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A new ichnotaxonomic name for burrows in vertebrate coprolites from the Miocene Chesapeake Group of Maryland, U.S.A

Stephen J. Godfrey^{1,2} and Alberto Collareta^{3,4*} 

Abstract

A new ichnotaxonomic name, *Transexcrementum cuniculus*, is applied to tubular (cylindrical) tunnelings in coprolites. The type series of *T. cuniculus* consists of burrowed vertebrate (probably crocodilian) coprolites that originate from the Miocene Chesapeake Group of Maryland, U.S.A. These complex trace fossils exhibit the following combination of characters: burrows not lined nor backfilled; opening and transverse sections sub-circular; diameter supra-millimetric, up to ca. 20 mm, rather constant throughout; inner termination(s) rounded/conical; tunnel morphology straight or gently curved, sometimes branching; internal sculpturing sometimes present in form of short and irregularly oriented scratches and gouges. Clusters of the same kinds of gouges may also mark the outer surface of the coprolite. The tunneling tracemaker likely engaged in coprophagy; however, it is unclear what kind of organisms could have produced these burrows. Judging from the overall rarity of *Transexcrementum cuniculus* occurrences in the fossil record, the tracemaker responsible for the burrows might also have been rare, or fed on faeces only occasionally.

Keywords: Burrowed coprolites, Calvert Cliffs, Calvert Formation, Choptank Formation, Coprophagy, *Transexcrementum* igen. nov., *Transexcrementum cuniculus* isp. nov., Langhian, Serravallian, *Thecachampsa*

Introduction

For much of the Miocene epoch (from approximately 22–8 Ma), the Chesapeake Bay region (i.e., the Salisbury Embayment) was intermittently flooded by the Atlantic Ocean. Some of the continental siliciclastic sediments that were laid down therein are now exposed as sea bluffs along the western shore of Chesapeake Bay and are known as Calvert Cliffs (Fig. 1). These naturally eroding cliffs abound with marine fossils, including the tests of planktonic organisms, shelled invertebrates, shark teeth, teleosts, marine mammals, and many other kinds of fossils numbering over 650 taxa (Godfrey, 2018; Vogt et al., 2018). In addition to innumerable body fossils, Calvert

Cliffs preserve trace fossils including invertebrate burrows (*Thalassinoides*, *Gyrolithes* and *Ophiomorpha*; Kidwell et al., 2015), shark bite marks, usually on cetacean bone (Godfrey, 2003; Godfrey et al., 2018; Godfrey & Lowry, 2021), and coprolites (Godfrey & Smith, 2010; Godfrey et al., 2022; Kent, 2018; Weems, 2018; Wetmore, 1943).

Coprolites attributed to the large marine crocodile *Thecachampsa* (Weems, 2018) are amongst the largest and most commonly found. Recently, one of these large vertebrate coprolites was reported as having been burrowed into by an unknown organism (Godfrey et al., 2022). The tunneling organism was thought to have engaged in coprophagy. Here, we describe that complex trace fossil and others like it. Because these burrows are unique in the fossil record, they are assigned herein to a new ichnogenus and ichnospecies.

