought to reflect diet or even external preservation (McAllister 1984, 1985, Hunt and Lucas 2012a) — raising doubts about the validity of the polarity criterion to systematically distinguish chondrichthyan faecal remains from actinopterygian and sarcopterygian ones. Non-spiral coprolites are even more difficult to assign to a producer taxon, mostly because the large terrestrial tetrapods of the Late Mesozoic have either gone extinct or drastically changed in ecologies (e.g. pterosaurs, dinosaurs). As a consequence, cylindrical coprolites are quite frequently attributed to crocodylomorphs (e.g. Waldman 1970, Schwimmer 2002, Nobre et al. 2008, Harrel and Schwimmer 2010, Souto 2010, Lucas et al. 2012, Milàn et al. 2018, Halaçlar et al. 2023, Rozada et al. 2024; see Hunt and Lucas 2012a for review) despite the very few studies involving comparisons with modern crocodilian examples (Sawyer 1981, Fischer 1981, Milàn and Hedegaard 2010, Milàn 2012, Rozada et al. 2024), and simply none with bird non-guano-like faeces. Modern crocodylomorphs are claimed to possess a recognisable highly corrosive digestive systems (pH < 4; Hunt and Lucas 2010; Milàn 2012), resulting in scale enamel degradation and only scarce large inclusions in faecal matrices. However, studies on enamel degradation in identified dinosaur coprolites are too few to truly figure out how pH and acids must have acted in their digestive system (aside of quantitative approaches as in Qvarnström et al. 2024, only two coprolites undoubtfully assigned to Dinosauria; Chin et al.

1998, Sorscher 2002). Lastly, very few publications have focused on describing reptilian digestive systems of similar corrosive effects (e.g. snakes, Secor 2008).

Kem Kem coprolites represent an unprecedented fossil assemblage to accurately estimate producers' diversity from retrieved faeces, provided that we dispose of a robust phylogenetic framework for the evolution of the intestine shape. Therefore, we here first reviewed the published literature on the morphology of the intestine in vertebrates and provide a phylogeny with robust ancestral character state reconstructions for the evolution of this organ. Appling microtomography and thin-sectioning to the coproassemblage, we here compare the relevance of different morphological features of the faeces to differentiate among producing taxa, depending on if they are externally or internally observed. Finally, we use faeces size and inclusions content to achieve discriminating between producers.

Geological context

The Kem Kem beds comprise two main formations: the Ifezouane and Aoufous formations (**Fig. 1**). This geological group is well-known for its emblematic aquatic vertebrate fauna and the over-representation of predators among its fossil remains (Cavin et al. 2015). The siliciclastic sediments of these formations are mainly derived from the erosion of the Anti-Atlas Massif, located west of the Kem Kem area (Ibrahim et al. 2020). Based on ichthyofaunal assemblages, the deposits are dated to the Albian–Cenomanian interval (Sereno et al. 1996, Forey and Grande 1998). However, due to the lack of stratigraphic fossils and the absence of absolute radiometric dating, the chronological resolution remains limited. The Kem Kem Group represents continental deposits dominated by an ancient south-to-north-flowing fluvial system, with occasional lacustrine horizons. Some rare marine environments have been documented further north, near the deltaic margin and close to the Atlas fault zone (Beevor et al. 2021, Adardor et al. 2021). Nevertheless, the majority of the Kem Kem Group reflects a freshwater to brackish setting. This is supported by the presence of taxa restricted to freshwater environments, such as lissamphibians (Rage and Dutheil 2008, Cavin et al. 2015), freshwater decapods (Garassino et al. 2006), and unionid bivalves (Ibrahim et al. 2020).

The Ifezouane Formation constitutes the lower unit (**Fig. 1B**), primarily composed of cross-bedded sandstones indicative of channel infill in a high-energy fluvial system. Its upper levels show tidal influence in northern localities (Ibrahim et al. 2020). This unit is overlain by the Aoufous Formation, consisting of alternating sandstone and claystone beds.

The fossil assemblage of the Kem Kem Group is dominated by vertebrates, including chondrichthyans, actinopterygians, actinistians, amphibians, squamates, crocodylomorphs, chelonians, sauropods, theropods, and pterosaurs (Ibrahim et al. 2020). In addition, some invertebrates are reported, including freshwater decapods (Garassino et al. 2006, Ibrahim et al. 2020), mollusks (Garassino et al. 2006, Cavin et al. 2015), and insects (Garassino et al. 2006).

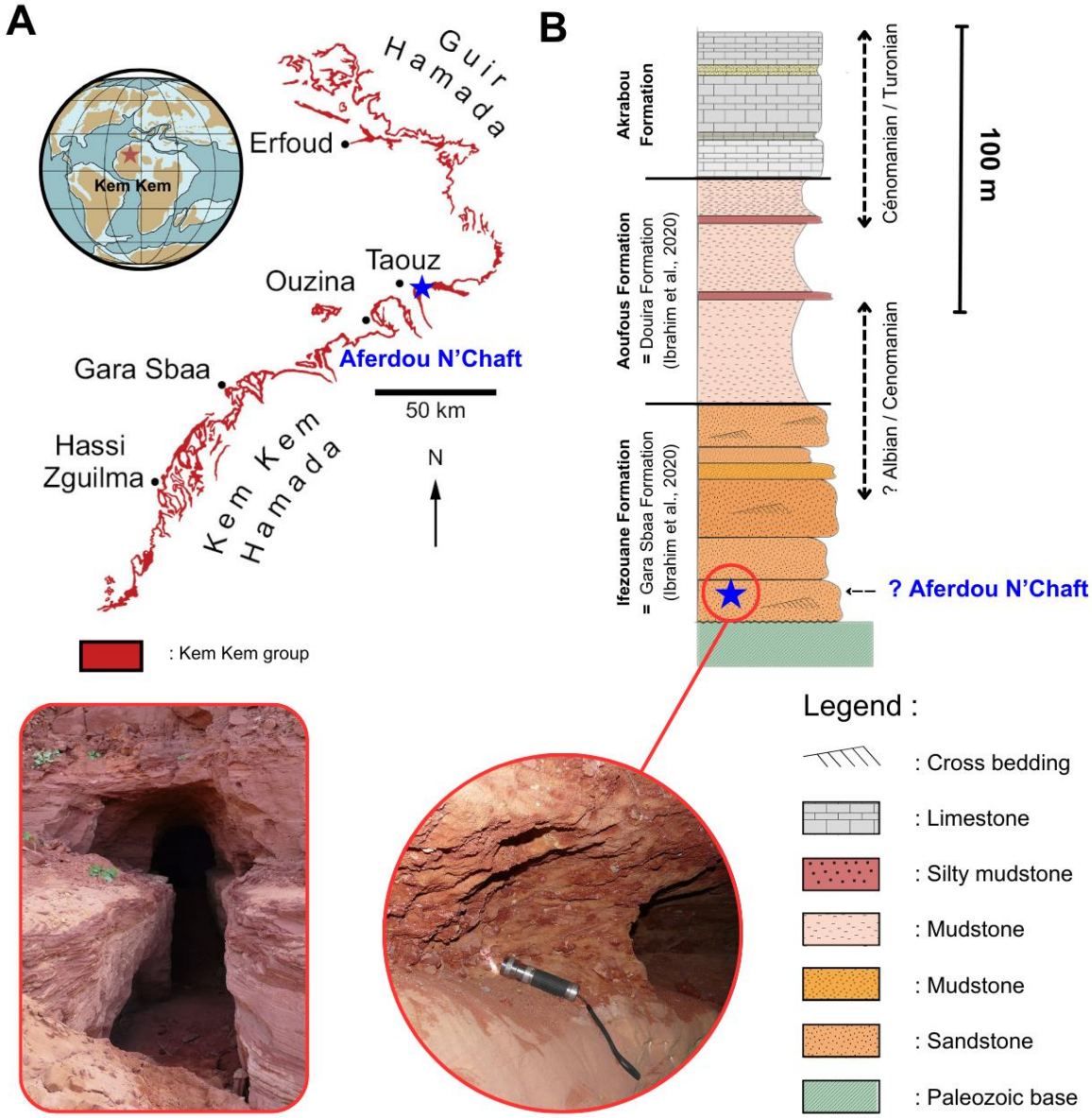

Figure 1. Geological context of the Kem Kem (Morocco). A. Paleogeographic map of the Cenomanian (94 Ma) and the current Kem Kem group (Aoufous and Ifezouane formations) (modified from Ibrahim et al. 2020). B. Simplified stratigraphic log of the Kem Kem and photographs of the Aferdou N'Chaft site (modified from Cavin et al. 2015).

Materials and Methods

147 Studied material and macroimaging

148 A total of 187 coprolites of vertebrates were gathered from the locality of Aferdou N'Chaft
149 (Kem Kem, Morocco) by one of us (B.H.) over a regional field visit. The collection
150 (MHNM.KK394–580) is deposited at the Natural History Museum of Marrakech, Morocco. It
151 consists of a total of 129 spiral and 31 non-spiral coprolites. All specimens were photographed
152 from two to three different views.

