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RESEARCH ARTICLE

Coprolite evidence for marine vertebrate migration in the warm Cretaceous Arctic

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ABSTRACT
Vertebrate migrations significantly impact the ecosystems they traverse, yet evidence for migration in the fossil record is difficult to identify. Here we infer the occurrence of seasonally driven marine migration in two exposures of the Upper Cretaceous Kanguk Formation on Devon Island, Nunavut, Canada. Four lines of evidence support the occurrence of migration at these sites: 1) the paleolatitude of Devon Island above the Arctic Circle indicates seasonal extremes in photoperiod, and abundant fossil diatoms in both sediments and coprolites reflect phytoplankton blooms that provided seasonally abundant food sources; 2) the greater abundance of coprolites relative to skeletal fossils suggests temporary vertebrate visitation; 3) coprolite contents and the internal tube-shaped structures we interpret as lumens suggest that at least 45 of the Devon Island coprolites can be attributed to sturgeons, a highly conserved clade with extant members that are predominantly migratory; and 4) paleobiogeographical occurrences of sturgeons and other Cretaceous Devon Island taxa in North America support migratory behaviour. Our analyses suggest sturgeons were migratory visitors that exploited rich food resources supported by seasonal planktonic blooms. This Cretaceous fossil assemblage thus offers rare coprolite evidence that supports the occurrence of migration in the Arctic that likely impacted resource cycling within the Western Interior Seaway.

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Introduction

Migration continues to be a difficult phenomenon to demonstrate in the fossil record. The passage of animals across landscapes has a major impact on modern ecosystems and likely had comparable effects in ancient environments (Albouy et al., 2019; Doughty et al., 2015). Extant migrating vertebrates adapt their routes to environmental changes (Ramp et al., 2015) and facilitate the cycling of nutrients from productivity hubs to the surrounding environments (Albouy et al., 2019; Doughty et al., 2015). Their travels shape and reshape food-web dynamics by introducing and removing predation and competition, thereby driving the evolution of other organisms in the ecosystems they cross and connect (Albouy et al., 2019). Recognising evidence for ancient migration in the fossil record makes it possible to connect small ecological snapshots from local fossil assemblages and may help explain differences in animal abundance and distribution. Previous work assessing evidence for ancient terrestrial vertebrate migration has included analyses of stable isotopes in hadrosaur teeth (Fricke et al., 2009), the morphological capacity to travel long distances in dinosaurs (Bell & Snively, 2008), and trackways of sauropods (Diedrich, 2010; Fricke et al., 2011; Meyer et al., 2021). In contrast, migration of ancient marine vertebrates has received less attention, likely because fewer methods exist to infer long-distance travel of marine animals. A handful of studies have investigated evidence for marine migration based on carbon, oxygen, and strontium isotope signatures in fish otoliths (Albertsen et al., 2021; Carpenter et al., 2003), ontogeny and oxygen isotope geochemistry of fossil whale barnacles (Bianucci et al., 2006; Collareta et al., 2018), bone histology of hesperornithiform birds (Wilson & Chin, 2014), and a monotypic fossil assemblage of ichthyosaurs in which all individuals show similar ontogenetic stages (Kelley et al., 2022). Nevertheless, the occurrence of diverse migration strategies in modern marine systems suggests that the scope and diversity of ancient marine migration may have been significant. Extant migratory marine vertebrates typically travel greater distances than terrestrial non-volant vertebrates when migrating (Stewart & DeLong, 1995) and can connect nearshore and open ocean environments over long distances and across latitudes (Burton & Koch, 1999;

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Doherty et al., 2017). Marine migrators can also be diadromous, travelling between freshwater and saltwater systems and facilitating the exchange of key nutrients between terrestrial and marine environments (Doughty et al., 2015). Additional lines of evidence for migration, particularly in marine settings, would improve our understanding of ancient marine ecosystems and the potential impacts caused by seasonal long-distance travel and resource exploitation. Here we describe the novel use of coprolites and their latitudinal and palaeoecological context to infer the migration of ancient marine vertebrates in the Cretaceous Arctic.

Modern Arctic marine ecosystems host many migrating species that travel north to take advantage of the productivity created by massive protist blooms that occur during the onset of extended daylight photoperiods after periods of winter darkness (Sauser et al., 2023; Tynan & DeMaster, 1997). As such, fossil assemblages from polar environments offer good opportunities to look for evidence of comparable ancient marine migration. Studies of the Upper Cretaceous Kanguk Formation on Devon Island in Nunavut, Canada, have revealed abundant planktonic microfossils that reflect high biological productivity in the Arctic during what was likely a warm temperate climate (Chin et al., 2008; Super et al., 2018; Witkowski et al., 2011). In this unique assemblage, marine vertebrate coprolites are the most common macrofossils, leading (Chin et al., 2008) to speculate that many of the defaecators were non-resident visitors.

Geologic setting

Exposures of the Upper Cretaceous Kanguk Formation are found throughout the islands of Nunavut in syndepositional down-faulted blocks in Palaeozoic strata (Mayr et al., 1998). The unit is characterised by organic-rich mudstones and silt-rich sandstones interbedded with layers of bentonite (Chin et al., 2008; Núñez-Betelu & Hills, 1998). The Kanguk Formation at Eidsbotn and Viks Fiord grabens comprises a thick regressive sequence from mudstone to glauconized greensands that are in turn overlain by the terrestrial Expedition Fiord Formation (Chin et al., 2008). Diatom biostratigraphy suggests that strata in these localities are around 93 to 72 Ma in age (Super et al., 2018). These greensands contain appreciable terrigenous inputs of wood and other organic detritus, suggesting that this unit represented a dynamic nearshore to offshore ecosystem (Chin et al., 2008; Davies et al., 2018; Super et al., 2018).

An expedition to Devon Island in 1998 led by Jaelyn Eberle and John Storer resulted in the first major collecting effort of the Eidsbotn graben locality (Figure 1). Eberle and Storer recovered various vertebrate and invertebrate fossils, as well as a number of coprolites. In 2003, a follow-up expedition to study the Cretaceous marine environment recovered additional body fossils, hundreds of coprolites, and sediment samples from both Eidsbotn graben and a new site, Viks Fiord graben (Figure 1).

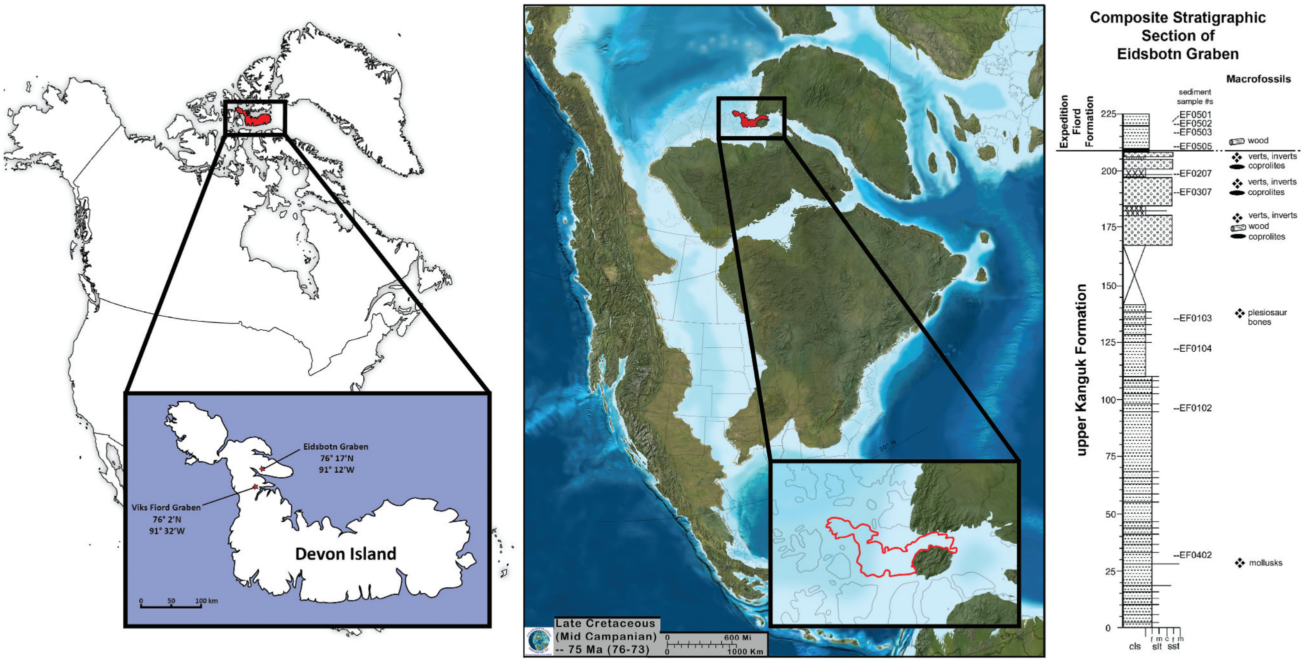

Figure 1. Left: Present Devon Island in Arctic Canada. Middle: Devon Island area during the middle Campanian (Base Paleomap created by Ron Blakey). Right: Composite section of Eidsbotn graben, borrowed from Chin et al. (2008).