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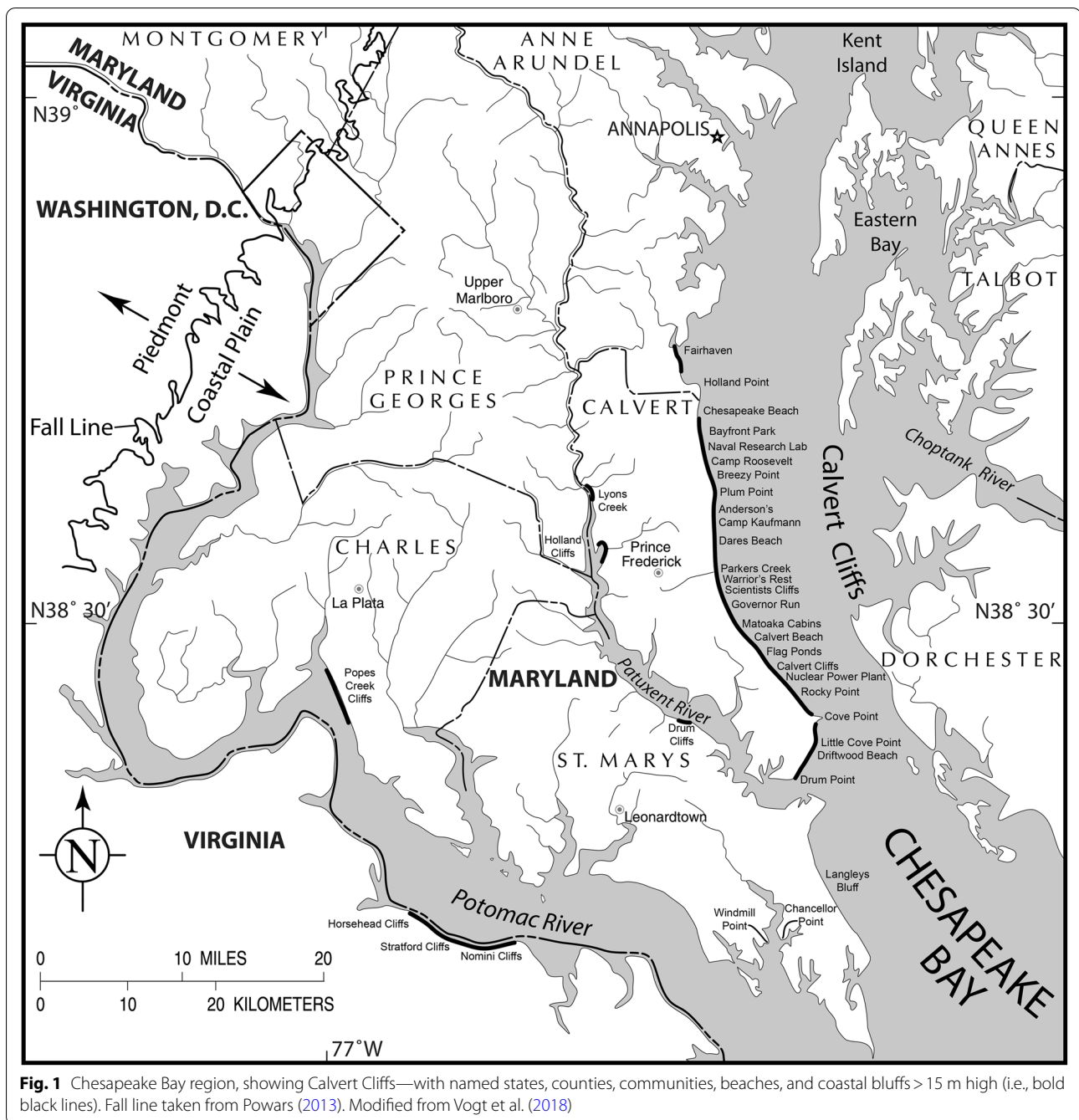
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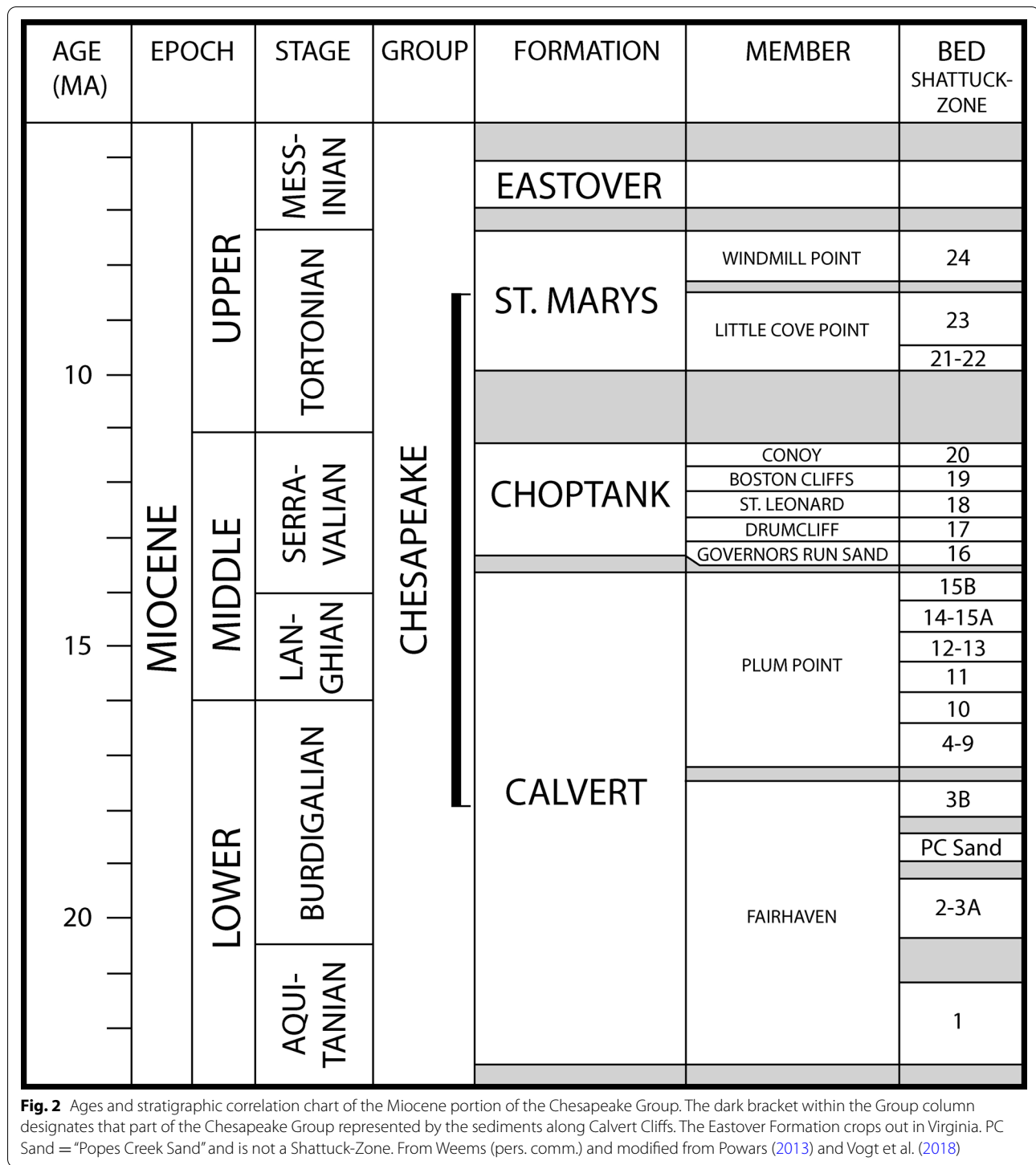