153 Reconstruction of ancestral character states for the spiral intestine
154
155 In order to infer ancestral characters at nodes based on robust support, we compiled an
156 exhaustive database of all published intestinal morphologies for non-teleostean and non-
157 tetrapod vertebrates (**Supp. Tab. 1**, fossil and modern evidences) The data displayed in Leigh
158 et al. (2021) were – after thorough exploration of the scanned data – chosen not to be included
159 due to some doubtful type assignations compared to the rest of the literature, implying possible
160 confusion within the published dataset (**Supp. Tab. 1**).
161 In order to reconstruct the ancestral character states of the intestine-type at nodes, we used
162 a topology-based consensus tree derived from published vertebrate relationships (recovered
163 from Liem 1988, Kuraku et al. 2009, Mirande 2017 and Amaral et al. 2018, see **SI**), using equal
164 branch lengths (set to 1) for comparative purposes. Ancestral state reconstruction was
165 conducted in R, testing the likelihood of intestinal morphologies at internal nodes under
166 different models of trait evolution. To identify the most appropriate model for ancestral
167 character state reconstruction, three models of character evolution were evaluated, each
168 differing in their assumptions regarding transition rates among spiral valve morphologies.
169 The first model, the equal-rates (ER) model, assumes a single transition rate for all changes
170 between character states. The second model, the symmetrical model (SYM), allows
171 different transition rates between character states but constrains forward and reverse
172 transitions between any two states to occur at the same rate (e.g., A → B = B → A). The
173 third model, the all-rates-different model (ARD) , estimates an independent transition rate
174 for every possible change between character states, including forward and reverse
175 transitions. Model performance was assessed using the Akaike Information Criterion (AIC),

with the model exhibiting the lowest AIC value considered to provide the best balance between goodness of fit and model complexity. Corresponding script is displayed in **SI**.

Microtomography

A subset of 58 specimens was scanned in micro-computed tomography to detect possible bone inclusions that could inform on dietary habits. Twenty scans were performed on the PLATINA platform (IC2MP, Poitiers University) and thirty-eight on the IMAGEO platform (OSERen CNRS, Rennes University). Reconstructions were performed using X-Act software (RX Solutions) with voxel resolutions ranging from 14 to 36 µm (90 keV; 20–30 W; 1018–2016 projections over 360°). 3D rendering and segmentation were conducted using Dragonfly BSD 6.4 (Dragonfly 2024.1).

Morphometric analysis

Morphometric measurements were performed both on coprolite surfaces using calipers (Fig. 2) and digitally, using FIJI v1.54g (Schindelin et al., 2012), on the spiral features observed within the coprolites on CT-scans. A number of qualitative morphological features relating on preservation, dimensions, ends shape, or categorization were compiled both from externally and internally observed features (e.g. completeness, degree of compression, polarity when spiral) for all 187 coprolites (non-spiral, **Fig. 2A**; spiral amphipolar, **Fig. 2B** and spiral heteropolar, **Fig. 2C**; see **Supp. Tab. 2**). Amphipolarity describes profiles with spirals extending along most or all of the coprolite; heteropolarity describes profiles with spirals restricted to the posterior portion of the coprolite (**Fig. 2B–C**). Quantitative discrete and continuous variables (measurements) were also reported, corresponding either to externally or to internally collected data (e.g. coprolite maximum length (L), maximum width (w_{max}), orthogonal width (w_{sec}), spiral part length (PS), whorl height (H) and width, or whorl angle relative to the horizontal plane (α), (**Fig. 2**, **Supp. Tab. 2**)). To minimize the impact of size on dimensional variations (e.g. relative shape), a log-shape ratio transformation has been performed on the measured data (Mosimann 1970). Principal component analyses (PCA) were performed on the ‘externally observed features” data subset (**Supp. Tab. 2,** exclusive of spiral features specific to only part of the dataset) in order to test for the variables explaining at most the global Kem Kem coprolite morphospace. The covariance between most possible pairs of variables were assessed by linear regression models, secondarily tested by ANOVA and HSD-Tukey tests (multiple comparison of the group obtained means). A linear discriminant analysis

focusing on spiral coprolites was secondarily performed (Fisher 1936) on the "externally observed features" data subset (**Supp. Tab. 2**), this time focusing on the spiral features in order to identify the variables explaining at most the heteropolar vs amphipolar morphologies (described in Neumayer 1904) among all the spiral coprolites of the Kem Kem. Among spiral coprolites, the data subset of "internally observed features" (**Supp. Tab. 2**) was screened for the morphological groups potentially existing among the coprolites consistent with a funnel-type spiral valve. To do so, a Partitioning Around Medoids clustering (Reynolds et al. 2006) was applied on a PCA. Clusters' robustness was tested by bootstrap resampling (Hennig 2007). Lastly, where possible, the length of the coprolite producer was inferred based on linear regressions performed on producer/faeces lengths compiled from literature (McAllister 1985, Milan 2012, Argyriou et al. 2016) for spiral and non-spiral types of intestines. Data were analysed in R v4.4.2 (R Core Team, 2018). Due to preservation limits, statistical analyses were performed only on the subset of the dataset preserving the targeted characterizing features. Statistical scripts are displayed in **SI**.

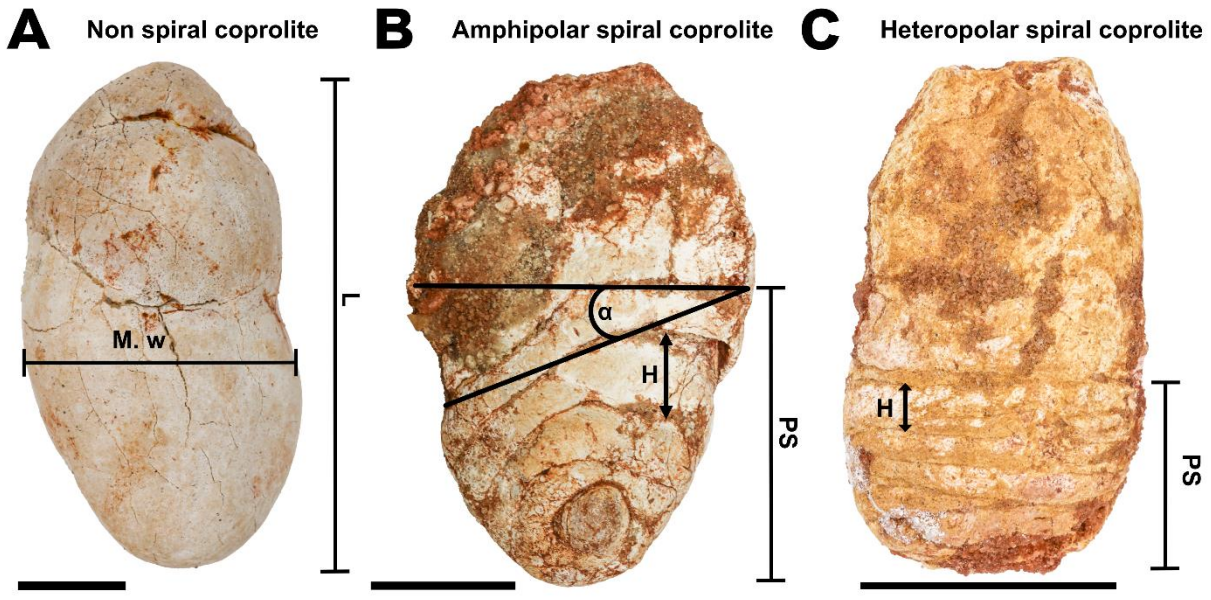

Figure 2. External measurements taken on spiral and non-spiral coprolites. A. example of width and length measurements on specimen MHNM.KK505. B–C. example of angle and height measurements for spiral coprolites MHNM.KK420 and MHNM.KK423. Abbreviations: M. w, max width; L, length; α, angle of the whorl; H, height of the whorl; PS, posterior spire. Scale bars = 2 cm.

Thin-section analysis

Twenty coprolites were selected for longitudinal and transverse thin sections, aimed at detecting features not visible in CT scans, such as microorganisms or soft tissue remains. The sections were analysed under a Leica M80 optical microscope and photographed using a Canon EOS 750D camera.

Results

Real variability of spiral intestines and ancestral character state reconstruction

Our exhaustive review of the existing literature confirms that two main classifications apply to the internal shape of spiral intestines; that of Parker 1880, and that of Compagno 1988. In both cases classifications, four main types are recognized: Type A, B, C and D. We would like to raise that the Type C, described by Parker (1880, and long cited since) shall actually be considered strictly inexistent. Indeed, Type C was never observed through any other evidence than this report of Parker; it is neither relevant in term of development of the typhlosole, nor of physiological function. Consequently, and after considering most options, we support Fee (1925) in the fact that Parker' type C is more susceptible to represent a tissue collapse owed to an inefficient intestine treatment (Fee 1925). We therefore removed this supposed state from our characters options and recommend to do always do so when considering the evolution of the spiral intestine. However, we add the "serpentine" type to our states list, describing the very atypical shape of most holosteans (different from that of chondrichthyans; **Fig. 3A**). Ultimately, five primary types shall be defined based on the literature (**Fig. 3A**):

- **Simple valve** type: Characterized by a small typhlosole (central columella) that twists around itself within the intestine.
- **Funnel valve** type: Characterized by several stacked cones, with tips pointing anteriorly and bases being horizontal, spanning on the entire width of the intestine. The typhlosole in the center strongly supports the whole structure.
- **Column valve** type: Composed of a central typhlosole connected to the valve wall by horizontal plans arranged in a slightly inclined spiral. This structure resembles a wood auger. Horizontal plans extend across the entire internal width of the intestine.
- **Serpentine valve** type: Characterized by the absence of a typhlosole, together with short horizontal plans emerging from the valve wall, and arranged in a spiral, similar in inclination to that in the column valve type.

- **Scroll valve** type: Characterized by several antero-posteriorly extended layers interlocked one within one another like a rolled-up parchment or cigar.