Methods and materials

The vertebrate and invertebrate fossils collected from Eidsbotn graben on Devon Island in 1998 are reposited in the Canadian Museum of Nature (CMN). Fossils collected from Eidsbotn and Viks Fiord grabens in 2003 belong to the Nunavut government and have Nunavut catalogue numbers but are cared for by the Canadian Museum of Nature until the Nunavut Government designates a different repository (NUVF and NUIF indicate Nunavut vertebrate fossils and invertebrate fossils, respectively).

The Devon Island coprolites were characterised by general morphology, groundmass composition, identifiable biotic inclusions, and volume determined by water displacement. Fifty-four thin sections were made of 18 coprolite specimens and the bulk chemical compositions of eleven coprolites and selected sediment samples were determined by inductively coupled plasma mass spectrometry (ICP-MS) by Actlabs. Four coprolite specimens were X-ray CT (computed tomography) scanned at the University of Texas High-Resolution X-ray CT Facility with a North Star ACTIS Scanner. We performed manual and artificial intelligence (AI) assisted segmentation of X-ray scans with the 3-D visualisation software Dragonfly to reconstruct the structure of three distinctive prey inclusions and one internal cylindrical structure within the coprolites.

Body sizes, dentition, locomotor capabilities, morphologic features, and feeding behaviours of extant relatives or analogs of the fossil vertebrate taxa from the Eidsbotn and Viks Fiord graben localities were examined to help identify the most likely defaecators at these sites. Tube diameters of coprolites with internal tube structures were analysed in a one-way ANOVA test run in R v2025.09.2 + 418 (R Core Team 2025). Biogeographic occurrence maps of the Devon Island vertebrate taxa were produced using occurrence data recorded in the Paleobiology Database. Mapped distributions were limited to Campanian occurrences in marine and nearshore environments. Both freshwater and marginal marine occurrences were included in the distribution of Acipenseridae as extant sturgeons are anadromous.

Results

Body fossils and coprolites

Previous studies have helped characterise the fossil assemblages from the Kanguk Formation on Devon Island. We summarise these studies here and include new unpublished information.

Microfossils

Mudstone facies at Eidsbotn and Viks Fiord preserve abundant and diverse siliceous and organic microfossils of autotrophic and heterotrophic plankton including more than 100 diatom taxa (Witkowski et al., 2011) and 75 dinoflagellate taxa (Chin et al., 2008). Radiolarians, silicoflagellates (McCartney et al., 2011), and sponge spicules are also present.

Invertebrates

Fossil cephalopods, bivalve molluscs (including inoceramids), and decapod crustaceans were recovered from both Devon Island localities and are often found as inclusions within the greensand coprolites (Chin et al., 2008) (Figure 2). Lingulid brachiopods and hexactinellid sponges (Rigby et al., 2007) appear to be unique to Eidsbotn graben and are rarely found within coprolites.

Vertebrates

Although vertebrate fossils occur in numbers similar to invertebrate fossils, most of the vertebrate material, especially fish fossils, are individual teeth (Figure 2). Vertebrate fossils from Devon Island include remains of chondrichthyans, actinopterygians, and reptilians (Chin et al., 2008). Hesperornithiform birds, lamniform sharks, holocephalans, sturgeons, *Xiphactinus* Leidy 1870, *Enchodus* Agassiz 1835, polycotylids, and elasmosaurs were found at both sites, whereas fossils of *Ichthyodectes* Cope 1870, *Pachyrhizodus* Agassiz 1850, and a mosasaur were recovered only at Viks Fiord.

Coprolites

Coprolites are highly abundant and widespread at both the Eidsbotn and Viks Fiord sites. Because they were ubiquitous, collection of coprolites at these sites was selective and biased; more than 450 specimens were collected that had distinctive sizes, morphologies, or conspicuous inclusions. Although most of the Kanguk Formation coprolites are generally fusiform, cylindrical, or ovoid, they are often broken and show considerable morphological variability. As such, the coprolites are grouped into three major categories based on the composition of the coprolite groundmass (Figure 3), because both the contents and phosphorus concentrations of each group were distinctive. *Phosphatic coprolites* are black or off-white in colour and are predominantly composed of microcrystalline calcium phosphate; three analysed samples contain 30.2 to 31.9 wt.% phosphorus oxide. *Greensand coprolites* have a groundmass dominated by greensand clasts but still contain appreciable phosphate; four analysed samples have 16.0 to 23.0 wt.% phosphorus. *Mixed phosphatic/greensand coprolites* contain abundant greensand clasts

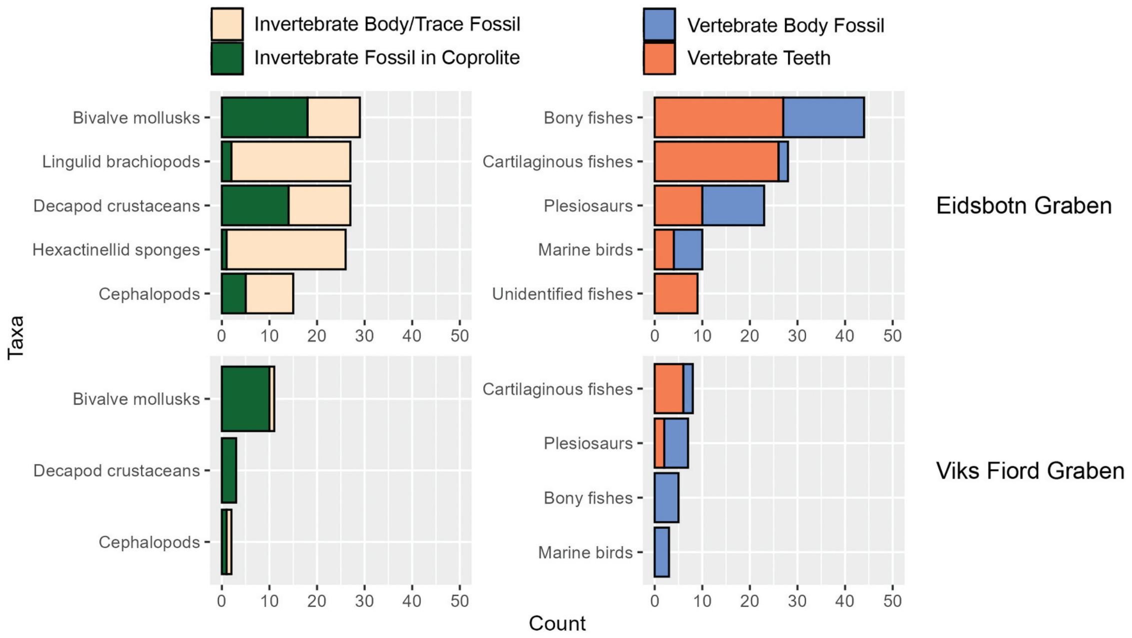

Figure 2. Invertebrate and vertebrate body fossils of taxa collected from Eidsbotn and Viks Fiord grabens in 1998 and 2003.

Figure 3. Three major categories of coprolite groundmass at Eidsbotn graben and Viks Fiord graben. Left Column: majority greensand (from top to bottom: CMN 52004, CMN 52011, NUVF-77/LO-8). Middle Column: mixed greensand and phosphate (from top to bottom: NUVF-92/IM-15, NUVF-70/RLO-29, NUVF-70/RLO-33). Right Column: majority phosphate (from top to bottom: NUVF-71/CO-7 NUVF-70/RLO-61, CMN 52038). All scale bars are 1 cm.

embedded in a microcrystalline phosphate; three analysed samples show 20.2 to 22.1 wt.% phosphorus.

Greensand coprolites were most common at Eidsbotn, whereas a majority of the coprolites collected at Viks Fiord are phosphatic or mixed phosphatic/greensand specimens. Measured coprolite volumes ranged from <1 mL to >130 mL with a few notable larger outliers. However, the majority (72%) of collected coprolites are between 1 mL and 30 mL in volume. Greensand coprolites generally tend to have higher volumes than both phosphate and mixed coprolites (Figure 4). We also observed a large differential between the numbers of body fossils relative to coprolites present at both sites, with coprolites being far more common at both localities (Figure 5). All invertebrate and vertebrate fossils were collected, whereas only a representative subset of the abundant coprolites was recovered. Thus, the histogram in Figure 5 shows the much higher number of preferentially collected coprolites relative to the completely collected body fossils, but does not fully capture the scale of the discrepancy between the relative abundance of coprolites and body fossils that were present at these sites.