Material and methods

Geologic setting

The Miocene stratigraphy of Calvert Cliffs and southern Maryland (Fig. 2) has recently been summarized by Kidwell et al. (2015) and Vogt et al. (2018). The locally exposed succession consists of three formations, namely, the Calvert, Choptank and St. Marys, in ascending stratigraphic order. These three largely

siliciclastic stratal packages belong to the broad-ranging Chesapeake Group and reflect a gradual shallowing within a Miocene bay known as the Salisbury Embayment. Intraformational subdivisions have been referred to as “zones” (i.e., informal but usually easily identifiable, and consequently useful, lithologic units) by Shattuck (1904), and later revised by Ward and Andrews (2008) and Kidwell et al. (2015), hence the



frequent mentioning of "Shattuck-Zones" (SZ) when referring to the stratigraphic whereabouts of Miocene fossils from Calvert Cliffs and surrounding areas. The inferred ages for each of the SZ are depicted in Fig. 2.

Specimen repository

All the specimens described herein are stored in the vertebrate paleontology (=CMM-V) collection at the Calvert Marine Museum.

Results

Systematic ichnology

Transexcrementum igen. nov.

Type and only known ichnospecies: *Transexcrementum cuniculus* isp. nov., herein designated.

Etymology: From the Latin prefix “trans”, meaning “through”, plus “excrementum”, the Latin word for “excrement”.

Distribution: As for the ichnospecies.

Diagnosis: As for the ichnospecies until further ichnospecies are described.

Transexcrementum cuniculus isp. nov.

Figures 3, 4

2022 “burrowed vertebrate coprolite”—Godfrey et al., p. 72, fig. 5

Holotype: CMM-V-5805 (Fig. 3), a burrowed vertebrate (probably crocodilian) coprolite.

Etymology: From “cuniculus”, the Latin word for “burrow”.