The spiral valve is here confirmed a plesiomorphic character for gnathostomes (**Fig. 3B**). Indeed, its expression as a simple valve in both petromyzontids and extinct jawed vertebrates appears as a distinct innovation in these groups (**Fig. 3B**), making the spiral valve appeared twice within vertebrates. Out of the four states here considered valid, the funnel valve type appears as the ancestral type in gnathostomes. It is indeed spread across most taxonomic groups, even highly phylogenetically distant ones (**Fig. 3B**). Our reconstruction of ancestral characters at node also confirms two convergent transitions from the spiral intestine to the non-spiral intestines: one in tetrapods and one in teleosts. The column spiral valve type is present in three chondrichthyan orders (myliobatiforms, orectolobiforms, lamniforms) supporting three convergences, highlighting plasticity degrees in these spiral shapes (**Fig. 3B**). The serpentine valve would be a holostean synapomorphy. Finally, the scroll valve type appears exclusively in carcharhiniforms, such as sphyrnids and carcharhinids (**Fig. 3B**).

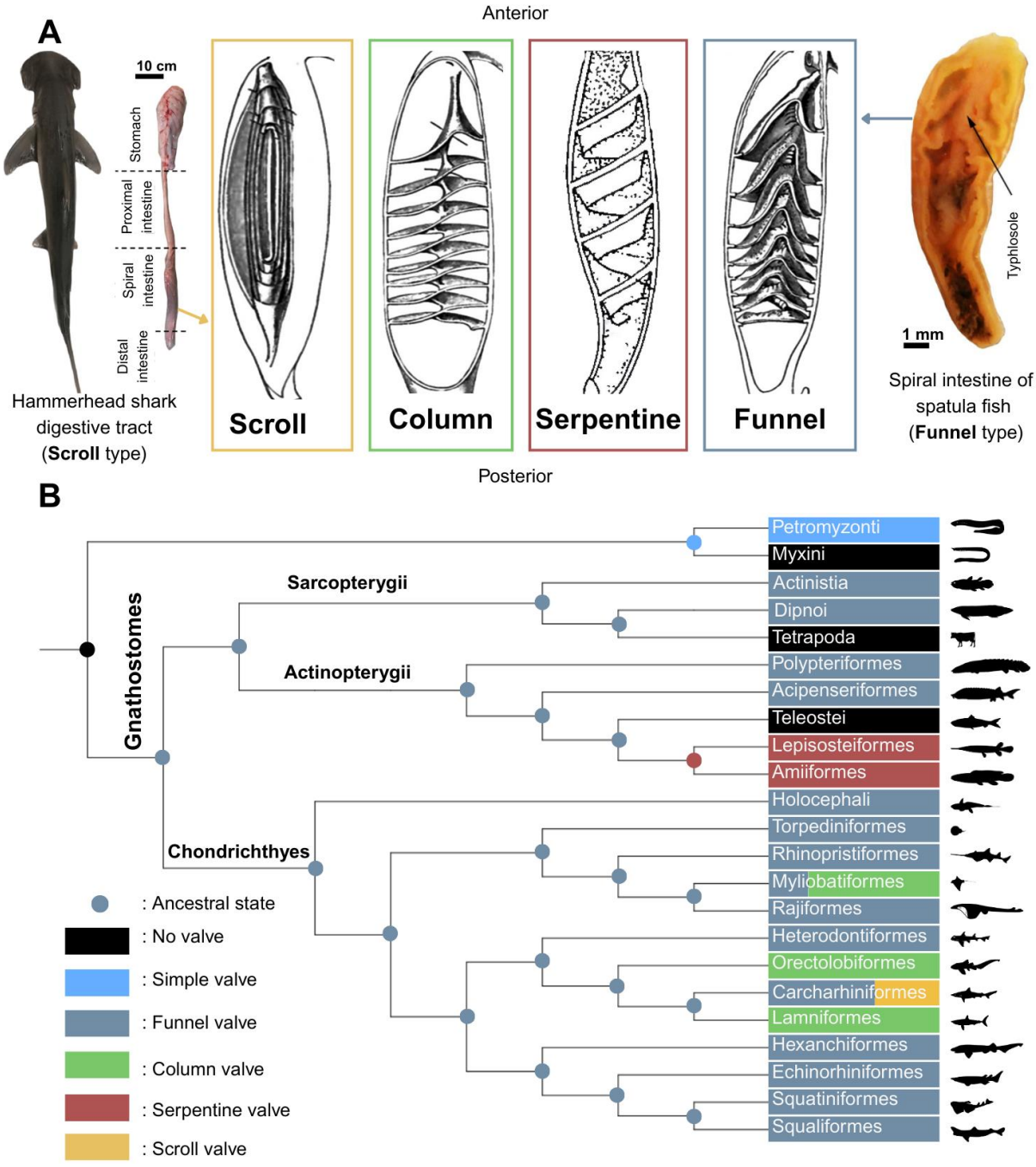

Figure 3. Description of the different forms of vertebrate spiral intestines and their evolution. A. Morphologies of spiral intestines (modified from Argyriou et al. 2016; Leigh et al. 2016). B. Simplified phylogenetic tree representing taxa with a valve (modified from Liem 1988; Kiraku and Kuratini, 2006; Mirande 2016; Amaral et al. 2018) and reconstruction of the ancestral state of the intestinal shape character.

Non-spiral coprolites (from external features)

- Cylindrical morphotype (**Fig. 4A–E**).

Abundance. 7 specimens/187

Diagnosis. Coprolites with an ovoid cross-section, a quite constant diameter and a width/length ratio about 2.5-3.5. Rounded ends.

Description. Most specimens with a highly constant diameter, such as MHNM.KK499 (**Fig. 4C**), including some with visible constrictions (such as MHNM.KK505, **Fig. 4D**). Average lengths: 4.9–9 cm, average width 3–3.2 cm. Coprolites corresponding to morphology B1 in Hunt and Lucas (2012a).

- Straight morphotype (**Fig. 4F**).

Abundance. 2 specimens/187

Diagnosis. Coprolites with an ovoid cross-section and a width/length ratio close to 4. Ends rounded when preserved.

Description. Most specimens ranging from 5.8 to 6.1 cm in length, average width around 1.5 cm. The only preserved end is located in MHNM.KK570. This type corresponds to morphology A4 and A5 in Hunt and Lucas (2012a).

- Rounded morphotype (**Fig. 4G**).

Abundance. 8 specimens /187

Diagnosis. Coprolites < 3.5 cm long, with a circular cross-section and a width similar in size to their length.

Description. Size variation is low for these specimens with a length between 1.8 and 3.3 cm and an average width between 1.4 and 2.2 cm. Some like MHNM.KK523 with a depression at one of their ends. This type corresponds to the C1 morphology in Hunt and Lucas (2012a).

Fourteen others are recognized as undetermined visibly non-spiral morphotypes (**Fig. 4H**).

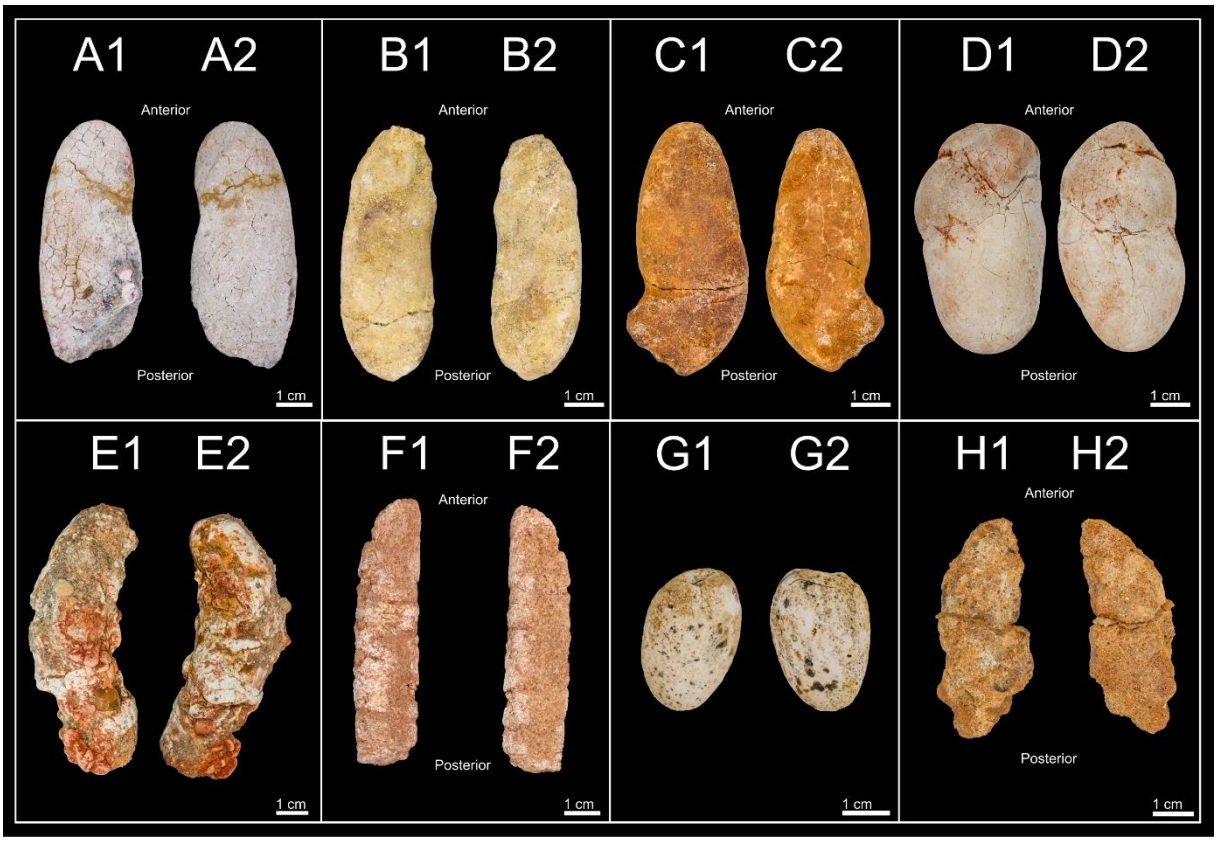

Figure 4. Non-spiral morphotypes in the Kem Kem coprolites. (A–E) Cylindrical morphotypes. A. MHNM.KK572 in longitudinal view (A1, A2). B. MHNM.KK571 in longitudinal view (B1, B2). C. MHNM.KK499 in longitudinal view (C1, C2). D. MHNM.KK505 in longitudinal view (D1, D2). E. MHNM.KK501 in longitudinal view (E1, E2). F. Straight morphotype. MHNM.KK570 in longitudinal view (F1, F2). G Rounded morphotype. MHNM.KK523 in longitudinal view (G1, G2). H. Undetermined morphotype. MHNM.KK503 in longitudinal view (H1, H2).