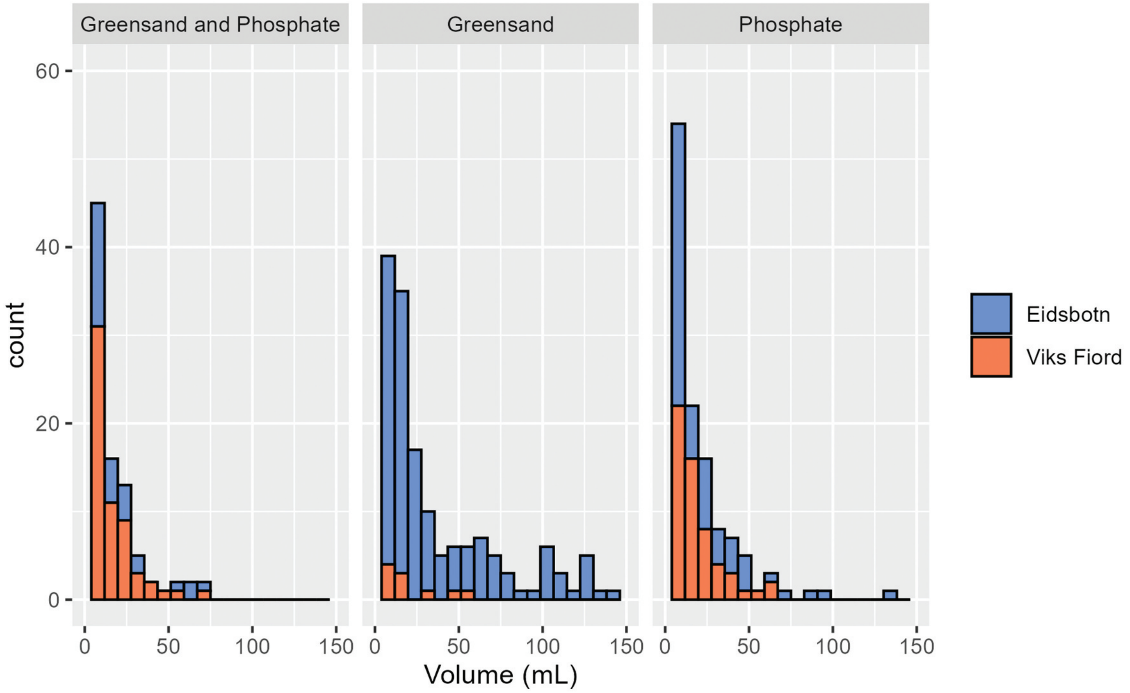

Figure 4. Stacked histogram of coprolite volumes (mL) faceted by predominant groundmass and differentiated by graben locality.

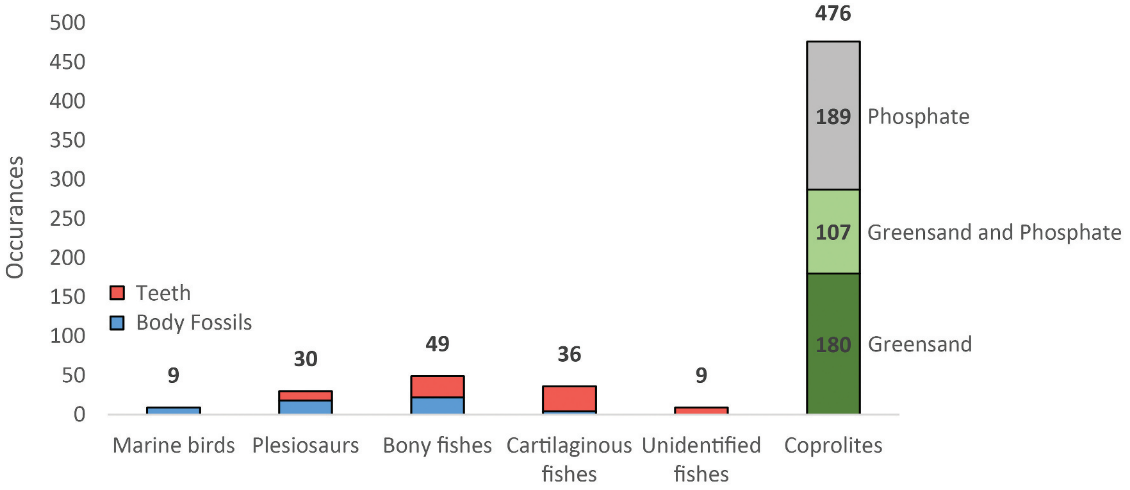

Figure 5. Relative numbers of coprolites and body fossils collected from both Eidsbotn graben and Viks Fiord graben. Collected coprolites significantly outnumber vertebrate body fossils even though all body fossils were collected while only a subset of coprolites were collected.

Macroscopic biotic inclusions within the coprolites are observed on broken or exterior surfaces or in thin sections (Figure 6). These biotic fragments are most common in greensand coprolites; inclusions are evident in ~60% of the greensand coprolites. Decapod fossils (claws and exoskeleton fragments in 22 coprolites) and squid fossils (beaks and phosphatic pens in 7 coprolites) are the most common recognisable invertebrates in greensand coprolites. Less common inclusions include bivalves, lingulid shells, hexactinellid sponge fragments, or wood fragments. Fragments of bone were observed in about 10 of the greensand coprolites/coprolite fragments collected.

Light microscopy of thin sections of phosphatic and mixed phosphatic/greensand coprolites reveal that countless siliceous microplankton dominate the groundmass (Chin et al., 2008) (Figure 6). Microfossils are much less common in greensand coprolites.

Some of the Devon Island coprolites show a distinctive structure in which a smaller-diameter cylinder is present within the cylindrical faecal mass (Figures 6 and 7). This cylinder-within-a-cylinder morphology is most conspicuous in phosphatic (Figures 6D,E,F and 7A,B,C) or mixed phosphatic/greensand coprolites that have fine-grained matrices (Figure 7D). The inner cylinder is usually solid but may be hollow if the internal contents have been lost

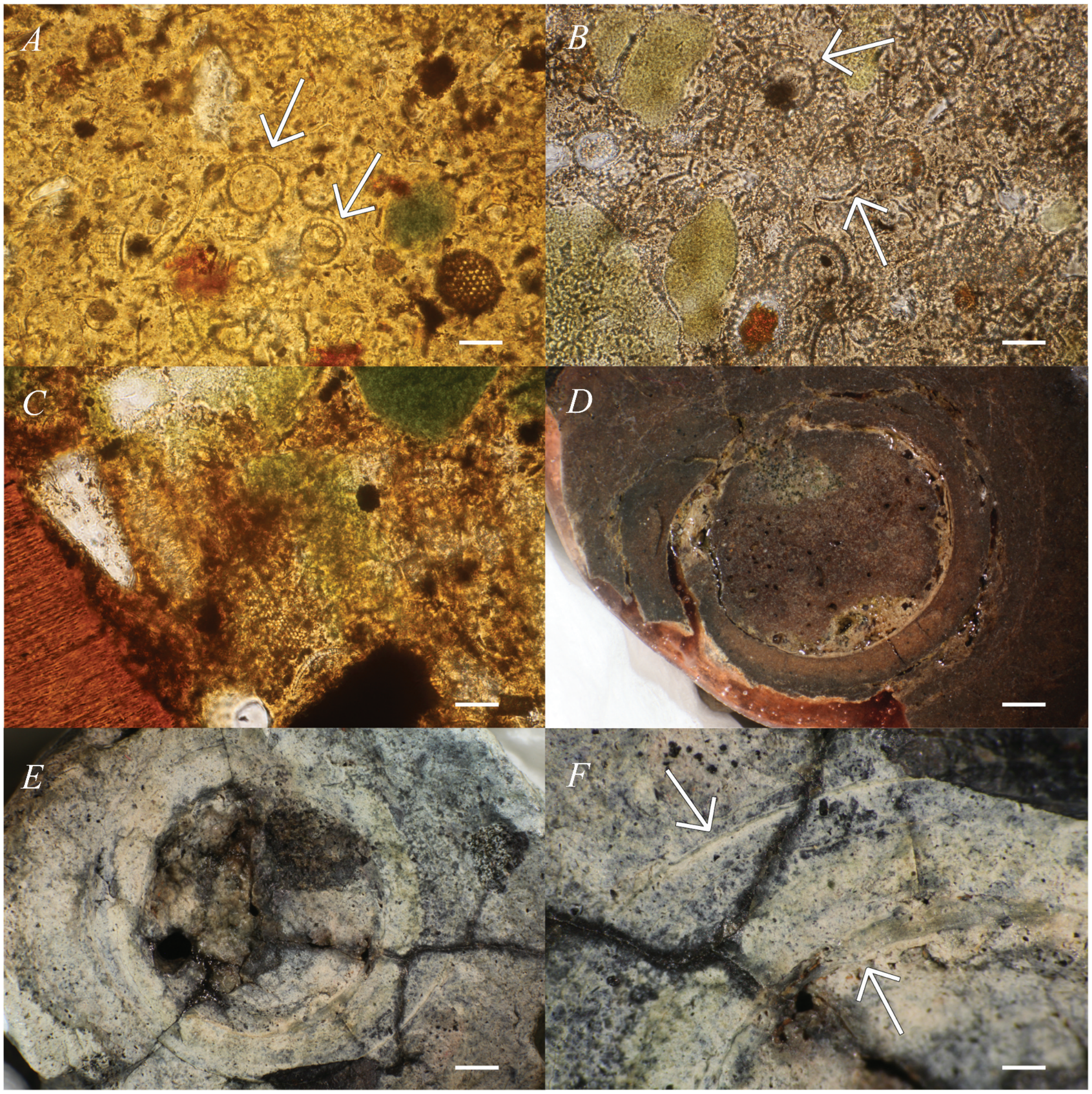

Figure 6. Thin section images of Devon Island coprolites (A) phosphate dominated coprolite containing abundant microfossils, (select diatoms are indicated by white arrows) (NUVF-75/UL-52c; scale bar = 25 μm) (B) 'mixed' coprolite in thin section showing microfossils and glauconized sand grains (select diatoms are indicated by white arrows) (NUVF-85/JM-2b; scale bar = 25 μm) (C) greensand dominated coprolite with a fragment of decapod cuticle (orange) in the lower left corner (CMN 52000/UL-98; scale bar = 25 μm) (D) lumen in cross-section of a coprolite that appears to spiral from an inner ring to an outer ring (NUFV-91/HR-2; scale bar = 1.25 mm). (E) &; (F) lumens in cross-section (NUVF-72/BD-8; scale bar (E) = 1.25 mm, (F) = .5 mm).

