Life in a Temperate Polar Sea: A Unique Taphonomic Window on the Structure of a Late Cretaceous Arctic Marine Ecosystem

Karen Chin
University of Colorado, karen.chin@colorado.edu

John Bloch
University of New Mexico

Arthur Sweet
Natural Resources Canada

Justin Tweet
University of Colorado

Jaelyn Eberle
University of Colorado

See next page for additional authors

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Authors

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Karen Chin,[1,2] John Bloch,[3] Arthur Sweet,[4] Justin Tweet,[1] Jaelyn Eberle,[1,2]
Stephen Cumbaa,[5] Jakub Witkowski,[6] and David Harwood[7]

[1] Department of Geological Sciences, University of Colorado, Boulder, CO 80309, USA
[2] Museum of Natural History, University of Colorado, Boulder, CO 80309, USA
[3] Department of Earth and Planetary Sciences, University of New Mexico, Albuquerque, NM 87131, USA
[4] Geological Survey of Canada, Natural Resources Canada, Calgary, Alberta, Canada T2L 2A7
[5] Research Services, Canadian Museum of Nature, Ottawa, Ont., Canada K1P 6P4
[6] Paleontology Section, Warsaw University, 00-927 Warszawa, Poland
[7] Department of Geosciences, University of Nebraska–Lincoln, Lincoln, NE 68588, USA

Corresponding author — Karen Chin, Department of Geological Sciences,
University of Colorado, Boulder, CO 80309, USA; karen.chin@colorado.edu

Abstract
As the earth faces a warming climate, the rock record reminds us that comparable climatic scenarios have occurred before. In the Late Cretaceous, Arctic marine organisms were not subject to frigid temperatures but still contended with seasonal extremes in photoperiod. Here, we describe an unusual fossil assemblage from Devon Island, Arctic Canada, that offers a snapshot of a *ca* 75 MYR ago marine paleo-ecosystem adapted to such conditions. Thick siliceous biogenic sediments and glaucony sands reveal remarkably persistent high primary productivity along a high-latitude Late Cretaceous coastline. Abundant fossil feces demonstrate that this planktonic bounty supported benthic invertebrates and large, possibly seasonal, vertebrates in short food chains. These ancient organisms filled trophic roles comparable to those of extant Arctic species, but there were fundamental differences in resource dynamics. Whereas most of the modern Arctic is oligotrophic and structured by resources from melting sea ice, we suggest that forested terrestrial landscapes helped support the ancient marine community through high levels of terrigenous organic input.

Keywords: paleoecology, polar, coprolites, diatoms, vertebrates, trophic

1. Introduction

Paleoclimatic analyses (e.g. Crowley & North 1991; Tarduno *et al*. 1998; DeConto *et al*. 2000) indicate that Late Cretaceous Arctic marine habitats were appreciably warmer than those of today; Campanian average sea surface temperatures may have been as warm as 15°C (Jenkyns *et al*. 2004). Such paleoenvironmental conditions have no modern analogue, i.e. seasonally extreme polar photoperiods in combination with a temperate climate. As such, Late Cretaceous marine environments would have been markedly different from those in the present-day Arctic, both in terms of warm polar conditions and having a Mesozoic suite of organisms. Little is known about the structure and dynamics of marine communities that inhabited such ecosystems.

Although more temperate conditions may have been favorable for a broader range of organisms, polar light regimes present special challenges. Whereas primary production at lower latitudes is not light limited and occurs whenever other conditions are favorable, polar phytoplankton can only photosynthesize during the relatively brief time when solar radiation is largely continuous, but lower in intensity than that found at lower latitudes (Fogg 1998). This timing has important implications for polar heterotrophs that must time their own activities (e.g. breeding and migration) to coincide with the relatively brief pulse of primary productivity.

Varying levels of primary productivity might be envisaged for ice-free Arctic waters. Sea ice plays a major role in structuring modern Arctic ecosystems: floes host dense concentrations of ice algae that provide rich, ephemeral food and nutrient sources during melt. Sea ice also facilitates open-water diatom blooms by fostering ocean stratification. On the other hand, floes reduce light intensity in the photic zone, cause fluctuations in salinity and can gouge benthic habitats (Fogg 1998; Kaiser *et al*. 2005). These observations suggest two possible scenarios for a temperate Arctic: productivity might have been poor without the interface of sea ice; conversely with adequate nutrient supply, greater solar radiation in the water column might have resulted in higher rates of photosynthesis (Sakshaug 2004).