Spiral coprolites (from external features)

- Amphipolar morphotype (**Fig. 5A–C, Supp. Tab. 2**).

Abundance. 8 specimens/187

Diagnosis. Spiral portion > 75% of the total coprolite length.

Description. Whorls located on the posterior part of the specimens (Hunt and Lucas 2012a). Average lengths 2.5–8.5 cm and average width 1.3–4.4 cm. Whorl angles with vertical 4–40°, whorl heights 0.3–1.7 cm, with high variance in all specimens. Three described morphogenera are recognized in the amphipolar specimens of the assemblage: four specimens of *Crassocoprus* (Hunt et al. 2012a), two specimens of *Hyronocopros* (Hunt et al. 2005), and one of *Elacacoprus* (Hunt et al. 2012a). This type of coprolites corresponds to the F2 morphology in Hunt and Lucas (2012a).

- Heteropolar morphotype (**Fig. 5D–F; Supp. Tab. 2**).

Abundance. 7 specimens/187

Diagnosis. Spiral portion < 75% of the total coprolite length.

Description. Whorls located on the posterior part of the specimens (Hunt and Lucas 2012a). Average lengths 4–12 cm and average width 2–4.1 cm. Whorl angles with vertical 2–18°, whorl heights 0.3–1.1 cm, with moderate variance in all specimens. Three described morphogenera are recognized in the heteropolar specimens of the assemblage: four specimens of *Saurocopros* (Hunt et al. 2007), one of *Heteropolacopros* (Hunt et al. 1998), and one of *Malericopros* (Hunt et al. 2007). This type of coprolite corresponds to morphology F3 and F4 in Hunt and Lucas (2012a).

Most spiral coprolites are incomplete and cannot be assigned to the different heteropolar or amphipolar morphogenera described in the literature. The organisation of the faecal matrix was in this case used to further describe the polarity of the incomplete spiral material.

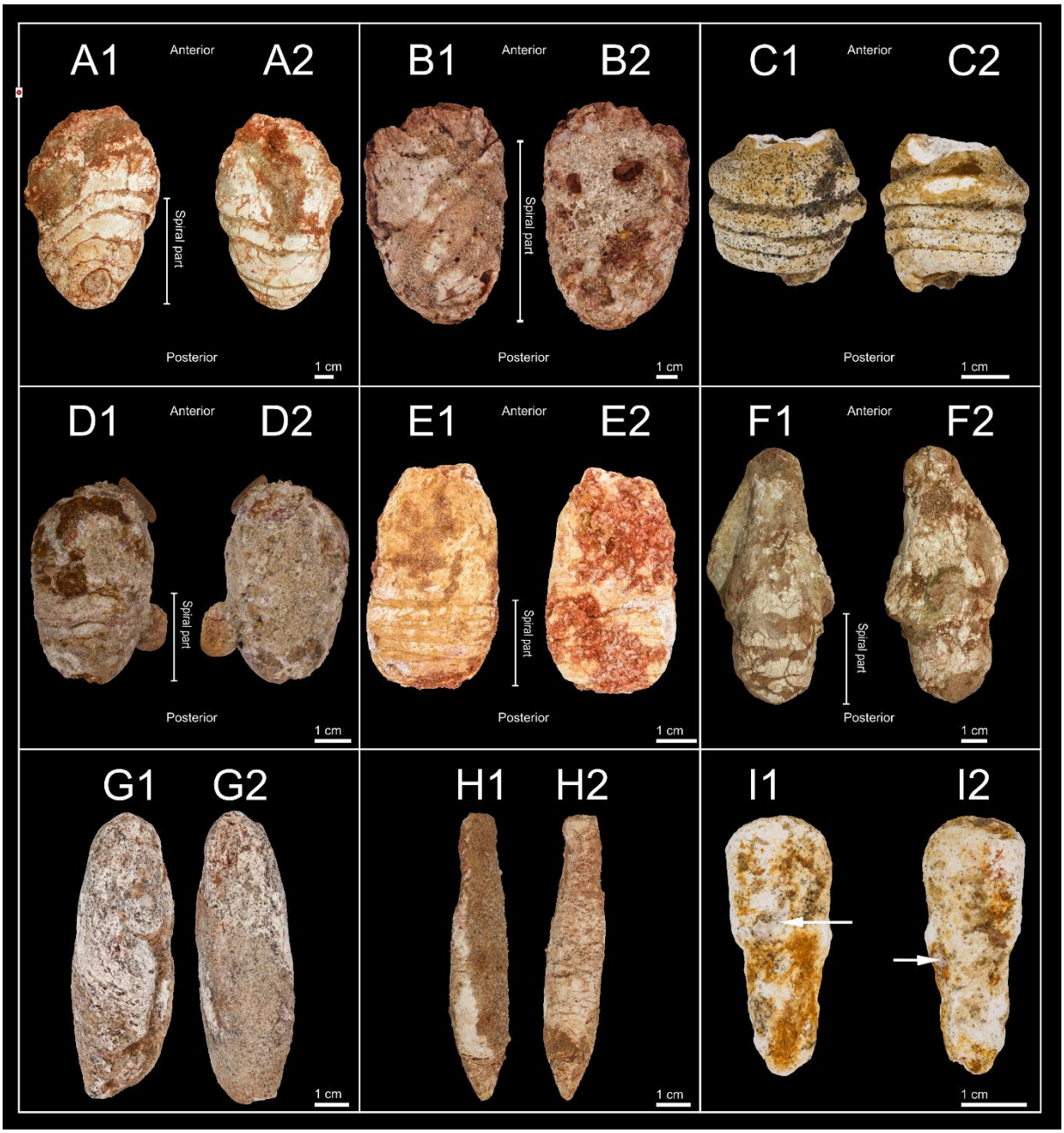

Figure 5. External morphotypes of the spiral coprolites from Kem Kem. (A–C) Amphipolar morphotypes. A. MHNM.KK420 in longitudinal view (A1, A2). B. MHNM.KK430 in longitudinal view (B1, B2). C. MHNM.KK456 in longitudinal view (C1, C2). (D–F) Heteropolar morphotypes. D. MHNM.KK436 in longitudinal view (D1, D2). E. MHNM.KK423 in longitudinal view (E1, E2). F. MHNM.KK487 in longitudinal view (F1, F2). G. Scroll morphotype. MHNM.KK488 in longitudinal view (G1, G2). (H–I) Spiral morphotypes with almost invisible whorls. H MHNM.KK497 in longitudinal view (H1, H2). I MHNM.KK522 in longitudinal view (I1, I2). White arrows pointing toward surface bone inclusions.

Spiral coprolites (from external and from internal features)

- Scroll (**Figs. 5G–I, 6E, Supp. Tab. 2**).

Abundance. 3 specimens /187

Diagnosis. Visible outer whorl forming a lip along the coprolite entire length giving a cigar-like appearance. Spires internally rolling up as parchment pages.

Description. Average length 4–8 cm and average width 1.9–3.4 cm. Many spiral specimens without evidence of the encompassing outermost lip whorl at surface (**Figs. 5G, 6E1–E3**). All specimens made of three whorls, the height of which vary little proportionally to coprolite length (0.1–0.18). This coprolite type corresponds to morphology F1 in Hunt and Lucas (2012a). All specimens are assigned to the described morphogenus *Bibliocoprus* (Hunt et al. 2012b). One with skeletal inclusions.

Spiral coprolites (from internal features)

- Funnel (**Fig. 6A–D, Supp. Tab. 2**).

Abundance. 24 specimens / 58 scanned

Diagnosis. Whorls forming cones nested within each other in longitudinal section. Cone tips are pointing anteriorly.

Description. Specimens with a highly variable number of whorls and height of whorls. Four groups are distinguished primarily based on the number of whorls. They have, respectively, an average of four (**Fig. 6A1–A3**), seven (**Fig. 6B1–B3**), ten (**Fig. 6C1–C3**), and fourteen (**Fig. 6D1–D3**) internal whorls. Some specimens contain a central cavity corresponding to the typhlosole found in the spiral intestine of modern animals (**Fig. 6F1–F3**). Among these 24 specimens, two show skeletal inclusions.

- Undetermined morphotypes

Abundance. 8 specimens / 58 scanned

Description. These coprolites do not contain visible whorls as in the other morphotypes, but the material within them is clearly organized in a helix, with no discernible whorl boundaries. An orientation across the entire internal part of the specimen can only be due to the presence of an originally spiral intestine (**Fig. 5H–I)**. Among these eight specimens, five present skeletal inclusions, i.e. more than 50% of the coprolites in this group.