(Figure 7D). This distinctive structure is not evident in cross sections of greensand coprolites, but faint vestiges of an inner cylinder are evident in greensand coprolites that fortuitously fractured along their long axes (Figure 7G,H).

X-ray CT scans of fossil inclusions

The 3-dimensional structure of prey inclusions revealed by digital segmentation allows assessment of damage likely caused by oral processing and digestion.

Coprolite UL-12/NUVF 74 contains a decapod claw ~62.9 mm in length. The claw is relatively complete but is missing part of the ventral-facing side of the palm of the propodus. There is a large break in the centre of the claw near the base of the thin elongated edge of the propodus mechanism from which many of the cracks in the claw appear to originate. The claw is still attached to the carpus and seems to have separated at the carpus/merus boundary (Figure 8A,B). Because the decapod is unidentified, it is difficult to estimate the animal's original length. However, a relatively complete crustacean abdomen with at least four abdominal segments and part of the cephalothorax was found in another coprolite (CMNIF 164) and is 47 mm in length. If we assume that the claw and abdomen belong to the same taxon, we can conservatively estimate that the crustacean was at least 110 mm in length without a tail.

The lower beak of a squid is present within coprolite UL-7/NUVF 74. The beak's original structure is clear (Lower Rostral Length (LRL) = 4.3 mm), with wings, lateral wall, and features of the crest remaining articulated. However, the edges of these features are eroded and permeated by cracks (Figure 8C,D). Although we do not know the taxon of the Cretaceous squid measured here, we can roughly estimate the size of the individual using the relationship between the LRL, mantle length (ML), and body mass of the extant squid, *Psychroteuthis glacialis* Thiele 1920. Using the regression of ML to LRL provided by (Gröger et al., 2000), the Cretaceous squid beak from Devon Island may have belonged to a squid with a mantle length of around 136 mm and a body mass of roughly 63 g.

Coprolite KG-1a&b holds a squid gladius, or 'pen' (length = 64.6 mm, max width = 8.9 mm). The gladius is broken off at one end of the coprolite so the original length cannot be determined. This inclusion retains its original shape within the coprolite but is considerably more

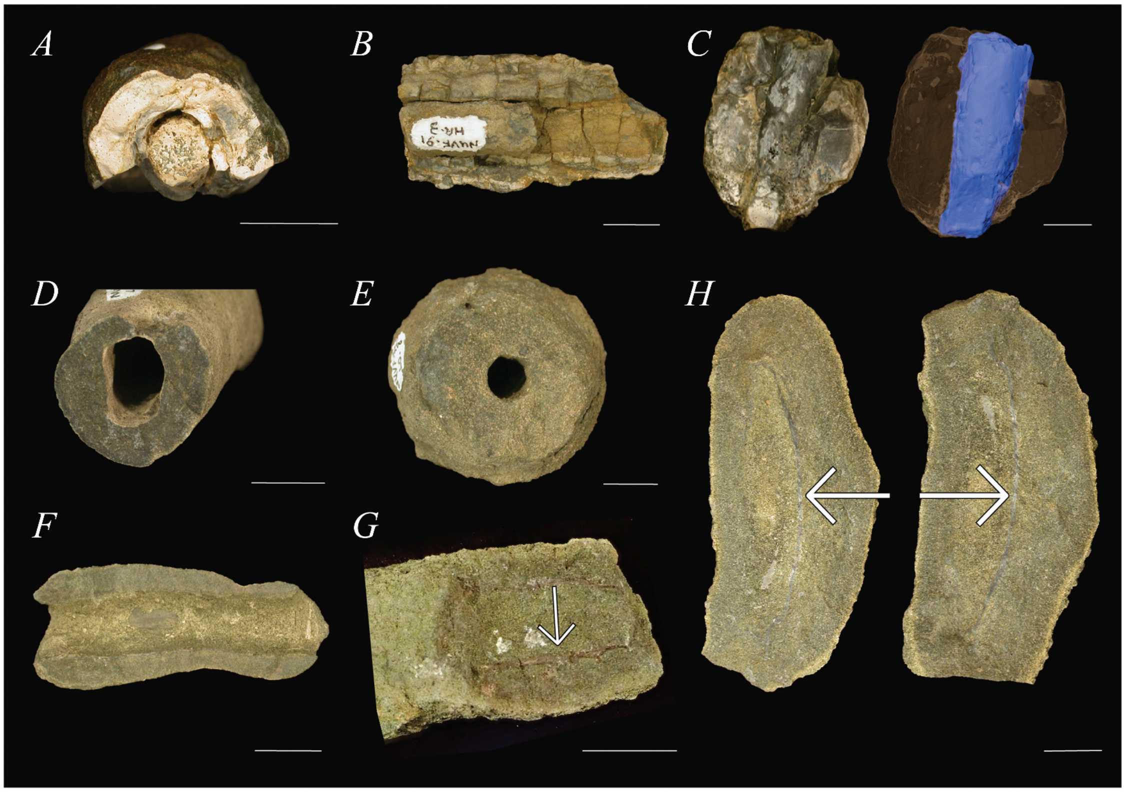

Figure 7. Lumen structures in coprolites with different ground mass fabrics. (A), (B) &; (C) majority phosphate, (D) mixed greensand and phosphate, and (E), (F), (G) &; (H) majority greensand. (A) &; (B) show partial internal cylinders still attached to the coprolites. (C) CT-segmented internal lumen cylinder (in blue) in a phosphatic coprolite. (D) and (E) show empty cylinders where lumen structures were once present within the coprolites. (F) shows longitudinal view of the absence of the internal cylinder within the coprolites. (G) &; (H) show longitudinal views of lumen structures as they appear within many of the fractured greensand coprolites. All scale bars are 1 cm.

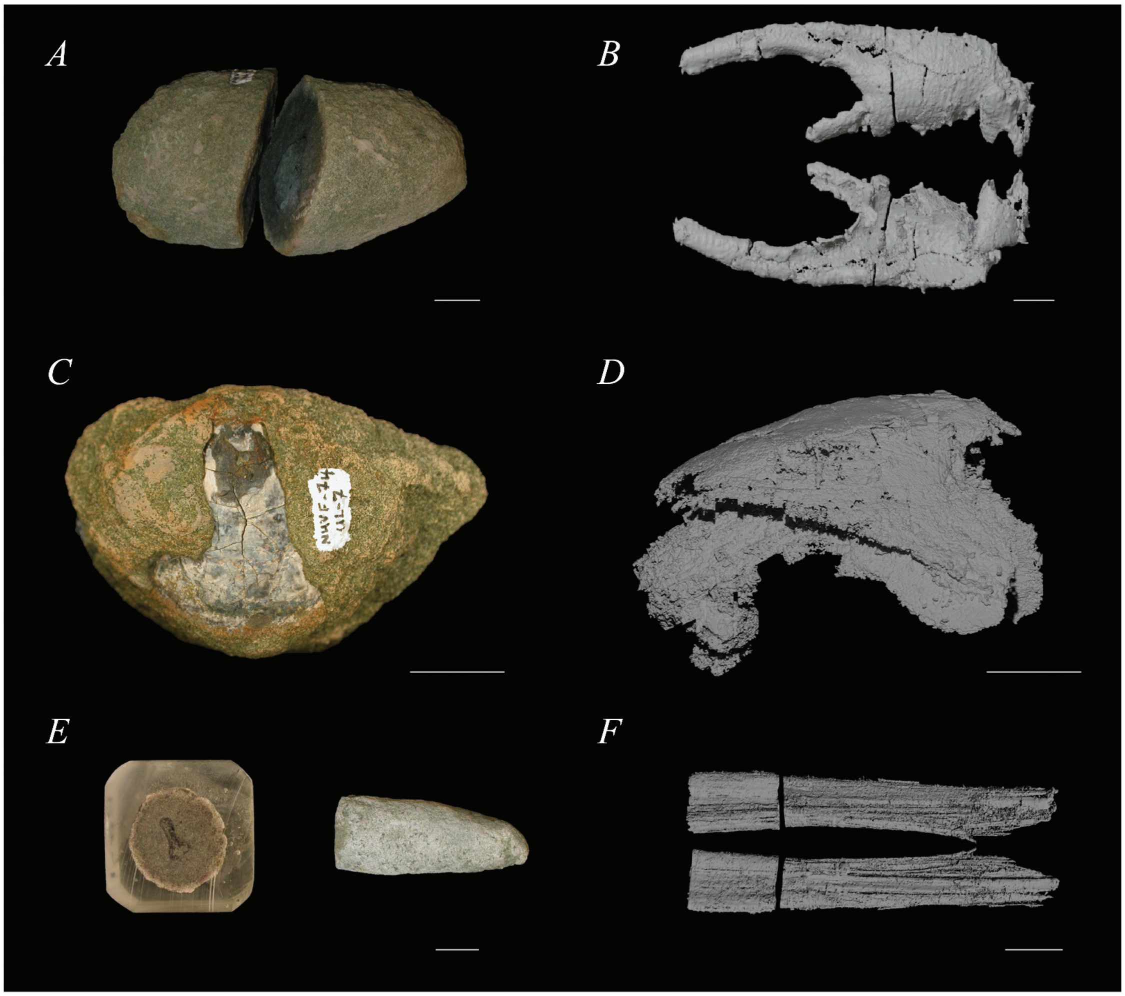

Figure 8. Devon Island coprolites with inclusions. Left column shows coprolite photos with views of contained prey items, right column shows prey inclusions segmented from CT-data. (A) &; (B) decapod claw (NUVF-74/UL-12), (C) &; (D) squid beak (NUVF-74/UL-7), (E) &;(F) squid pen (KG-1a, KG-1b). All scale bars are 1 cm.