Different climates and terrestrial floras influence the composition of riverine discharges into the marine system. In the cold present-day Arctic, rivers drain landscapes dominated by short-stature tundra. Channels frozen by permafrost generally discharge little water from autumn to the spring freshet, and the intermittent discharge causes fluctuations in salinity (Dunton *et al*. 2006). The timing and composition of run-off into the marine environment would have been significantly different in a warmer, forested Arctic.

Testing these theoretical constraints on extinct polar communities presents a challenge because methods employed to analyze modern ecosystems (e.g. remote sensing of chloro-

phyll, direct observation, etc.) are not available. A number of studies have described specific organisms found in Late Cretaceous Arctic marine sediments, including diatoms (e.g. Dell'Agnese & Clark 1994; Tapia & Harwood 2002), dinoflagellates (Núñez-Betelu & Hills 1992*a*) and vertebrates (Russell 1967, 1990; Hills *et al.* 1999; Friedman *et al.* 2003), but the paucity of fossiliferous deposits has made it difficult to determine how these organisms were integrated within Cretaceous polar communities. Unique fossil deposits on Devon Island in the Canadian High Arctic, however, reveal a spectrum of fossil invertebrates, vertebrates, wood, siliceous microfossils, palynomorphs and coprolites that shed light on the flow of energy and nutrients through the ancient coastal ecosystem. Moreover, abundant coprolites provide rare direct evidence of trophic structure. Reconstructing aspects of a Late Cretaceous temperate ecosystem offer evolutionary and paleoenvironmental perspectives on the modern Arctic. In essence, it presents an opportunity to examine the paleo-ecosystem data as a proxy for experiments on high-latitude systems that cannot be run in today's world.

2. Material and methods

Two fossil localities were investigated on northwestern Devon Island, Nunavut, Canada, at Eidsbotn (approx. 76°17′N, 91°12′W) and Viks Fiord (approx. 76°2′N, 91°32′W) grabens (Figure 1). Stratigraphic sections were measured at both localities, and numerous fossils and sediment samples were collected. Fossils collected in 1998 were catalogued in the collections of the Canadian Museum of Nature; those collected in 2003 were assigned Government of Nunavut numbers for repository at the Canadian Museum of Nature. Thin sections of coprolite samples were prepared, photographed and analyzed with image analysis at the University of Colorado. Mudstones were examined by backscattered electron microscopy, and bulk chemical compositions of samples were determined by X-ray fluorescence at the University of New Mexico. Palynological, Rock-Eval 6 (kerogen characterization; Whelan & Thompson-Rizer 1993) and maceral analyses were performed at the Geological Survey of Canada, where the palynological residues and slide mounts are reposited. Siliceous microfossils were extracted from sediment samples and analyzed at the University of Nebraska and Warsaw University; scanning electron micrographs of diatom specimens were taken at Johann Wolfgang Goethe University.