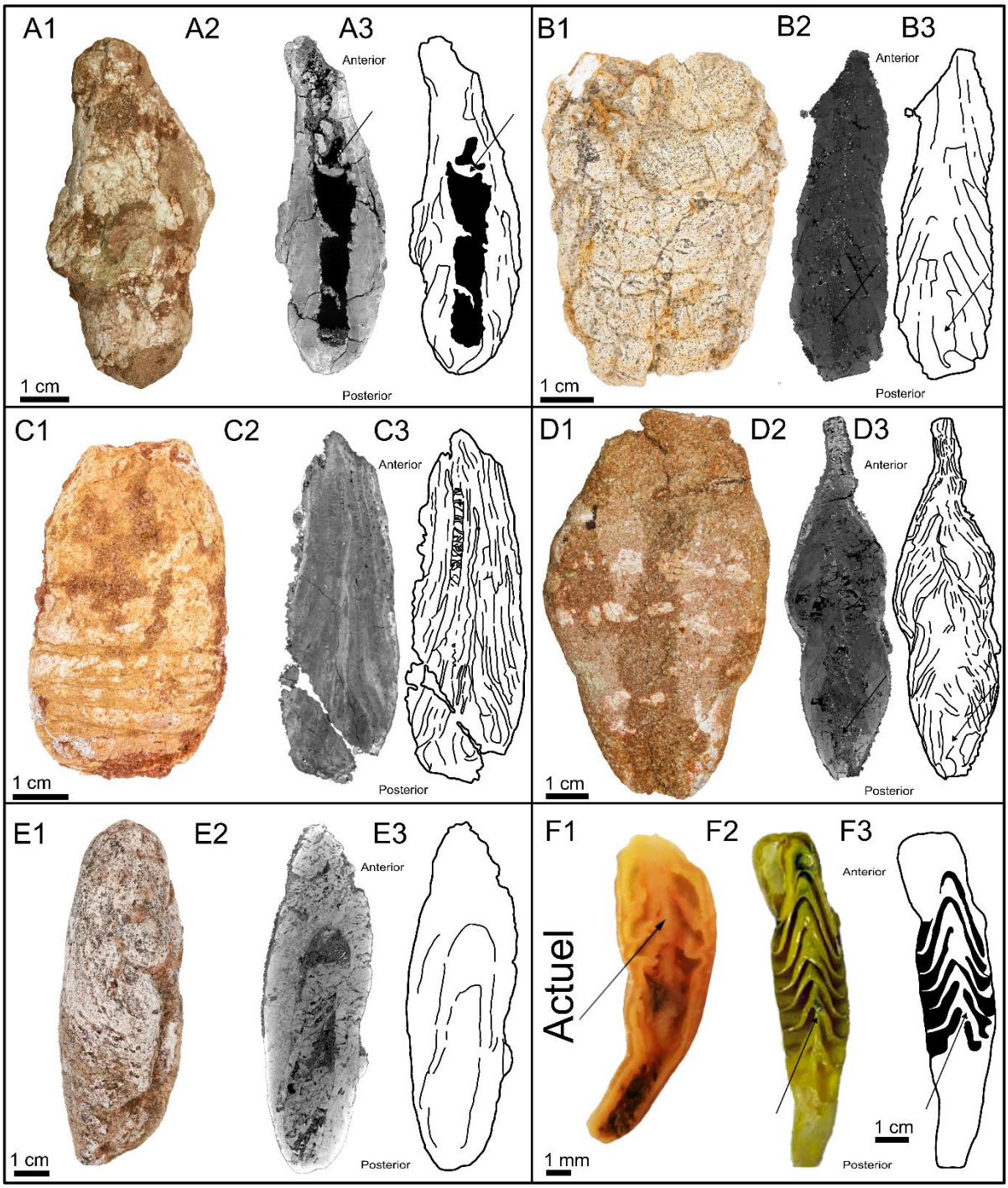

Figure 6: **Internal morphotypes of the Kem Kem spiral coprolites**. A–D. Funnel morphotypes; E. Scroll morphotype; F. Vertebrate modern spiral intestines for comparison. A. MHNM.KK487; B. MHNM.KK424; C. MHNM.KK423; D. MHNM.KK509; E. MHNM.KK488. 1. Longitudinal external views, 2. Axial tomographic virtual sections, 3. Interpretative drawings of (2). F1. Axial section of chondrostean fish *Polyodon spathula* (Argyriou et al. 2016); F2. Axial section of dipnoan fish *Neoceratodus forsteri* (Hassanpour and Joss 2009); F3. interpretative diagram of (F2). Black arrows indicate intestinal typhlosoles.

Statistical discrimination of coprolite shape

Multivariate analysis of the global shape of all coprolites

A Principal Components Analysis was used to compare coprolites relative shape (e.g. general dimensions variables) and degrees of compressions both in spiral (n = 129) and in non-spiral coprolites (n = 28). PC1 and PC2 account for all the variance among the dataset, in relatively comparable proportion (PC1= 60% and PC2 = 40% of variance) comprising similar contributions from L, w_{max} and w_{sec} (≈ 33% each) in opposite directions. As a result, degrees of compressions group separately following a gradation of degrees "flattened", "slightly flattened" to 'not flattened" coprolites, from negative/low to positive/high PC2 values. A linear regression model (p-value = $4.4e^{-12}$, R = 0.3) indicates that the relative shape of the coprolites depends on degrees of compression. On the opposite, spiral and non-spiral coprolites largely overlap on the entire morphospace. When tested by linear regression model, the variation of the relative shape is not linked to the spirality feature (p-value = 0.12). This hold true even in the case of selecting only the non-flattened portion of the coprolites (p-value = 0.84); implying that, in this setting of the Kem Kem, both spiral and non-spiral types of producing intestines had been of comparable diameters.

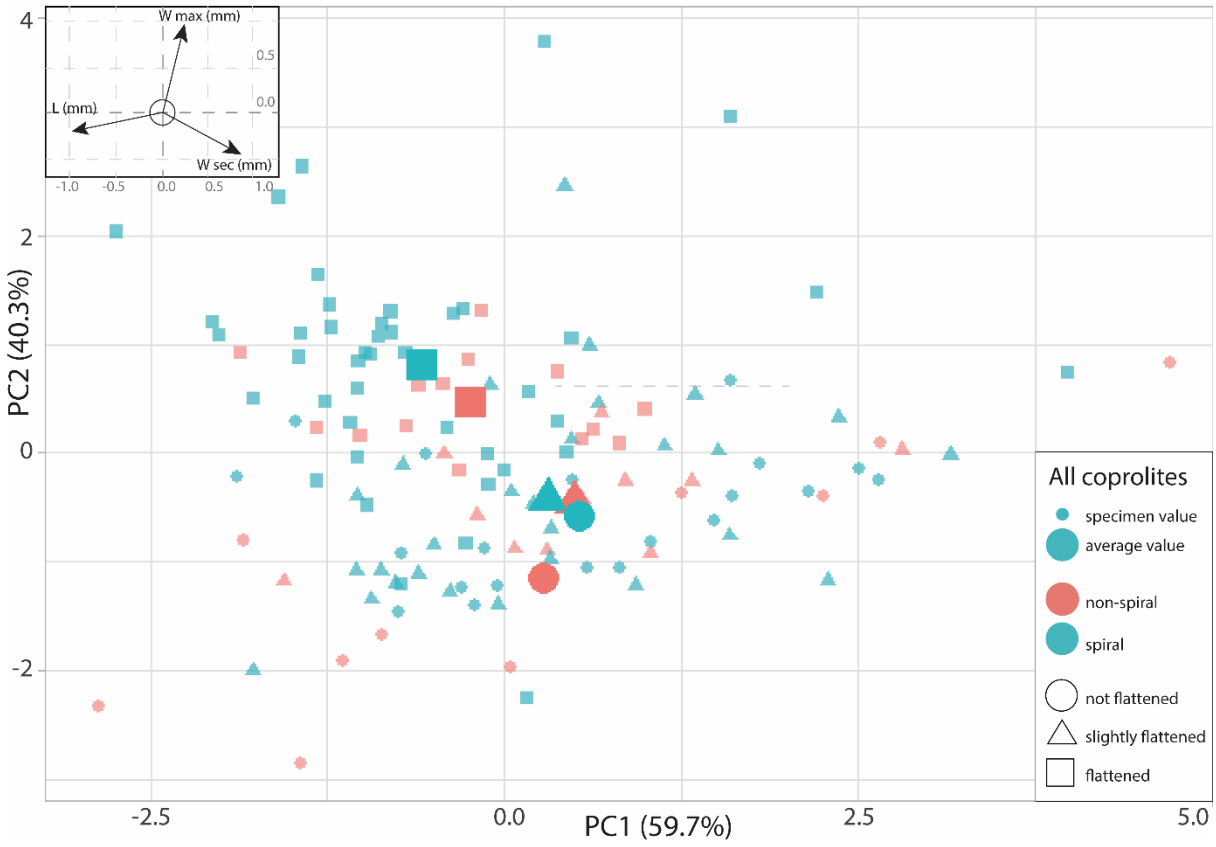

Figure 7. Multivariate analysis on all the Kem Kem coprolites. Principal Components Analysis of the externally observed global shape (= general dimensions) and the degrees of compression in all coprolites.

Multivariate analysis of the externally observed features of spiral coprolites

A Linear Discriminant Analysis was applied on spiral coprolites to identify the variables (among spiral part length, external whorl angles and widths, number of whorls, heteropolarity rate) explaining at most the heteropolar (n = 20) vs amphipolar (n = 10) morphologies of these types. The entire dataset variance is explained by LD1 (LD2 = 0%; **Fig. 8A)** revealing the highly dominant (and almost exclusive) contribution of the variable "number of external whorls" explaining the distribution of the data on the LD1 horizontal axis (**Fig. 8A**). The provided prediction model reveals separated heteropolar vs amphipolar clusters (**Fig. 8A**); the Kem Kem heteropolar spiral coprolites bear significantly more whorls than amphipolar spiral ones. It is noteworthy that polarity assignment is here only poorly predicted by the model (**Fig. 8A**); however, morphotypes can be robustly differentiated by their numbers of surface whorls (p-value = $0.4e^{-3}$, $R^2 = 0.42$).