damaged than the other reconstructed prey items. The gladius is split partially along its long axis starting at the narrow end of the structure but otherwise appears to be mostly intact (Figure 8E,F).

In cephalopods, gladius length has occasionally been used as a substitute for mantle length, as the gladius and the mantle are typically similar in length in younger squids and the gladius grows to be slightly shorter than the mantle in adults. This allows us to again use the analysis by (Gröger et al., 2000) to estimate the minimum LRL and body mass. With a ML of at least 64.6 mm, this individual would have had a LRL of at least 1.9 mm translating to a body mass of at least 6 g.

Paleobiogeographic distribution of Cretaceous marine vertebrates from Devon Island

Campanian occurrences of the major marine vertebrate groups represented at Devon Island show a wide distribution ranging across much of the North American continent. Cretaceous teleosts and sharks occupied much of the Western Interior Seaway and the modern south-eastern coast of the United States spanning some 45 degrees of latitude across mostly marine to marginal marine environments (Figure 9). Plesiosaurs and sturgeons follow a similar distribution across 38 degrees of latitude with far fewer individuals discovered in the southeastern US and most occurrences falling within marine to near-shore deposits in the Western Interior Seaway.

Feeding habits of Cretaceous marine vertebrates from Devon Island

Our review of previous analyses of the dentition, fossil stomach contents, and hypothesised feeding strategies of fossil vertebrates found on Devon Island during the Late Cretaceous allows us to evaluate which animals likely produced the ancient faeces (Table 1) (Figure 10).

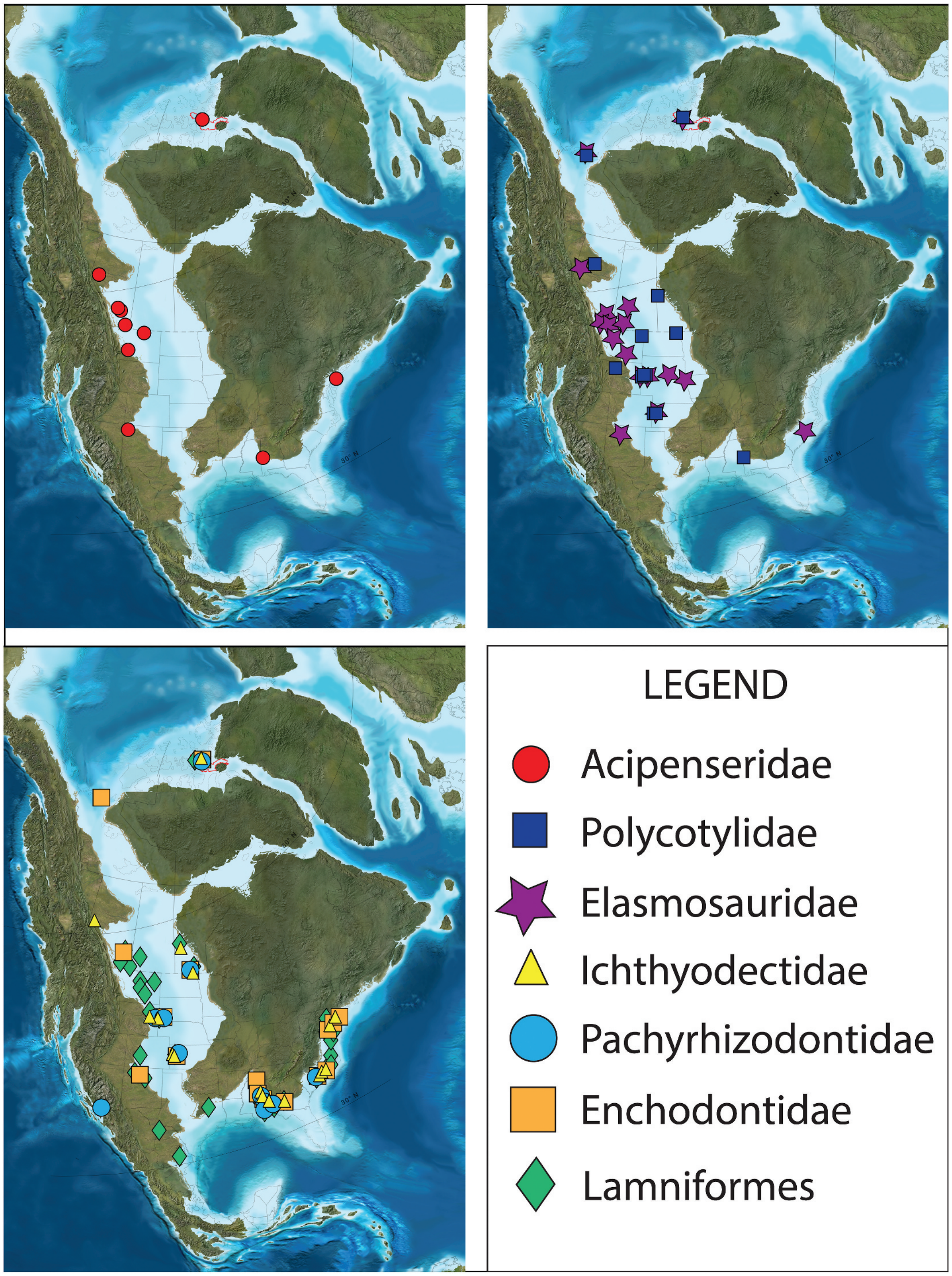

Figure 9. Biogeographic occurrence maps of Cretaceous Devon Island vertebrates in the mid Campanian. Upper left: sturgeon localities. Upper right: plesiosaur localities. Lower left: lamniform and teleost localities. Locality data sourced from the Paleobiology Database.

Vertebrate criteria that are congruous with features of the greensand, phosphatic, and mixed coprolites include an adult size greater than one metre (accounting for the range of coprolite sizes observed), and the physical ability to consume large amounts of sediment, benthic invertebrates, and/or plankton.

Chimaeriformes

Tooth plates of chimeras, also known as ratfish, have been found at both Devon Island sites. Extant ratfish have been observed feeding predominantly in the benthos and on rare occasion in the water column (Huber et al., 2008; Quigley, 2011). Ratfish grab hard-

Table 1. Body length, tooth morphology and documented stomach contents of Cretaceous Devon Island vertebrates.

Potential defaecator	Typical adult length (m)	Tooth morphology	Potential Prey	Spiral Intestinal Valve
Ratfish	0.5–1	Mineralised grinding tooth plates	*Crustaceans, *polychaetes, *mollusks, * *starfish	Yes
Lamniform Sharks	3–5	Sharp/pointed often serrated	*Various marine fishes, (including *Xiphactinus)* cephalopods and turtles; scavenging of plesiosaurs and mosasaurs	Yes
Sturgeon	3–5	No teeth	*Crustaceans, *bivalves, *gastropods, *insects, *benthic and *nektonic fish	Yes
Enchodus	0.5–1	Needle-like	Fish, cephalopods	No
Pachyrhizodus	2	Sharp/conical	Ichthyodectiforms and other fish	No
Xiphactinus	4–5	Needle-like	*Enchodus, Gillicus* Hay 1898, and other fish	No
Polycotylid Plesiosaur	6–8	Conical, slender, fairly pointed	Ammonites, *Enchodus*, and other fish	No
Elasmosaurid Plesiosaur	8–14	Large and robust, slightly pointed and delicate	Bivalves, brachiopods, crustaceans, crinoids, *Enchodus*, and other fish	No
Hesperornithiform Birds	1–2.8	Sharp/pointed, recurved	Fish, cephalopods	No

*Denotes stomach contents from extant taxa, see text for references.