3. Results

(a) Geologic setting

At Eidsbotn and Viks Fiord grabens, Upper Cretaceous sediments are preserved in syndepositional down-faulted blocks within the Paleozoic carbonate that covers much of Devon Island today (Mayr *et al.* 1998). The two field sites are approximately 30 km apart, and are dominated by sediments of the upper Kanguk Formation, a unit that spans much of the Upper Cretaceous (Mayr 1998). Paleogeographic reconstructions indicate that Devon Island was no farther south than approximately 70°N in the Campanian (Tarduno *et al.* 1998; Scotese 2002), so the region was located well above the Arctic Circle at that time.
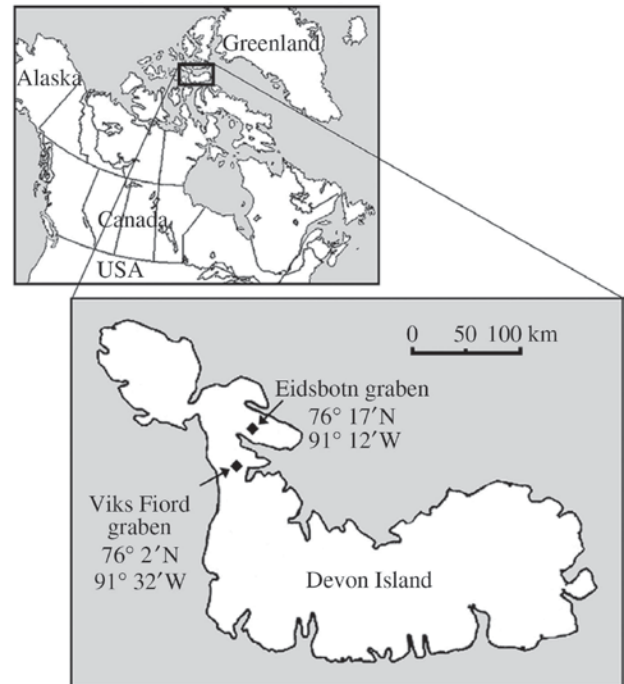

Figure 1. Map showing fossil localities at Eidsbotn and Viks Fiord grabens on Devon Island in the Canadian High Arctic.

Stratigraphic sections reveal over 200m of clastic sediments at Eidsbotn graben and 40m at Viks Fiord graben, demonstrating a conformable stratigraphic succession from Kanguk Formation marine mudstones through glaucony sandstones (greensands), up to terrestrial sediments (Expedition Fiord Formation; Figure 2) at the top of the sequence. The patchy exposures at Viks Fiord graben cannot be accurately correlated with each other, or with the more extensive sections at Eidsbotn graben, but sediments and fauna from both the localities are broadly similar.

An unusual feature of both Devon Island localities is the occurrence of thick (up to 75m at Eidsbotn), friable, greensand deposits that include interbedded mudstone and bentonite. The greensand grains are dominantly fine sand-sized glaucony with approximately 3.1–4.2 wt percent K_2O, and many grains are clearly derived from glauconitization of radiolarian tests. Scattered skeletal fossils and abundant coprolites occur in the greensands, although steep slopes, slumping and frost heaving made it difficult to determine the original stratigraphic position of the fossils. Dark marine mudstones underlying or intercalating the greensands are rich in biogenic siliceous microfossils with some volcaniclastic debris and little detrital silt; macrofossils are uncommon in the extensively bioturbated mudstones.