Multivariate analysis of the internally observed features of funnel-type coprolites

While externally observed features do not allow the recognition of specific spiral valve types, internally and especially topographically investigated specimens (n = 54) allowed to identify several of the valve-types reported in Parker 1880 (updated with exclusion of the non-existing Type C, see 4.1. *Real variability of modern spiral intestines*). Here, 23 funnel-valve types of coprolites were recognized along with three scroll ones (**Supp. Tab. 2**). The shape of the funnel-valve types was explored with a Partitioning Around Medoids clustering (Reynolds et al. 2006) on a Principal Component Analysis of the internally observed general dimensions (L and w_{mean}) and spiral relative dimensions (number of internal whorls, H_{mean}, H_{var}, **Supp. Tab 2**). The PAM evidenced four significantly different clusters tested by bootstrap resampling, with values between 0.73 and 0.87 (valid stable cluster show mean bootstrap similarity ≥ 0.75; Hennig 2008; **Fig. 8B**). The plotting of *funnel group 1* (p-value = 0.83) on the positive PC1 side (= 68% of the variance) indicates it displays higher whorls on average than all other groups, with considerable whorl height variance in a single specimen (**Fig. 8B**). *Funnel group 2* (p-value = 0.86) displays more constant whorls height than the rest of the groups. *Funnel group 3* (p-value = 0.73) and *funnel group 4* (p-value = 0.87) are similar to *funnel group 2* but exhibit more whorls (with *funnel group 4* displaying more whorls than *funnel group 3*; **Fig. 8B**).

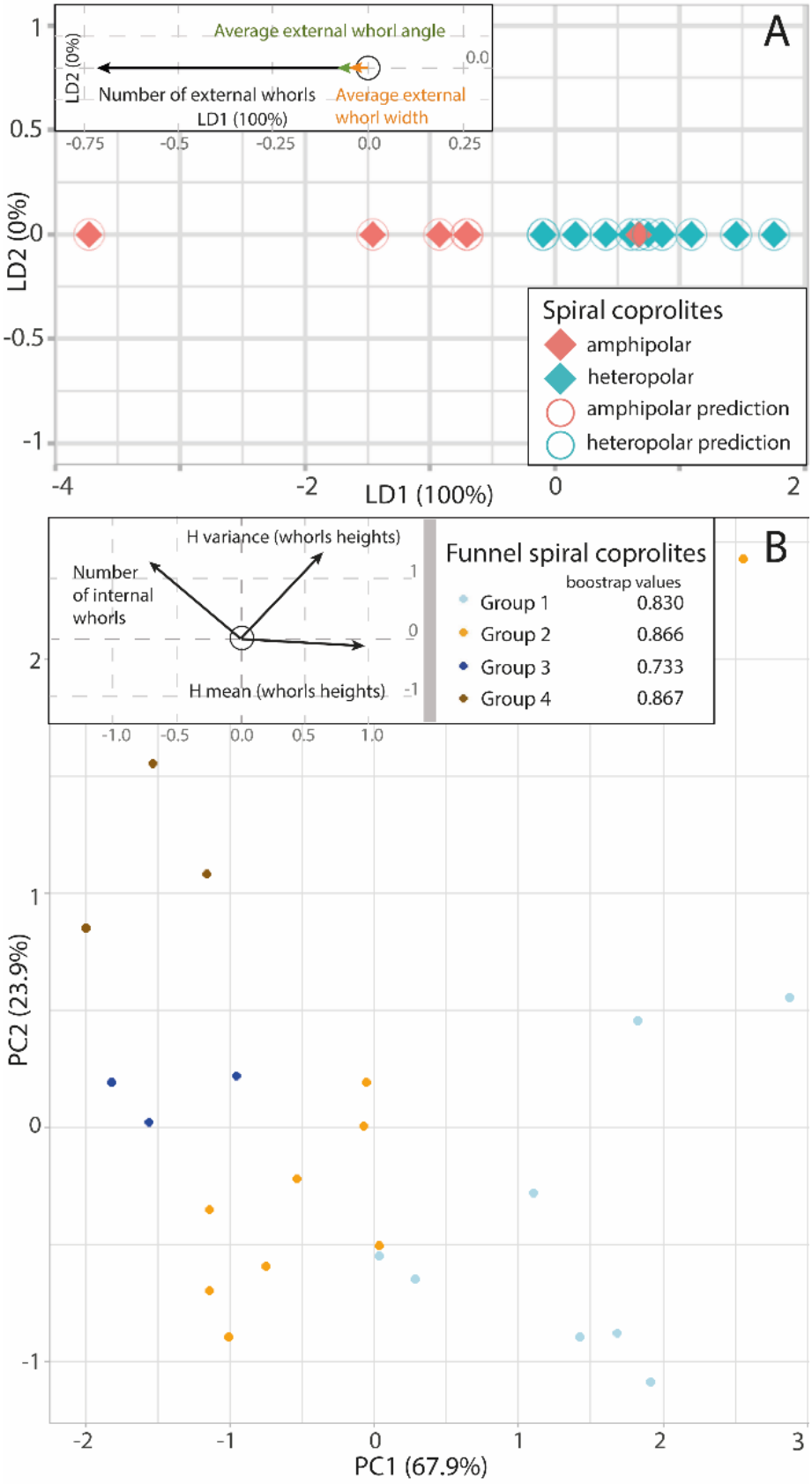

Figure 8. Multivariate analyses on the spiral coprolites only (on externally and internally observed features). A. Linear Discriminant Analysis of externally observed spiral features and their relative

dimensions. B. Principal Components Analysis with Partitioning Around Medoids clustering (internally observed features only).

Internal inclusions evidenced by tomography and thin sectioning.

Out of the 54 scanned specimens, ten revealed large enough skeletal inclusions. Most of the inclusions correspond to hard remains, which do not allow for a diagnosis of the possible vertebrates that may have been ingested. The vast majority of inclusions found are scales. In the spiral coprolite MHNM.KK443, numerous ganoid scales form one of the whorls (**Fig. 9A–B**). They show a typical diamond-rhomboedral shape, no ornamentation, and an average size of approximately 5 mm. According to the fish assemblage known from the Kem Kem beds, these scales could belong to the stem lepidosteid *Oniichthys* (Cavin and Brito 2001, Cavin et al. 2015). Other scales are present in the spiral MHNM.KK477 (**Fig. 9D)** with average length being 5 mm for the largest scales. The diamond shape and the ornamentation of a main ridge on this scale are characteristic of the species *Obaichthys africanus* for the Kem Kem (Meunier et al. 2016). Other bones are present, but their interpretation is often more difficult. Nevertheless, a few actinopterygian vertebrae and a possible preopercularis (**Fig. 9C**) were identified. This bone has a sigmoid shape, and numerous radially arranged canals are visible on its internal portion (**Fig. 9C2**). Out of the 20 coprolites examined in thin-sections, only one contained large skeletal inclusions consisting of three similar vertebrae and unidentified short bone elements.

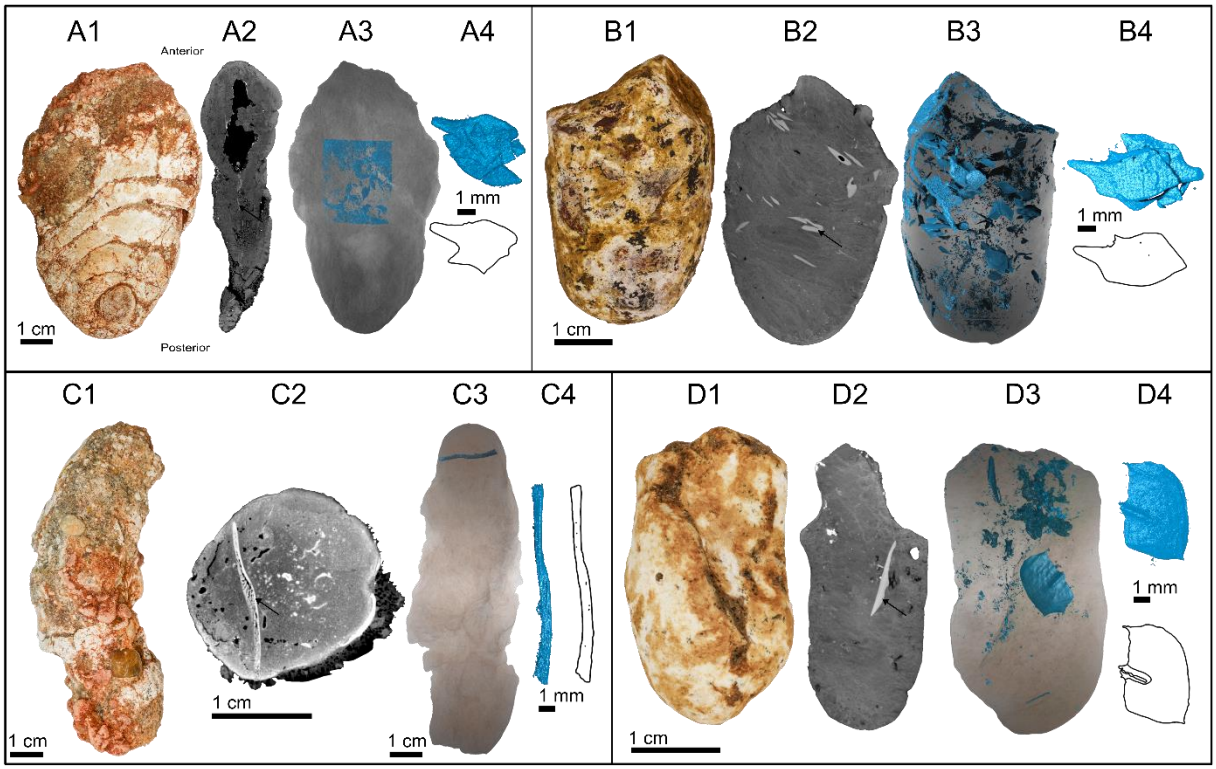

Figure 9. Various skeletal inclusions within coprolites. A. MHNM.KK420. B. MHNM.KK443. C. MHNM.KK501. D. MHNM.KK477. 1. External longitudinal view; 2. Longitudino-central tomographic virtual section, 3. Segmented skeletal inclusions *in situ*, 4. Selection of segmented inclusions and their interpretative drawing: ganoid scale (A); ganoid scales (B), pre-opercular bone (C); *Obaichthys africanus* ganoid scale (D). Black arrows indicate skeletal inclusions.