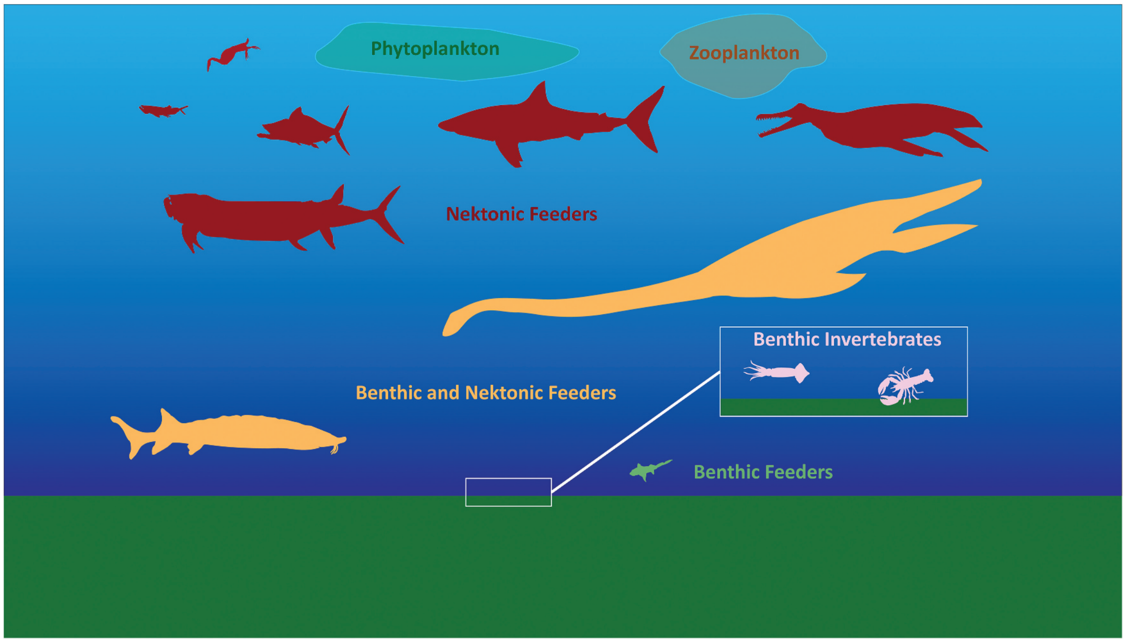

Figure 10. Schematic of vertebrate feeding guilds and food sources within the Devon Island ecosystem.

bodied invertebrates from the substrate with their jaws, ingesting some sediment in the process, and use their strong bite force to break shells with their hardened tooth plates (Quigley, 2011). Chimaeriformes also possess a spiral intestinal valve, a plesiomorphic intestinal morphology found in many groups of fish (Burton & Burton, 2017). The valve creates a recognisable spiral or coiled morphology in faeces that is often preserved in coprolites (Dentzien-Dias et al., 2021; Gilmore, 1992).

Lamniform sharks

Lamniform shark teeth are some of the most common body fossils found at the two Devon Island sites with 19 teeth collected over both expeditions. Extant members of this order have only been observed feeding in the water column but have evolved specialised traits for both carnivorous and planktivorous feeding strategies within different families (Shimada & Everhart, 2004; Strasburg, 1958). Only one described planktivorous lamniform shark has been reported from the Late Cretaceous (Vullo et al., 2021), suggesting that most lamniform sharks during this period primarily fed upon nektonic teleosts, mosasaurs, and possibly plesiosaurs (Shimada, 1997). The sharp fossil teeth of *Squalicorax* Whitley 1939 and *Cretalamna* Glikman 1958 found on Devon Island support this hypothesis and are consistent with piscivory. Lamniforms and other sharks also possess a spiral intestinal valve and produce distinct spiralled faeces (Burton & Burton, 2017; Dentzien-Dias et al., 2021).

Acipenseriformes

Sturgeons have undergone few morphological changes since they first appeared in the Late Cretaceous (Hilton & Grande, 2006). Extant sturgeons have been observed feeding in both the benthos and the water column, using sensory barbels on their lower jaw to detect prey (Saadatfar & Shahsavani, 2007; Williot et al., 2011). Juvenile sturgeons possess small teeth but are gape-limited and cannot ingest the benthic invertebrates and fish that adult sturgeons consume. They instead feed on zooplankton until they reach a certain length and eventually lose their teeth (Zarri & Palkovacs, 2018). Adult sturgeons feed by applying suction to the benthos, often ingesting large volumes of sediment at a time. Modern sturgeon gut contents have been shown to contain up to 75.4 weight % sand (Johnson et al., 1997), and some speculate that sturgeons are responsible for the creation of feeding pits in sand where large populations of shrimp live (Dumbauld et al., 2008). Extant adult sturgeon diets include crustaceans, bivalves, gastropods, insects, oligochaetes, and benthic and nektonic fish (Billard & Lecointre, 2001; Brooks & Sulak, 2005; Dumbauld et al., 2008; Guilbard et al., 2007; Harrison et al., 2014; Nilo et al., 2006). Like sharks, sturgeons possess a spiral intestinal valve (Williot et al., 2011).

Teleosts

Teleosts such as *Enchodus*, *Pachyrhizodus*, and *Xiphactinus*, found at Eidsbotn and Viks Fiord (Chin et al., 2008), were also likely nektonic feeders (Bazzi et al., 2015; Diedrich, 2012; Shimada, 2015). All possessed dentition, fossil gut contents, or a body shape that suggest a diet dominated by swimming prey in the water column (Allen & Shimada, 2022; Becker et al., 2010; Carpenter, 1996; Lindsey, 1978; Shimada, 2015; Shimada et al., 2006). They also lacked a spiral intestinal valve (Cooper et al., 2022).

Plesiosaurs

The variable morphology of the different plesiosaur subgroups enabled them to feed in diverse ways (Massare, 1987; McHenry et al., 2005; Zammit et al., 2008). Some of the skeletal fossils from Devon Island are attributed to polycotylids and pliosaurs. These groups have been characterised as nektonic feeders because their teeth are best adapted for piercing flesh (Massare, 1987). Elasmosaurids are also well represented at the Devon Island localities and generally possessed robust teeth that could pierce fleshy nektonic organisms and crush benthic organisms with hard parts (Massare, 1987). Chin et al. (2008) speculated that elasmosaurid plesiosaurs may have produced the Cretaceous greensand-filled faeces on Devon Island because (McHenry et al., 2005) showed that fossil gut contents within an Australian elasmosaur were dominated by molluscs. The latter study (McHenry et al., 2005) suggested that elasmosaurs used a 'benthic grazing' strategy in which they tilled or filtered the substrate with their teeth to unearth or disturb potential benthic prey. This feeding strategy appears to have been possible because of the inferred flexibility of the elasmosaur neck as modelled by Zammit et al. (2008).

Hesperornithiform birds

Hesperornithiforms likely occupied a trophic niche similar to modern foot-propelled diving birds like cormorants, loons, and grebes (Chiappe & Witmer, 2002; Dumont et al., 2016; Wilson, 2019). Their recurved unicuspid teeth appear to have been effective in catching slippery, fast-moving prey in the water column, suggesting a predominantly piscivorous diet (Dumont et al., 2016; Martin & Tate, 1976). Even so, the lack of fossil evidence for abundant small fish at higher latitudes led (Wilson et al., 2016) to speculate that these Cretaceous birds might have fed on a variety of other prey depending on the season. In place of fish, they may have consumed cephalopods or other soft-bodied invertebrates that are rarely preserved in the fossil record (Wilson et al., 2016).

Discussion

Fossil distributions and taphonomy

Nearly all vertebrate fossils found on Devon Island were located in greensand horizons of the Upper Kanguk Formation, with only one plesiosaur and an ichthyodectid fish located lower in section in siliceous mudstones. Slight differences in invertebrate and vertebrate diversity between the two Devon Island sites suggest at least minor differences in nearshore habitats. It is possible that the Eidsbotn locality offered a more sheltered environment that allowed colonisation by the hexactinellid sponges and lingulid brachiopods found there. In contrast, the Viks Fiord locality may represent more open water, thus accounting for the slightly higher diversity of nektonic fossil vertebrates. The marine macrofossil assemblages recovered from Eidsbotn and Viks Fiord grabens are highly unusual in the prodigious number of coprolites relative to skeletal fossils.

Several complex biological and taphonomic factors would have influenced the relative abundances of different types of fossils in these assemblages. A major factor is the relative supply of faeces, teeth, and bone deposited in the sediment before fossilisation. Vertebrates deposit faecal masses frequently (likely at least daily), and fish and reptile teeth can also be regularly added to sediments as they are often continually shed. The rate of tooth loss is highly variable, but one study documented that Pacific lingcod can shed 20 teeth per day (3.6% of their ~555 teeth) (Carr et al., 2021). Although most bones only enter the fossil record when an animal dies, we note that a single vertebrate carcass contributes multiple bones and teeth to the sediment. Preservation potential also plays a major role in the relative abundance of coprolites and body fossils in a deposit. Whereas mineralised bones and teeth have a high preservation potential when they enter the depositional environment, soft faecal matter requires specific conditions for mineralisation to occur (e.g. inferred rapid burial, appropriate redox conditions, etc.) (Hollocher & Hollocher, 2012). In most depositional settings, we might expect the lower preservation potential of faeces to reduce the abundance of coprolites in the sediment. As such, the mismatch in numbers of coprolites versus body fossils is surprising – particularly since the body fossils in the Devon Island assemblages are dominated by teeth which are deposited more frequently than bones. These relative numbers suggest that sizeable vertebrates engaged in extensive feeding activity while experiencing relatively low rates of tooth loss or attritional death in the area. This scenario is consistent with an influx of non-resident vertebrates exploiting a burst of seasonally abundant resources. We recognise that it is possible that conditions at the Devon Island sites were unusually conducive to fossilisation of faeces. However, the presence of epifaunal organisms (sponges, decapods, lingulid brachiopods, bivalves, etc.) and inferred nearshore depositional environment (Chin et al., 2008; Witkowski et al., 2011) do not indicate hypoxia or other unusual taphonomic conditions that would cause such differential preservation. Even if the number of fossilised faeces was skewed by conditions that favoured faecal preservation, the abundance of coprolites reflects considerable feeding activity at these sites.