Total organic carbon (TOC) of the sediments ranges from 0.11 to 3.34 percent in eleven mudstone samples (mean = 0.73%) and from 0.08 to 0.22 percent in four greensands (mean = 0.14%). Rock-Eval 6 analyses of mudstones with TOC ≥ 0.9 show consistently low hydrogen indices (HI) that are typical of type III kerogens derived from terrigenous plant precursors. Even fully marine samples exhibit a terrestrial pyrolysis signature (Figure 3). Maceral analyses of three coprolites reveal nearly equal contributions of terrigenous and marine organic matter in one; the other two are dominated by marine macerals, with trace amounts of terrigenous debris.
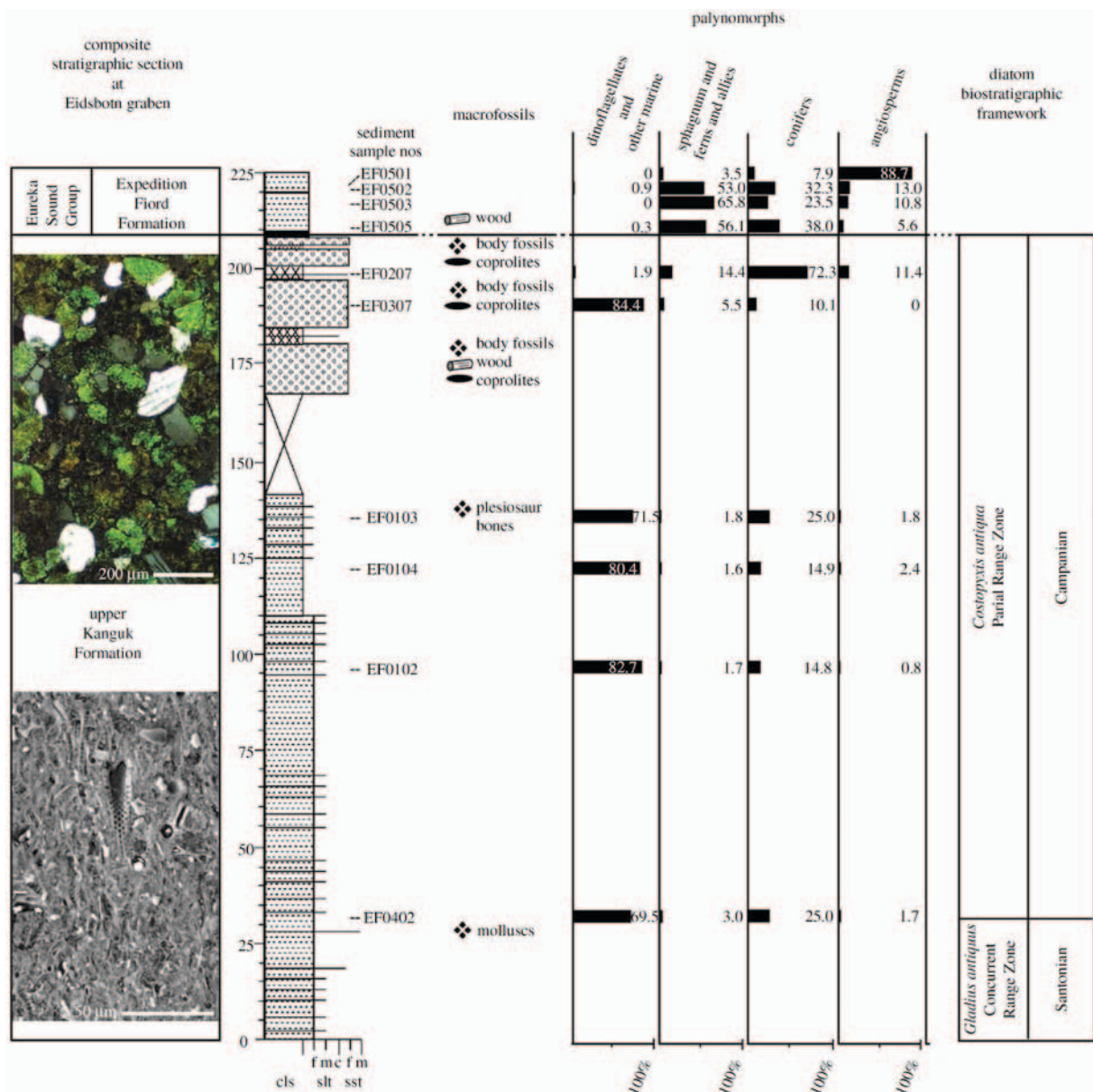
Figure 2. Composite stratigraphic column of Upper Cretaceous sediments exposed at Eidsbotn graben on Devon Island. Inset photomicrographs are of glaucony sandstone (above; crossed nicols) and siliceous mudstone (below; scanning electron micrograph). Column also shows distribution of macrofossils, relative percentages of palynomorph types in samples and diatom biostratigraphic zones.

(b) Marine microfossils

Mudstones from both Eidsbotn and Viks Fiord grabens show surprisingly diverse assemblages of organic and siliceous microfossils (Figure 4). The density of siliceous fossils in the mudstones is particularly striking. These biogenically rich sediments are dominated by diatoms (Figure 4,*a–h*), indicating large populations of autotrophic phytoplankton. Over one hundred diatom taxa representing around 40 genera are identified, including planktonic taxa (approx. 43%), resting spores (approx. 27%), and benthic and tychoplanktonic forms (approx. 20%; J. Witkowski 2008, unpublished master's thesis). Diatom biostratigraphy of the upper portion of the composite section of Eidsbotn graben indicates a stratigraphic position within the Campanian *Costopyxis antiqua* Partial Range Zone of Tapia & Harwood (2002) based on the presence of *C. antiqua* and absence of *Gladius anti-*

quus. The presence of *G. antiquus* in stratigraphically lower mudstones, however, suggests that the Santonian–Campanian boundary occurs in the lower part of the section, based on the last known occurrence of this taxon (Figure 2; Tapia & Harwood 2002). Radiolarians, silicoflagellates and sponge spicules are common in samples from both sites.