Length assessment of the animal producer

Only a handful of study have simultaneously reported producer and faeces dimensions, while simply no study have applied linear regression to spiral faeces and producers' sizes. Gathering the very limited literature existing on the topic (excreted modern crocodilian faeces from Milan 2012; in situ small-spotted catshark faeces in McAllister 1985 and saurichthyid cololites from Argyriou 2016; **Supp. Tab. 3**), we obtained two linear regression models (significant for non-spiral faeces, p-value = $2.63e^{-7}$, R^2 =0.83; non-significant for spiral faeces, n = 4) for the assessment of the length of the Kem Kem coprolite producers (**Fig. 10**). Cylindrical-straight morphotypes (1.5–3.2 cm in diameter) provide together an animal length estimate of 64–180 cm. Rounded morphotypes (1.2–1.7 cm in diameter) gives an estimated animal size of 61–75 cm. Funnel types ranges from 1.7 to 4.3 cm in diameter, indicating a 40–110 cm size range for their producers; with *funnel group 1* producer: 1.16–2 m, *funnel group 2* producer: 92–1.78 m, *funnel group 3* producer: 1–1.35 m and *funnel group 4* producer = 1.60 m. Scrolls' producers are estimated as animals 1–1.7 m long.

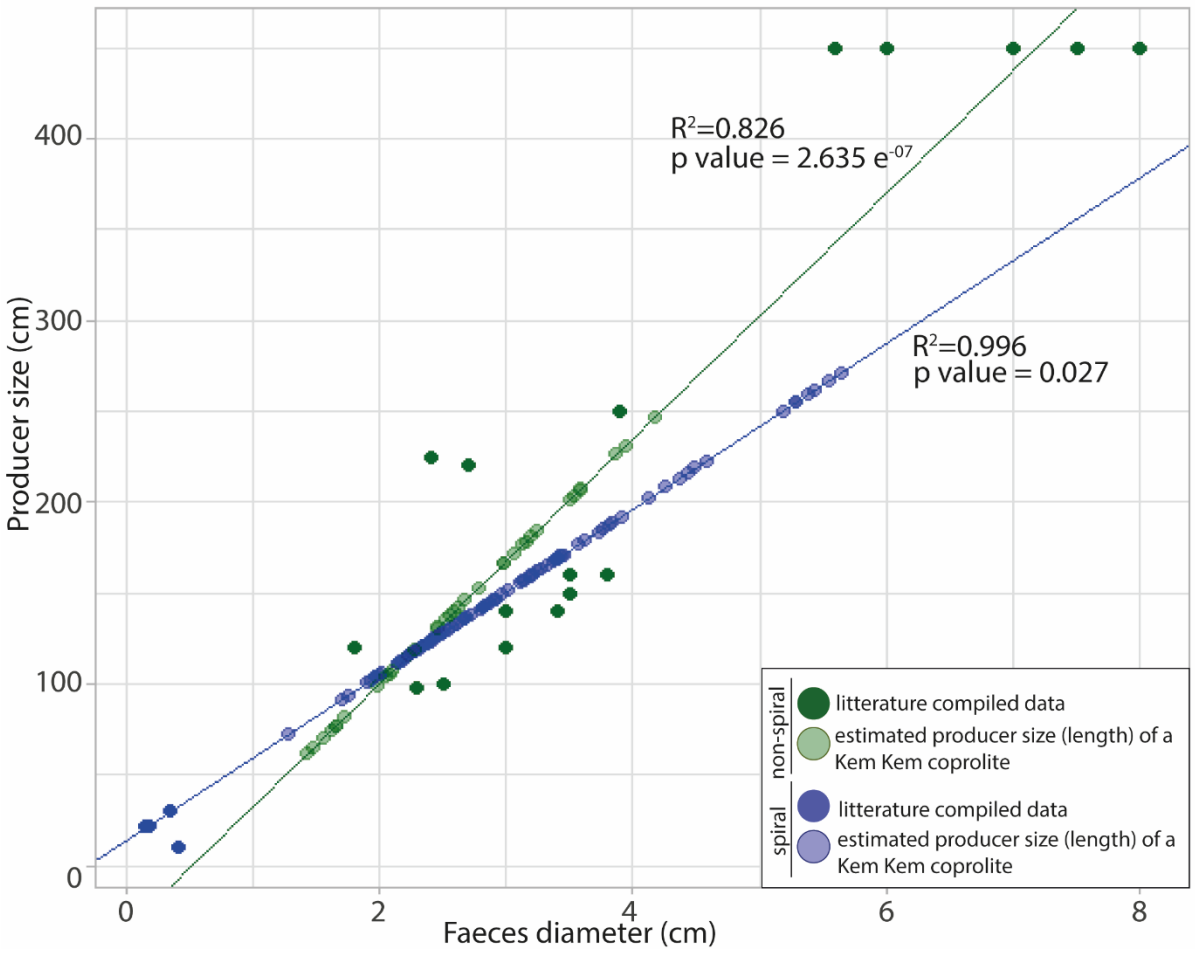

Figure 10. Linear regression models linking producer size vs faeces diameter, obtained for the assessment of the length of the Kem Kem coprolite producers from gathered relevant literature (see **Supp. Tab. 3**).

Discussion

Evolution of the spiral valve

The reconstructed evolutionary pattern involves degrees of transformation between some of the valve character states. Studies only recently explored which evolutionary constraints could have forced drastic changes in the shape of the gut spiral valve. When comparing valve variety within chondrichthyans, it appears that these significant changes are not linked to differences in diet (Leigh et al. 2021). Interestingly, no alternative hypothesis for such changes has been so far been suggested in the literature. At birth, the spiral valve is generally fully formed and remains morphologically stable throughout the whole individual life (Theodosiou and Oppong 2019). Ontogenetically, it is known that the spiral valve forms through an asymmetric mesenchymal growth occurring during the embryogenesis. This asymmetry is at the origin of the formation of a fold elongating and coiling helically along the main conduct (Theodosiou and Oppong

2019), creating the spiral valve wall. Such simple conformation is the one observed in petromyzontids. The funnel-type morphology develops through the additional formation of horizontal walls that progressively tilt, forming stacked, cone-shaped layers with apices directed anteriorly. Whorls first form horizontally before forming anteriorly oriented cones (Theodosiou and Oppong 2019). Therefore, the transition to a columnar valve could result of a simple pedogenesis during embryonic development from the posterior side, omitting - posteriorly first - the secondary tilting. Such transitionary event is suggested by the double existence, in some orectolobiforms, of both anterior funnel-type whorls and posterior column-type whorls in one same spiral valve (Borucinska and Caira 1993), indicating plasticity between these two morphologies and likely explaining the minimal three convergences. The scroll-type restricted to Carcharhiniforms may result from one event of extreme modification of the funnel type (McAllister 1985), with antero-posterior elongation of walls along the typhlosole. The number of whorls within the spiral valve shows little intraspecific variation (Chu et al. 1986, Compagno 1988), but important interspecific variation, which does not appear to follow phylogenetic trends. This variability may rather be correlated to body size (Argyriou et al. 2016).

Relevance of descriptive features of spiral coprolite for producer assignments

The polarity of a spiral coprolite as always been largely considered as diagnostic feature for producer assignment (cf. introduction). Heteropolar morphology is assigned to chondrichthyans; amphipolar morphology is assigned to non-teleost actinopterygians or non-tetrapod sarcopterygians (Eriksson et al. 2011, Anagnostakis 2013, Dridi 2018). The latter is based for amphipolarity on the few reports of modern dipnoan and gar-fish faeces (Dean 1903, Williams 1972; no reports for modern actinistians, polypteriforms, acipenseriforms nor halecomorphs), as well as fossil holostean cololites. Heteropolarity is assigned to chondrichthyans from modern shark's valve dissections (McAllister 1985), as well as from cololite reports. For instance, *Scyliorhinus* revealed "consolidated" faecal material exiting the intestine is spiral-shaped, consistent with some fossil coprolites (McAllister 1985). However, no modern shark faeces have yet been ever documented, which raises doubts on the assignment of the abundant heteropolar fossil faeces to extinct chondrichthyans. Little is actually known on if these morphologies reflect true differences in producers' valve morphology, diet (see McAllister 1985) or faeces excretion modes. Here, our results however suggest that external features of polarity are likely to discriminate producer taxonomic differences, being driven by

a different number of externally visible whorls. The sole character of external polarity (amphipolarity vs heteropolarity) can therefore indeed be reflective of producers' differences, but is not necessarily always driven by such extraspecific feature. On top of that, and accounting for the limited proportion of 58 scanned specimens, features as the numbers of whorls whorl angle and whorl heights (**Supp. Tab. 2**) are readily more often accessible as internally observed features than externally. In our case, internally measured features have has allowed for the detection of more statistically supported morphological groups of spiral coprolites (their vast majority being of the funnel type) than using externally measured ones.