Identifying the likely faecal producers

The Devon Island coprolites reflect distinctive feeding strategies used by ancient vertebrates at these two sites: 1) feeding on benthic organisms by ingesting large volumes of sediment; 2) ingesting plankton or soft-bodied planktivores; and 3) a combination of both benthic and pelagic feeding. The fact that coprolites of different sizes can have phosphatic, greensand, or mixed phosphatic/greensand coprofabrics suggests that defaecators of different sizes engaged in one or both of the benthic and planktonic feeding strategies. We consider the unique features of the Devon Island coprolites along with our analysis of the likely feeding behaviours of the coeval fossil vertebrates to infer which ancient vertebrates were most likely to engage in these feeding behaviours (Table 2).

Benthic feeders and greensand coprolites

Based on coprolite size, abundance of ingested sand, and the size, types, and completeness of prey inclusions, the greensand-dominated coprolites were likely produced by large deposit feeders.

Hesperornithiform birds were unlikely to be deposit feeders because they had relatively small narrow beaks and sharp, unicuspid recurved teeth. It is also implausible that *Squalicorax, Cretalamna*, *Enchodus, Pachyrhizodus*, ichthyodectiforms, polycotylids, or pliosaurs produced sediment-filled faeces because their dentition and body types were consistent with chasing and catching fast nektonic prey (and with the exception of *Squalicorax* and *Cretalamna*, they all lacked a spiral intestinal valve). The three remaining groups, ratfish, sturgeons, and plesiosaurs were more likely producers of the greensand faeces because of their inferred diets and feeding

Table 2. Devon Island vertebrates organised by characters involved in the creation of sediment dominated faeces or faeces that contain lumen structures.

Potential Defecator	Typical Adult Length > 1 m	Spiral/Scroll Valve	Benthic/Sediment- Dominated Stomach Contents	Durophagous Dentition/No Teeth
Hesperornithiform bird	X			
Enchodus				
Pachyrhizodus	X			
Xiphactinus	X			
Polycotylid plesiosaur	X			
Lamniform shark	X	X		
Ratfish		X	X	X
Elasmosaurid plesiosaur	X		X	X
Sturgeon	X	X	X	X

An X indicates that the potential defecators possesses the character.

strategies. Ratfish initially appear to be strong candidates for the producer of the greensand faeces because of their exclusively benthic diet. However, their small body size and the prey-crushing feeding behaviour observed in extant representatives are not a good match with the sizeable Devon Island greensand coprolites that contain relatively intact dietary inclusions (Figure 8).

Evidence suggests that elasmosaurid diets included both benthic and nektonic prey (Cicimurri & Everhart, 2001; Massare, 1987; McHenry et al., 2005; Noè et al., 2017; Zammit et al., 2008). The range of motion inferred for elasmosaurids likely allowed them to forage within the benthos (McHenry et al., 2005; Zammit et al., 2008) and possibly ingest sediment during feeding, ultimately resulting in sediment-filled faeces. The diets of extant sturgeons are also consistent with the contents of the greensand coprolites. The large amount of ingested sediment combined with a mix of mostly benthic prey items suggests that toothless adult sturgeons could have produced the greensand faeces. This is also consistent with the observation that some of the inclusions appear to be intact and show minimal evidence of oral processing.

Planktonic feeders and phosphatic coprolites

The density of siliceous microfossils and the paucity of macro-skeletal elements in the phosphatic faeces suggest that they were either produced by sizeable filter-feeding planktivores or carnivores feeding on soft-bodied planktivores (such as krill, jellyfish or poorly ossified fish that targeted microplankton but left little or no skeletal remains of their own). No fossil material clearly derived from specialised filter-feeding Cretaceous vertebrates was recovered from either locality. However, most Devon Island vertebrate taxa, with the exception of benthic-feeding ratfish, could have consumed soft-bodied planktivores.

Mixed greensand/phosphatic coprolites

The occurrence of coprolites with mixed greensand and microplankton contents is surprising because it indicates that some vertebrates employed two seemingly disparate feeding strategies. Organisms that produced these faeces would have been capable of deposit-feeding to consume benthic invertebrates as well as feeding on plankton or nektonic planktivores. Extant sturgeons are known to feed in the benthos (Johnson et al., 1997; Zarri & Palkovacs, 2018) and the water column and interpretations of the functional morphology of elasmosaurs suggest they also had similar varied feeding capabilities (Massare, 1987; McHenry et al., 2005; Zammit et al., 2008). This suggests that the mixed greensand and phosphatic faeces were produced by sturgeons or elasmosaurs.

Defaecators with spiral intestinal valves

Chondrichthyans, non-teleost actinopterygians, and non-tetrapod sarcopterygians have spiral (also known as scroll) intestinal valves (Burton & Burton, 2017). The unique shape of this structure improves digestion and absorption without requiring a longer intestinal tract (Burton & Burton, 2017). Evidence of spiral intestinal valves can be seen in coprolites in the form of spiral patterns visible in coprolite cross sections (Dentzien-Dias et al., 2021). These patterns may vary as valvular intestines have different morphologies (Leigh et al., 2021), and the number of intestinal whorls can be variable (Argyriou et al., 2016). Although the distinctive internal cylindrical structures in many of the Devon Island coprolites do not show a conspicuous spiral structure, the cylindrical structure resembles the central lumen that is often associated with valvular intestines and allows ingesta to bypass the spiral valves (Leigh et al., 2021) (Figures 6 and 7). This lumen structure can also be observed in the gut contents of modern chondrosteans which retain the plesiomorphic spiral intestinal valve condition (Figure 11). We know of no other intestinal structures that can shape the internal structure of faeces like this, so we infer that the cylinder-within-a-cylinder structures evident in 45 of the Devon Island coprolites were likely shaped by the passage of intestinal contents through a spiral or scroll intestinal valve. Sharks, ratfish, and sturgeons are the only groups from Devon Island known to have possessed spiral/scroll intestinal valves.

Most of the coprolites from Devon Island lack a clear cylinder-within-a-cylinder structure, so many may have been produced by vertebrates without valvular intestines. However, relatively few greensand coprolites are longitudinally fractured in such a way that reveals internal cylinders. (Byrne et al., 2022) observed that external views of some Devonian coprolites often suggest a non-spiral morphology, even though synchrotron analyses of the same specimens reveal an internal spiral configuration accentuated by the orientation of tiny acanthodian scales inside the coprolites. The subtle evidence for valvular intestines observed in longitudinally fractured greensand coprolites from Devon Island could indicate that the high sand content in the greensand coprolites may be responsible for concealing evidence for extrusion through valvular intestines. This suggests that more coprolites beyond the 45 Devon Island coprolite specimens with an identified lumen can likely be ascribed to vertebrates with valvular intestines.