Type locality and collector: CMM-V-5805 was collected by Mike Ellwood from Warrior’s Rest, Calvert Cliffs, southern Maryland, U.S.A. (Fig. 2).

Type horizon: SZ 14 of the Plum Point Member of the Calvert Formation (Langhian, Middle Miocene) (Fig. 2).

Paratypes: CMM-V-6500 (Fig. 4B–D), a burrowed vertebrate (probably crocodilian) coprolite, collected by Mike Ellwood as beach float along Calvert Cliffs at Warrior’s Rest, Calvert County, Maryland, U.S.A.; CMM-V-7958 (Fig. 4A), a burrowed vertebrate coprolite, collected by Paul Murdoch as beach float along Calvert Cliffs at Warrior’s Rest, Calvert County, Maryland, U.S.A. Although neither of the paratype specimens were found in situ, there is no reason to think that they were not locally derived from the adjacent cliffs at Warrior’s Rest Sanctuary. At the point where these coprolites were found, SZ 11–19 are exposed, which include the upper portion of the Plum Point Member (SZ 11–15B) of the Calvert Formation along with the Governors Run Sand (SZ 16), Drumcliff (17), St. Leonard (SZ 18), and Boston Cliffs (SZ 19) members of the Choptank formation (Kidwell et al., 2015). The sediments comprising this section of the cliffs range in age from approximately 16 Ma to 12 Ma (Perez et al., 2019: fig. 1).

Distribution: Middle Miocene (but see Discussion for a possible occurrence from Lower Cretaceous deposits).

Diagnosis: Tubular (cylindrical) tunneling in coprolites, not lined nor backfilled; opening and transverse sections sub-circular; diameter supra-millimetric, up to ca. 20 mm, rather constant throughout; inner termination(s) rounded/conical; tunnel morphology straight or gently curved, sometimes branching; internal sculpturing sometimes present in form of short and irregularly oriented scratches and gouges.

Description: Godfrey et al. (2022) described the holotype specimen (Fig. 3) as follows: “CMM-V-5805 is a fairly large specimen with a maximum length of 178 mm [...]. Its long axis is bent to an angle of about 90 degrees. The surface opening is sub-circular in outline and approximately 15 mm in diameter (part of the perimeter of the outer opening was damaged and lost). Within the coprolite, the burrows range in diameter from 13 to 17 mm. The walls of the cylindrical burrows are pervasively marked by many short burrowing/feeding gouges with no apparent preferred orientation. The same kinds of gouge markings are scattered about on the outer surface of this coprolite, a surface characteristic of most of the vertebrate coprolites from Calvert Cliffs (SJG pers. obs.). Within the coprolite, the tunnels curve and branch.”

The paratype specimens (Fig. 4) are CMM-V-6500 and CMM-V-7958. The first of these coprolites (CMM-V-6500, Fig. 4B–D) was originally cylindrical, at least 65 mm in diameter, and 131 mm in length. This specimen is now preserved in two roughly equal-sized pieces (Fig. 4B–D). From what remains of this burrowed coprolite, we estimate from the ubiquity of the short linear gouges, that at least one-third of the faecal mass was consumed prior to its final preservation. Figure 4B shows the most heavily burrowed internal surface of one half of this coprolite. The curvature of the tunneling walls, presumed to have been originally cylindrical burrows, suggests an original diameter of approximately 19 mm. These curved surfaces are heavily marked with short linear gouges. In this same moiety of CMM-V-6500, there is one small burrow into one of the ends of the coprolite that is 7.7 mm in diameter (not visible in Fig. 4B). That burrow is only about 13 mm deep.