Taxonomic attributions of producers

Associating coprolites with ancient intestinal morphologies, implies to validate correspondence with modern faeces morphology. However, little information exists on the faecal morphology of non-mammalian vertebrates (Seton 1925, Halfpenny 2015, Robin et al. 2016, Rozada et al. 2024, Rey et al. 2026). Indeed, no reliable chondrichthyan faeces has ever been identified either in the literature (Dean 1903, McAllister, 1985). Additionally, zoos and sea parks are always negative at recovering chondrichthyan faeces, the latter immediately disintegrating in water after being expelled (multiple pers. comms., e.g. P. Ternat, Oceanopolis Brest; V. Pueyo, Aquarium St. Malo, France; L. Peel, Western Australia Uni., Australia, France) at the exception of in the case of some rays. Indeed, *Raja clavata* appears to produce stable faeces (pers. comm. N. Hirel, Planet Ocean Montpellier, France). Spiral faeces are observed for dipnoans (Dean 1903), with morphology varying according to age and diet (pers. obs. A. Kemp, Queensland Uni., Australia; L. Gesch, https://www.areallycrappystory.com/, USA). Juvenile individuals produce non-spiral faeces, which become spiral after several weeks, indicating changes either in diet or in the intestine formation at this early stage. Deposited spiral faeces are reported in gar-fish (*Lepisosteus*, Williams 1972).

Non-spiral coprolites

Cylindrical and straight coprolites provide an animal length between 64 and 180 cm. These morphotypes correspond to coprolites most often attributed to crocodylomorphs (Halaçlar et al., 2023; Rozada et al., 2024). Indeed, this form of dropping is observed in extant crocodylomorphs (Milàn, 2012; Rozada et al., 2024). Furthermore, some specimens (e.g. MHNM.KK499) have an angular break along their length axis (**Fig. 4C**). This rupture could be explained by the fact that its producer had its cloaca close to the ground during excretion,

modifying the cylindrical shape of the excreted faecal matter (Milàn, 2012). Out of the six scanned specimens, one contains skeletal inclusions occurring in small quantity, though well preserved (**Fig. 9C**). Apart from this specimen, this suits what is known for the digestive system of crocodylomorphs (Milàn 2012), letting aside it could totally fits that of other archosaurs as pterosaurs or theropods of the Kem Kem whose digestive system is not readily accessible for accurate comparison (Chin et al. 1998; Farlow 2012, Rozada et al. 2024). The rounded morphotypes can be attributed to small tetrapods, but do not allow for a more precise attribution. Taking into account the Kem Kem faunal list, these faeces could also be attributed to lissamphibians or non-ophidian squamates (**Fig. 12F–G**). Turtle and snake droppings displaying rather elongated shape are less likely to be their producers (Brachaniec et al. 2022, Falcón et al. 2020).

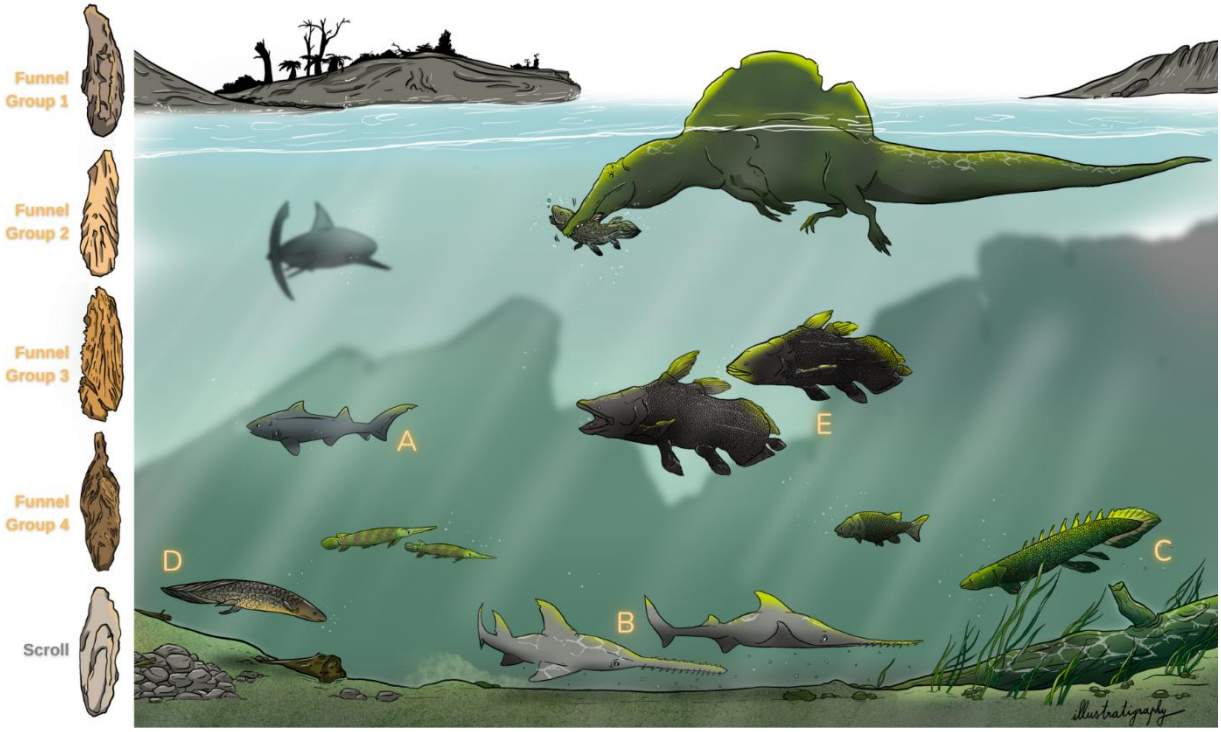

Figure 11. Synthetic producer-assignations of the five significantly differing categories of spiral coprolites. Funnels groups 1–4 assignable to either (A) distobatid Hybodontoidea, (B) Batoidea (*Onchopristis numidus*), (C) Cladistia (*Bawitius* sp.), (D) Dipnoi (*Arganodus tiguidens*is) or (E) Actinistia (*Axelrodychtys lavocati*). Scroll lacks being assignable by actualism. Tetrapods (*Spinosaurus aegyptiacus*), lamniform sharks (a galeomorph) and holostei (*Adrianaichthys pankowskii* and *Obaichthys africanus*) are excluded producers. Illustration by L. Thibault.

Spiral coprolites

A funnel morphotype could have produced correspond to the majority of Kem Kem taxa with a spiral valve. Only lamniforms and holosteans can be excluded, suggested to already have

583 acquired respectively a column-valve and a serpentine valve (**Fig. 3A, Fig. 11**). Possible
584 remaining producers attaining 110 cm in length are distobatid hybodontiforms, the batoid
585 *Onchopristis*, the cladistia *Bawitius*, the lungfish *Neoceratodus*, and mawsoniid actinistians
586 (**Fig. 11A–E**). The four identified funnel groups, defined on different numbers of internal
587 whorls, indicate four potential producers for these coprolites. However, in the herein tested
588 coproassemblage, the coprolite size is not correlated with the number of whorls (p-value = 0.63,
589 see **SI**). This aspect differs from what has been observed for modern intestines (Argyriou et al.
590 2016). As a consequence, and awaiting for the discovery of fossil intestines preserved in situ in
591 the Kem Kem fauna, results prevent further attribution (**Fig. 11A–E**). The scroll morphotype is
592 nowadays solely present in carcharhiniforms, the latter being never reported from the Kem Kem
593 fauna (Ibrahim et al. 2020). We suggest the possible earlier appearance (by convergence) of a
594 scroll-type spiral valve in the vertebrates represented at that time. Indeed, scroll-shaped
595 coprolites are found in the Paleozoic (Gilmore 1992) well before the appearance of the order
596 Carcharhiniformes. The scroll-type specimens here recovered are 1.9–3.4 cm. The scroll
597 morphology being very specific, the previously used linear regression shall not be used for
598 producer estimate. However, based on the intestine width of a hammerhead shark (Jhaveri et
599 al. 2015) a cross product gives a minimum size range 60–120 cm long. This corresponds to the
600 minimum size for its producers, knowing that the smallest coprolite contains a scale of
601 *Obaichthys africanus*, an animal measuring between 30 and 60 cm (Cavin et al. 2015). This
602 size does not provide constraints allowing discrimination of taxa (**Fig. 11**). The Kem Kem
603 assemblage provides no evidence for the column-like specimens to be identified. This absence
604 could correspond to a collection bias, as lamniforms are relatively rare in the formation. It could
605 also suggest that the mid-Cretaceous lamniforms had their funnel-type valve yet non-modified
606 into the modern column-type. The same applies to the serpentine-type of valve and holosteans,
607 present in much larger amount in the Kem Kem.

608 **Conclusion**

609 This Kem Kem coproassemblage (almost 200 fossil faeces) provides an unprecedented
610 opportunity to accurately estimate vertebrate producers' diversity from retrieved Mesozoic
611 faeces. It demonstrates that both tetrapod and non-tetrapod faeces were likewise deposited and
612 preserved at burial and deposit, but that it was mostly four different types of non-tetrapod
613 producers (with funnel-type spiral guts and one another with a scroll-type spiral gut
614 representing an extinct convergence) which were the most prompt to deposit faeces in the

system. Globally, in the sample locality, spiral and non-spiral types were produced by intestine of comparable diameters. The assemblage evidences that external features can be indicative of interspecific differences of the producers, but that equivalent internally measured features are more efficient at indicating groups of producers. The absence of specific types of valves in the assemblage corresponding to likely abundant taxa (e.g. holosteans) could evidence some ancestral state of the spiral valve in the mid-Cretaceous, relatively to its suggested evolution among vertebrates.

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