Palynological samples are also productive and show a gradient from marine Kanguk Formation samples dominated by organic-walled cysts of marine dinoflagellates to wholly terrigenous assemblages of pollen and spores from the overlying Expedition Fiord Formation. Approximately 75 different dinoflagellate taxa are present in sediments from both sites. Common genera include *Laciniadinium*, *Heterosphaeridium* and *Fromea* (Figure 4,*i–o*). Although some dinoflagellates are mixotrophic or heterotrophic, approximately half of extant species are autotrophic (Larsen & Sournia 1991). This suggests that some of the Devon Island dinoflagellates were photosynthetic,

along with substantial numbers of *Leiosphaeridia* prasinophyte algal cysts also found in the mudstones.

(c) Marine invertebrate and vertebrate fossils

Modest numbers of invertebrate and vertebrate fossils occur in the greensands or within coprolites from both sites (Figures 5–7a), representing bivalve mollusks (inoceramids and *Teredolites* borings), decapod crustaceans, cephalopods, cartilaginous fishes (lamniform sharks and ratfish), bony fishes (*Xiphactinus* and *Enchodus*), plesiosaurs (both elasmosaurids and polycotylids) and hesperornithiform birds. Hexactinellid sponges (Rigby *et al.* 2007) and lingulid brachiopods were found only at Eidsbotn graben, whereas teeth from *Squalicorax* (a shark), *Ichthyodectes*, cf. *Pachyrhizodus* (bony fishes) and a mosasaur were recovered at Viks Fiord graben.

The only calcareous fossils evident in the greensands are bivalve mollusks preserved within coprolites or as moulds or casts in sediment. Other mollusk material was found in mudstones at one site low in the section at Eidsbotn graben. Skeletal elements representing approximately 30 sponges, 30 lingulids and 30 bivalves were collected. Roughly 30 cartilaginous fish, 50 bony fish, 30 marine reptile and 6 hesperornithiform bird fossils were collected, most of which were individual teeth. These are relatively small numbers considering the volume of bioclastic sediment and the fact that all vertebrate fossils encountered were collected.

(d) Coprolites

Nearly 300 partial to entire coprolites were collected from Eidsbotn and Viks Fiord grabens for analysis, and countless more remain in the field. Unbroken specimens are generally fusiform, oblong, spheroidal or irregular variations on these morphologies. Although the specimens display considerable morphological and size variation, they can be characterized by two distinct compositions: a high phosphate/siliceous microfossil coprofabric, or a greensand coprofabric (Figure 6). High phosphate specimens (*n* = 70) are black or tan in color and are composed of microcrystalline calcium phosphate; analyzed specimens contain approximately 29.0–37.8 wt percent P_2O_5. Thin sections of these high phosphate specimens reveal that most have high concentrations of siliceous microfossils in the phosphatic groundmass; other recognizable inclusions such as fish bone or mollusk shell are rare. The majority of the high phosphate/microfossil coprolites are conspicuously burrowed, with open or filled burrows up to more than 5 mm in diameter. Greensand coprolites (*n* = 208) are distinguished by having significant quantities of greensand clasts (approx. 25–63% as measured by image analysis). These specimens also contain substantial apatite (approx. 17.8–21.5 wt% P_2O_5) and a variety of inclusions, including crustacean carapace parts, mollusk shell fragments, lingulid shell, sponge spicules and wood fragments. Invertebrate fecal pellets and burrow traces are common on the surfaces of these specimens, and tiny (approx. 40 µm diameter) open burrows have been found in the interiors.