The other half of CMM-V-6500 is also pervasively marked, both internally and externally, with short linear gouges. Three cylindrical burrows are visible in Fig. 4C, one in the upper left quadrant of the coprolite and the other two on the right half, one directly above the other. The one in the upper left quadrant is 9 mm in diameter and approximately 16 mm deep. Of the two on the right hand side of the coprolite, the upper one is 12 mm in diameter and approximately 9 mm deep. Conical would describe the overall shape of this incipient hole. (We interpret this shallow conical tunnel as an incipient burrow instead of a fully developed one.) The lower burrow is also conical and 11 mm in diameter where it opens on the surface of the coprolite. It is approximately 11 mm in depth. Some of the external surface of this coprolite is marked by the same kind of short linear gouges that mark the walls of the burrows (Fig. 4D). Furthermore, small circular dimples approximately 4 mm in diameter and only a few millimeter deep occur on the outer surface of this coprolite. They too are marked by the linear gouges

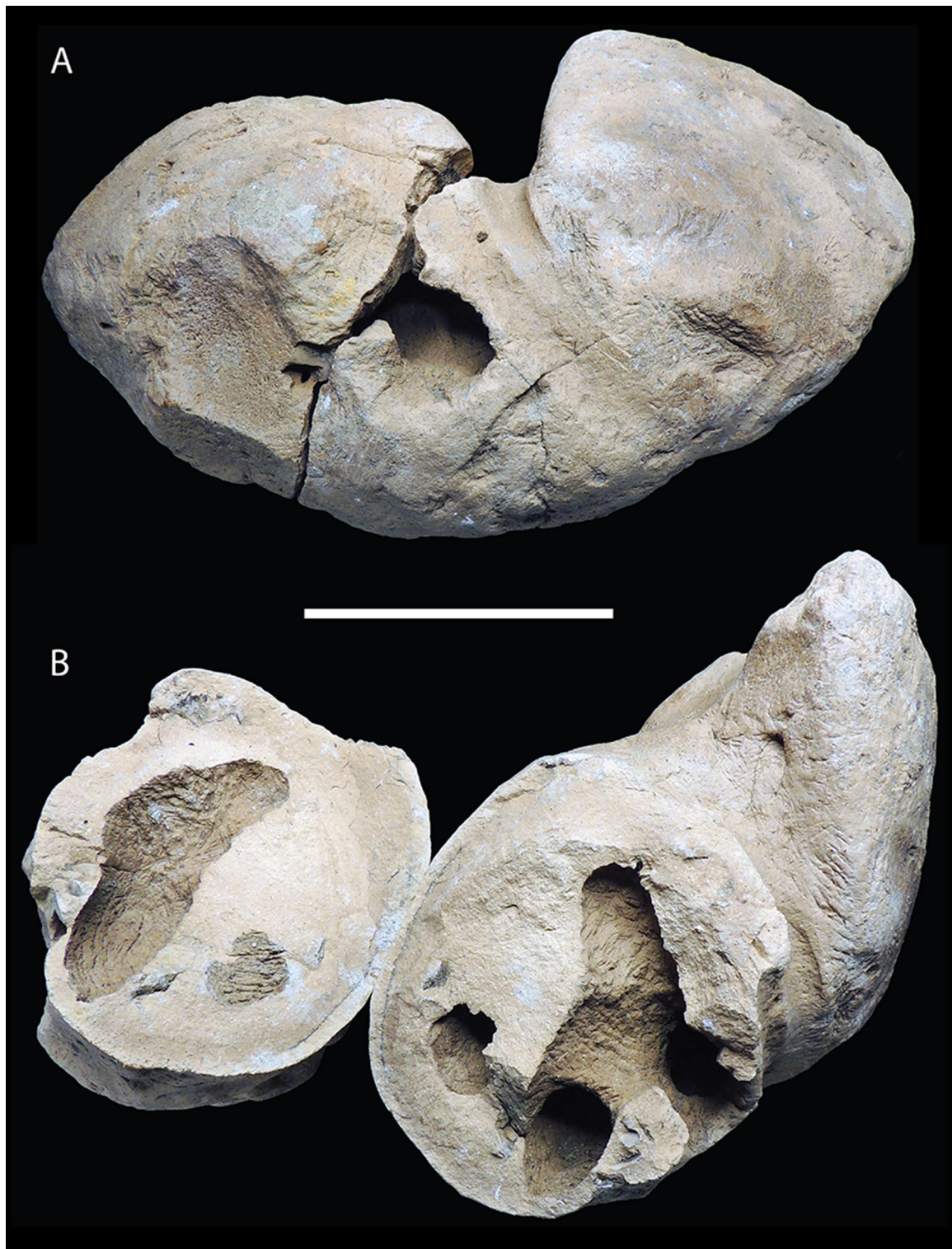


Fig. 3 CMM-V-5805, holotype of *Transexcrementum cuniculus* igen. et isp. nov., a burrowed vertebrate (probably crocodilian) coprolite from Shattuck-Zone 14 of the Plum Point Member of the Calvert Formation, Calvert Cliffs, Maryland, U.S.A. **A** General overview of the specimen, showing the circular opening through which the coprolite was burrowed. **B** The coprolite opened up along the crack seen in **A**, showing the interconnected cylindrical burrows within the coprolite. Notice the linear striations on the walls of the burrows. Scale bar equals 50 mm