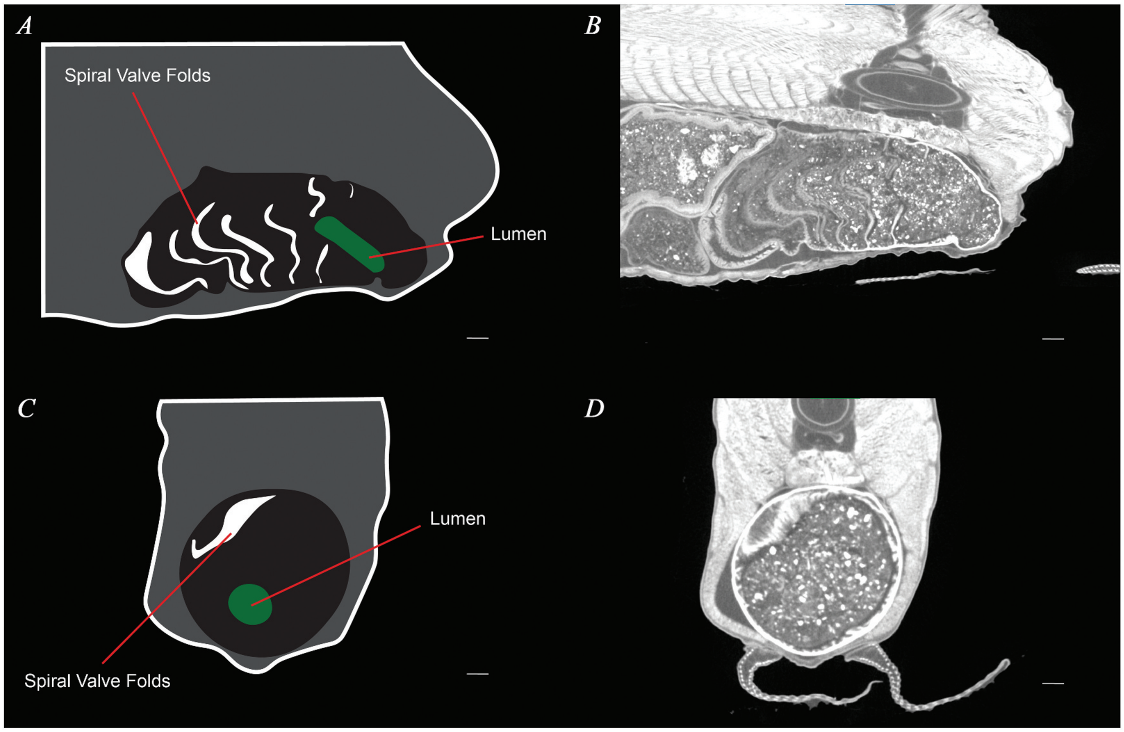

Figure 11. Image slices from Dice-CT scan of VIMS 42992, stained with buffered Lugol's iodine, scanned by Jaimi Gray. (a) &; (b) Sagittal section of *Polyodon spathula (American paddlefish)* showing a lumen structure in lateromedial view. (c) &; (d) Cross section of *Polyodon spathula* showing a lumen structure in anteroposterior view. All scale bars are 1 mm.

Synthesis: most likely defaecators

The cylinder-within-a-cylinder structures likely created by spiral/scroll valves are found at both Devon Island localities and in all three types of coprolites: these structures are evident in at least 7 greensand coprolites, 29 phosphatic coprolites, and 9 mixed coprolites. Moreover, these coprolites show a narrow range of internal cylinder diameters (~9–12 mm) across both localities and within all coprolite types (Table 3). Our standard one-way ANOVA test demonstrated that these diameter averages do not differ to a statistically significant degree across predominant groundmass. This consistency suggests that many of the coprolites with tube structures were likely produced by similar sized individuals, possibly of the same species. Because sturgeons are the only known vertebrates from the ancient Devon Island ecosystem that possessed a spiral intestinal valve and could feed in both the benthos and the water column, we conclude that the 45 coprolites with these structures were most likely fossilised sturgeon faeces.

Inferring Cretaceous marine migration in the Devon Island area

Although evidence for migratory behaviour can be difficult to recognise, we found several lines of evidence suggesting seasonal exploitation of resources in the Devon Island area during the Late Cretaceous. These include evidence from microfossils, coprolites, behaviour of extant taxa, and palaeogeographical distributions.

Seasonal resources in the Cretaceous Arctic

The abundant microfossils found in both Eidsbotn and Viks Fiord grabens (Chin et al., 2008; Witkowski et al., 2011) demonstrate that the Devon Island area supported massive diatom blooms during the seasonal onset of extended daylight during the Late Cretaceous. These planktonic blooms would have supported large numbers of heterotrophic organisms at multiple trophic levels. We have fossil evidence that these heterotrophs

Table 3. Coprolite specimens with observed lumen structures organised by locality, dominant coprolite groundmass, and average lumen diameter.

Coprolites with Lumens	Eidsbotn	Viks Fiord	Total	Average Lumen Diameter
Greensand	7	0	7	10.5 mm
Mixed	4	5	9	10.2 mm
Phosphate	12	17	29	9.1 mm

included zooplankton (e.g. dinoflagellates and radiolarians), invertebrates (e.g. sponges, lingulid brachiopods, squid, decapods, molluscs), and the sizeable vertebrates whose faeces became fossilised. At a minimum, the abundant plankton-filled coprolites document extensive vertebrate feeding activity that was coincident with diatom blooms. Since Arctic plankton blooms would have occurred with the onset of long photoperiods, such seasonal resource windfalls would have likely attracted mobile non-resident visitors from other locales that the environment could not have supported year-round. Thus, we infer that the disproportionately high number of coprolites not only records utilisation of resources by local residents but also reflects exploitation of seasonal foods by migratory visitors to the area. Because we identified at least 45 likely sturgeon coprolites, it appears that a population of sturgeons seasonally inhabited the Cretaceous Devon Island environment.

Modern analogs of migratory sturgeons

The migratory behaviour of extant anadromous sturgeons may serve as a modern analog for their Late Cretaceous ancestors because sturgeon morphology is highly conserved (Hilton & Grande, 2006). Despite a lack of soft-body preservation, the biogeographic occurrence data of sturgeons during the Late Cretaceous (Figure 9) suggest the key metabolic and osmoregulatory features that support anadromy and extended marine migration in extant sturgeons were also present in their Late Cretaceous ancestors. Extant anadromous sturgeons spend most of their lives in marine systems but migrate to shallow marine or estuarine systems to exploit seasonal food resources before moving into freshwater habitats to spawn in protected environments (Krayushkina, 2006; McKeown, 1984; Moser et al., 2016; Secor, 2015; Taylor et al., 2016). Like other anadromous fish, sturgeons follow predictable routes, and aggregate in great numbers when migrating to their spawning sites (Secor, 2015). They often travel thousands of kilometres and have been observed migrating up to 58 kilometres per day (Lindley et al., 2008; McKeown, 1984). If the migration of Cretaceous sturgeons was similar to the behaviour of their modern descendants, the nearshore Devon Island ecosystem may have served as a shallow marine waypoint with abundant food resources for anadromous sturgeons making their way towards protected spawning grounds in nearby freshwater systems.

Migration of other Cretaceous marine vertebrates

We ascertained that at least 45 of the Devon Island coprolites can be attributed to sturgeons and it is likely that many more of the abundant coprolites were also preserved sturgeon faeces. Nevertheless, it is possible that some of the fossilised faeces from Devon Island were produced by other Cretaceous vertebrates that also took advantage of abundant food resources supported by seasonal planktonic blooms. The occurrence data of other vertebrates (lamniform sharks, teleosts, plesiosaurs) that may have produced the coprolites found on Devon Island suggest populations of these taxa might have travelled north and south within the Western Interior Seaway (Figure 9) depending on the season. This suggests that the Devon Island paleoenvironment could have hosted populations of other visiting marine vertebrates in addition to sturgeons.

Conclusions

The Cretaceous marine fossil assemblages recovered from two sites on Devon Island are highly unusual in the great abundance of coprolites relative to body fossils. Analyses of the contents and chemical composition of more than 450 coprolites revealed three distinctive feeding strategies: 1) deposit feeding in the benthos; 2) ingestion of plankton or planktivores in the water column; and 3) a combination of both benthic and planktonic feeding. Correlation of these feeding strategies with the valvular internal structure of the coprolites and with the feeding capabilities of coeval fossil vertebrate taxa from the same sites singles out sturgeons as the source of at least 45 of the coprolite specimens.

Four lines of evidence support the interpretation that Devon Island was likely the temporary residence of at least one population of migratory vertebrates: 1) fossil evidence of countless diatoms in the sediments and in coprolites indicate the occurrence of large phytoplankton blooms that would have provided seasonally abundant resources that supported multiple trophic levels in the Devon Island paleoecosystem; 2) coprolites occur in far greater numbers than fossil skeletal material, suggesting that some vertebrates were seasonal visitors that only temporarily occupied the area while feeding; 3) at least some of the ancient faeces were likely created by sturgeons, a group whose extant members are predominantly migratory; and 4) the biogeographical distributions of several Devon Island fossil taxa within the Western Interior suggest that some of these taxa may have migrated during this period.

This study suggests that seasonal planktonic blooms at the Devon Island localities helped provide reliable resource-rich destinations or waypoints for non-residential fish and/or marine reptiles in the Cretaceous. The maximum extent of the Late Cretaceous Western

Interior Seaway in the mid-late Campanian (Figure 1) opened wider connections between the southern part of the seaway and the Arctic (Burgener et al., 2021). The nutrient-rich waters from phytoplankton blooms in the Devon Island area would have been highly attractive and accessible to a variety of Cretaceous marine vertebrates. The impacts of migrating organisms can be far-reaching; extant migratory marine fauna can transport key nutrients such as carbon, nitrogen, and phosphorus through defaecation. This can translocate nutrients away from productive hubs both laterally across ecosystems and vertically within the water column, connecting many isolated marine environments (Doughty et al., 2015). The cycling of nutrients within the Devon Island paleoecosystem, as well as in and out of the Arctic, suggests vertebrate-aided redistribution of resources through parts of the Western Interior Seaway in the Late Cretaceous.

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Author contributions

CRediT: **Franklin Duffy:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Visualization, Writing – original draft, Writing – review & editing; **Karen Chin:** Conceptualization, Investigation, Resources, Supervision, Writing – original draft, Writing – review & editing; **Steve Cumbaa:** Resources, Supervision, Writing – review & editing; **Laura Wilson:** Data curation, Formal analysis, Methodology, Writing – review & editing.

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Data availability statement

The data that support the findings of this study are openly available on Morphosource at https://www.morphosource.org/projects/000821614/temporary_link/Ss6KHpvpr8ch8Aw5qqLCsBZ5?locale=en

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