Several lines of evidence corroborate a fecal origin for both phosphatic and greensand specimens. The high phosphorus content relative to the host sediment (less than 0.5 wt% P_2O_5) is particularly significant because most coprolites are phosphatic (Bradley 1946; Häntzschel *et al.* 1968). The clustering of invertebrate fecal pellets on the surface of many
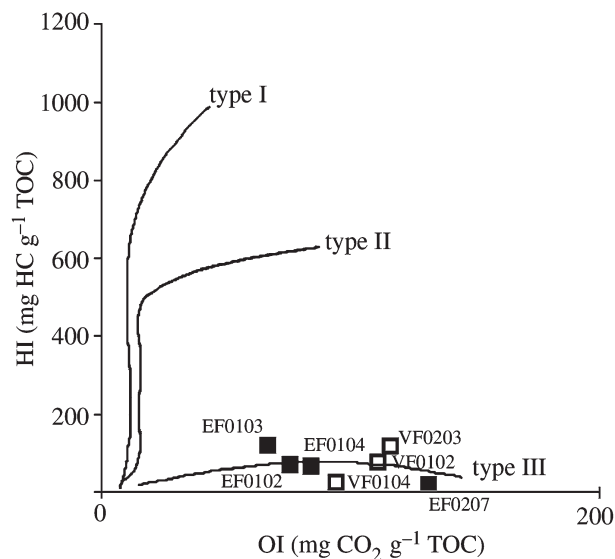

Figure 3. Modified Van Krevelen diagram showing kerogen types of Cretaceous Devon Island samples determined by hydrogen (HI) and oxygen indices (OI; measured by Rock-Eval 6 pyrolysis). All samples are marine mudstones (three from Viks Fiord graben (open squares) and four from Eidsbotn graben (filled squares); see Figure 2) that behave as type III kerogens typically composed of vascular plant components.

specimens (Figure 6,*a,d*) helps define the outer surfaces of the feces and argues against concretion development by radiation from organic nuclei. Similarly, voids and open burrows inside specimens (Figure 6*e*) indicate that lithification occurred as replacement of existing substrate rather than as void-filling cementation; the high bacterial content of feces appears to facilitate rapid phosphatization (Chin *et al.* 2003). Finally, the recurring sizes and fusiform shapes with tapered ends are consistent with fecal masses. Non-fecal marine concretions may show a laminated internal structure, sub-angular shapes (Marshall-Neill & Rufell 2004), collateral growth into surrounding sediments or morphologies that conform to the body fossils they enclose (Hall & Savrda 2008). A non-fecal concretion from Eidsbotn graben differs from coprolite specimens in having less P_2O_5 (approx. 14.5 wt%), significantly more silicon (38.2 wt% versus 3.8–26.2 wt% SiO_2) and greensand clasts (approx. 90%), and no burrows.

Excavation and sieving of $0.2m^3$ of sediment from each of two selected sites at Viks Fiord graben revealed densities of approximately 1.6 and 2.8l of coprolite m^{-3} of sediment; no body fossils were found in these sediments. Calculation of volume by water displacement indicates individual coprolite volumes up to 0.3l, signifying sizeable fecal producers.