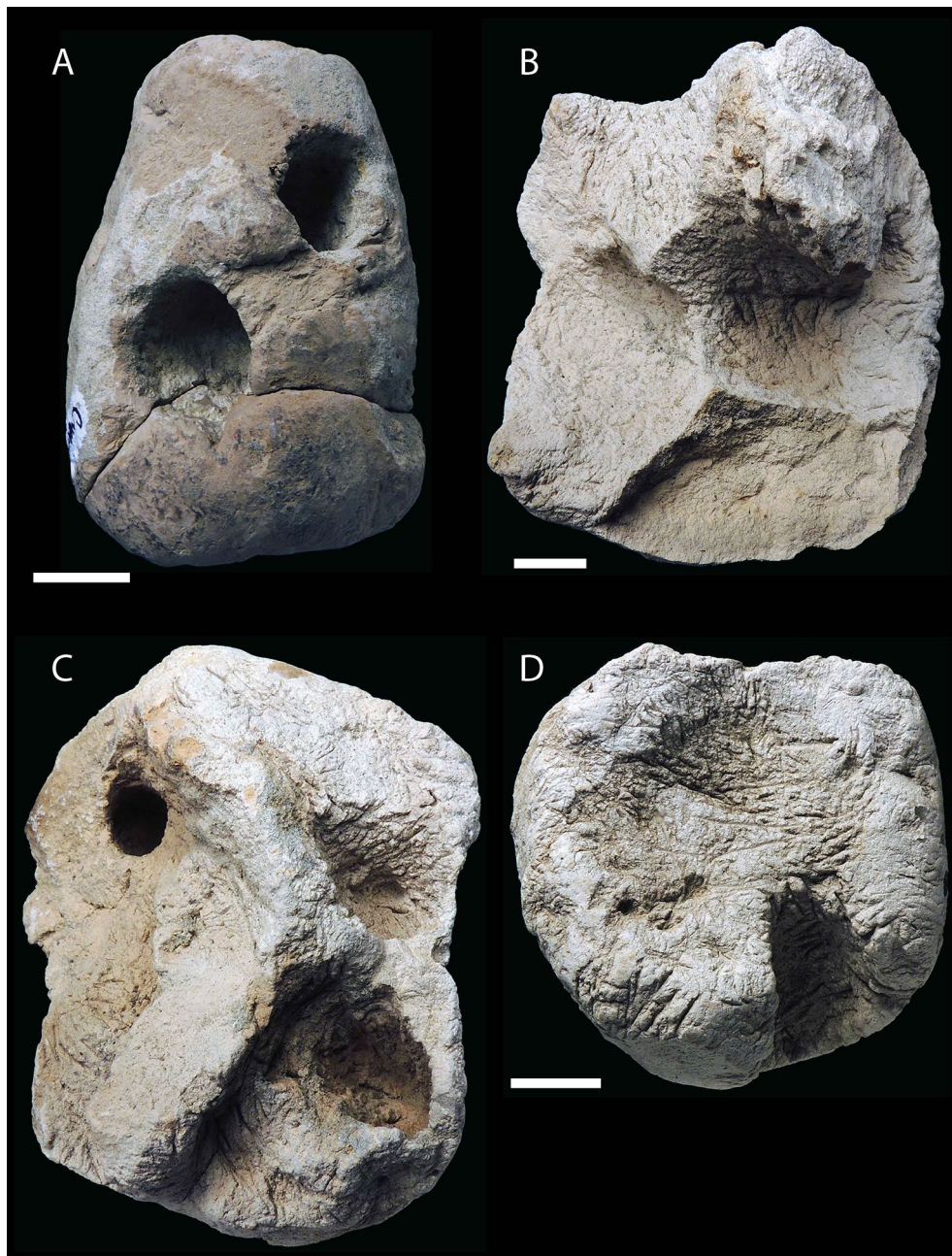


Fig. 4 *Transexcrementum cuniculus* igen. et isp. nov., paratypes. **A** CMM-V-7958, a burrowed vertebrate (probably crocodilian) coprolite from Calvert Cliffs, Maryland, U.S.A. **B–D** CMM-V-6500, a single vertebrate (probably crocodilian) coprolite broken in two roughly equal-sized pieces. **B** is a view of the heavily burrowed internal surface of one of these pieces, and **C, D** are two views of the other part of this same coprolite. In **D**, notice all the gouge marks over much of the outer surface of this portion of the coprolite. Scale bars equal 10 mm

and are interpreted as representing sites where tunneling was initiated but not pursued.

CMM-V-7958 (Fig. 4A) is broken into two pieces; it has a maximum diameter of 47 mm and a length of 66 mm. The surface displays two sub-circular openings,

12–14 mm in diameter, connected by a U-shaped tunnel with the same diameter throughout.

Remarks: As traces on coprolites, the *Transexcrementum cuniculus* burrows can be referred to the *Gaspeichnus* ichnofacies as defined by Hunt et al (2018).

Discussion

Burrowing versus boring

The physical properties of the medium that an organism tunnels into determine whether the resulting cavity is described as a boring or a burrow (Dorgan, 2015). Borers employ abrasion or chemical secretions to penetrate hard materials such as rock or wood, whereas burrowers move through softer substrates. Distinguishing between borings and burrows is not always straightforward, and many fossil tunnels may represent both, depending on the consistency of the substrate at the time it was engaged by the tunneling organism. As the kind of sculpturing that ornaments the internal walls of the *Transexcrementum cuniculus* holotype also occurs locally on the outer surface of CMM-V-5805 (Fig. 3), and the same can be said for paratype CMM-V-6500 (Fig. 4D), the faeces appear to have been incised and excavated prior to lithification (cf. discussion in Eriksson et al., 2011). At the same time, the faeces would have been firm enough to record and preserve the rasping/gouge marks made by mouthparts or other appendages as distinct wall ornaments. Firm substrates are generally associated with soft rather than hard (e.g., lithic) substrates in terms of consistency (Bertling et al., 2006), hence *T. cuniculus* should be interpreted in terms of burrowing rather than of boring.

Comparisons with similar coprolite burrows/borings

Burrows and/or borings affecting coprolites have rarely been reported in the literature. In many cases, such cavities are distinctly sub-millimetric in diameter (e.g., Brachaniec et al., 2015; Eriksson et al., 2011; Hunt et al., 2018), thus differing from the kind of tunneling described herein.

Larger examples include the clavate excavations of boring bivalves in Eocene phosphatic coprolites of Mali (Tapanila et al., 2004). Recognized as representatives of *Gastrochaenolites*, these flask-shaped cavities were excavated into partly to fully lithified faeces (paleocoprolites) (Tapanila et al., 2004). As *Transexcrementum cuniculus* is not a clavate trace, its diameter being fairly constant throughout, an attribution to *Gastrochaenolites* as well as an origin from the boring activity of bivalve tracemakers can be ruled out (Godfrey et al., 2022).

Other similarly sized (i.e., ranging in diameter between 1 and 31 mm) burrows were described from herbivorous dinosaur coprolites from Cretaceous deposits of Montana, U.S.A. (Chin, 2007; Chin & Gill, 1996). Interpreted as dung beetle tunnels, these burrows are distinctively backfilled; as such, they are not representative of the same ichnotaxon as *T. cuniculus*.

Finally, Milàn et al. (2012) described two deep cylindrical burrows, which they interpreted as made by coprophagous organisms, excavating a turtle (or

theropod) coprolite from the Lower Cretaceous Jydegaard Formation exposed at Bornholm (Denmark). CT-scans of this coprolite, MGUH 29,809, showed, among other things, two cylindrical tunnels. They extend from the surface into the coprolite, preserving an almost constant diameter throughout their length with a rounded terminal end (Milàn et al., 2012: fig. 3C, D and fig. 4). While smaller in size (i.e., less than 5 mm in transverse diameter), these burrows appear as morphologically consistent with *T. cuniculus*, and future analyses may reveal they belong to the same ichnotaxon as the Calvert Cliffs burrows described herein.

Hypotheses on the ethology and identity of the tracemaker

It is unclear what kind of organisms and behaviours could have resulted in the production of *Transexcrementum cuniculus*. We concur with Godfrey et al. (2022) in interpreting this trace fossil as due to coprophagy rather than to, e.g., the manufacturing of a living place. Since the type series of *T. cuniculus* occurs within vertebrate coprolites from a subaqueous depositional setting (i.e., the Salisbury Embayment), and immersed bodies are generally isolated from being colonized by maggots (Higgs & Pokines, 2013; Hughes, 2018), an origin from the excavating activity of fly larvae seems rather unlikely. (Note however that Milàn et al., 2012 interpreted similar burrows in a vertebrate coprolite from the brackish/freshwater Jydegaard beds to have been left by maggots on the basis of actuo-paleontological considerations). Different considerations apply to the backfilled burrows from Montana, which were formed in a subaerial paleoenvironment (Chin, 2007; Chin & Gill, 1996). Judging from the overall rarity of *T. cuniculus* occurrences in the fossil record, the tracemaker responsible for these burrows might also have been rare, or engaged in coprophagy only occasionally. Many aquatic invertebrates are known to feed on faeces, including polychaetes, gastropods, bivalves, crustaceans and echinoderms (e.g., Brendelberger, 1997; Collareta et al., in press; Frankenberg & Smith, 1967; McClintock, 1994).

Is faecal matter a unique substrate?

In the ichnotaxonomic literature, ichnogenera have often been distinguished on the basis of the type of substrate (Bertling et al., 2006). At present, the ichnological community is nonetheless divided on what kind of substrates are “unique”, i.e., useful to differentiate traces, and even on whether the substrate nature is suitable as an ichnotaxobase (e.g., Bertling et al., 2006; Höpner & Bertling, 2017; Donovan & Ewin, 2018; Zonneveld et al., 2021). Basic substrate categories that are often used to differentiate traces include unconsolidated sediment, rock,

wood and bone (Zonneveld et al., 2021). Although faeces have not often been identified as a unique substrate, they have recently been recognized as such by Hunt et al. (2018), who diagnosed the ichnogenus *Gaspeichnus* as “[e]longate and irregularly sinuous borings of small size (diameter 0.1–0.2 mm) with irregular width in a coprolite substrate.” (Although Hunt et al. (2018) used the term borings for referring to *Gaspeichnus* traces, they interpreted the latter as the likely product of coprophagy, tunneled into nutrient-rich faeces.) Further on, the same authors contended that “[t]he coprolite substrate alone differentiates it [= *Gaspeichnus*] from other sinuous trace fossils.” At present, we concur with Hunt et al. (2018) that a faecal substrate may prove ichnotaxonomically relevant in case of traces hinting at a deliberate and targeted exploitation of the faeces, as is the case for both *Gaspeichnus complexus* and *Transexcrementum cuniculus*. Although this position is not without concerns, we regard it as ultimately consistent with some of the main conclusions by Bertling et al. (2006), i.e., that ichnotaxonomic criteria resulting from behaviour are the most important, and that ichnotaxa should not always be distinguished on the basis of morphology alone. Hopefully, the present contribution will spark a broader debate on whether and under what conditions faecal matter comprises a unique, ichnotaxonomically informative substrate.

Conclusions

Some coprolites attributed to the crocodilian *Thecachampsa* from the Middle Miocene deposits exposed along the Calvert Cliffs (Maryland, U.S.A.) were tunneled into, likely reflecting coprophagy by some unknown tracemaker. This resulted in the production of burrows that excavate the coprolites, the sides of which are sculptured by scratch/gouge marks. These highly idiosyncratic, overly rare trace fossils are referred herein to the new ichnogenus and ichnospecies *Transexcrementum cuniculus*. Whereas the exact origin of such burrows is largely unknown, their fossil record may be as old as at the Early Cretaceous.

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Author contributions

AC and SJG contributed equally in writing the manuscript. SJG created all the figures. Both authors read and approved the final manuscript.

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Availability of data and materials

The specimens described herein will be made available to qualified researchers.

Declarations

Competing interests

The authors declare that they have no conflicts of interest.

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