(e) Terrestrial plant and palynomorph fossils

Pollen and spores are present in both the terrestrial Expedition Fiord and marine Kanguk Formations. These miospores reveal a diverse terrestrial flora that included sphagnum, ferns, gymnosperms and angiosperms (Figure 7,*b–e*). Substantial percentages (13.1–98.1%) of terrigenous miospores are present in the Kanguk Formation samples; conversely, sparse dinoflagellates (0.3–0.9%) in two Expedition Fiord samples confirm proximity to the marine environment (Figure 2). The most common gymnosperm palynomorphs
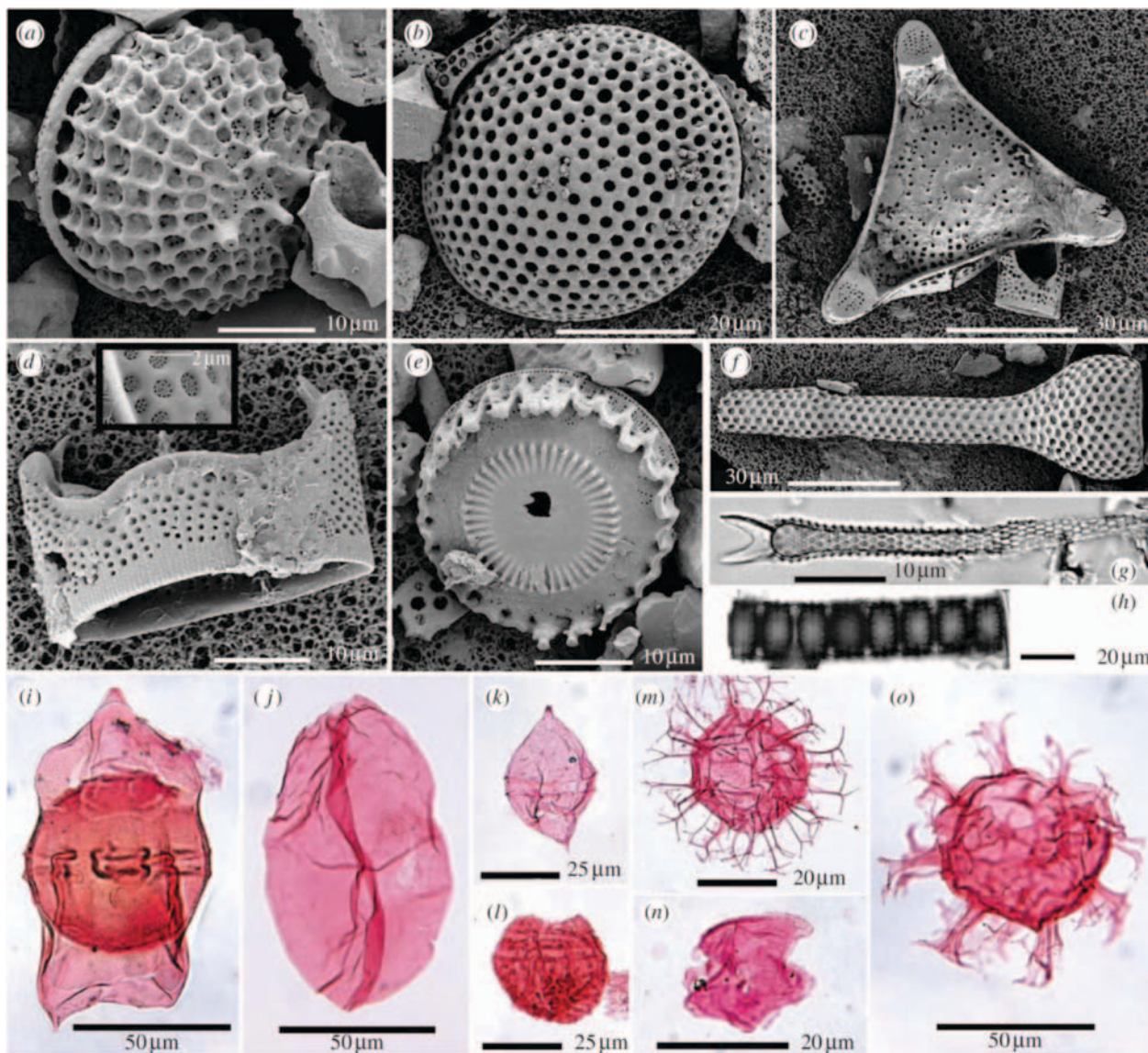
Figure 4. Late Cretaceous marine microfossils from Devon Island, including (*a–h*) diatoms and (*i–m*) dinoflagellates. Mudstone sample numbers are given in parentheses. (*a*) *Costopyxis antiqua* (EF0102), (*b*) *Stephanopyxis dissonus* (EF0103), (*c*) *Trinacria indefinita* (EF0103), (*d*) *Hemiaulus antiquus* (EF0304); inset is close-up of areolae. (*e*) *Paralia crenulata* (EF0102), (*f*) *Gladiopsis speciosus* (EF0103), (*g*) *Gladius antiquus* (EF0402), (*h*) chain of *P. crenulata* (EF0103), (*i*) *Chatangiella granulifera* (EF0402; GSC type no. 124280), (*j*) *Fromea fragilis* (EF0307; GSC type no. 124281), (*k*) *Laciniadinium arcticum* (EF0307; GSC type no. 24282), (*l*) *Alisocysta brevivallata* (VF0303; GSC type no. 124283), (*m*) *Spiniferites ramosus* (VF0305; GSC type no. 124284), (*n*) *Horologinella apiculata* (VF0301; GSC type no. 124285) and (*o*) *Heterosphaeridium difficile* (VF0303; GSC type no. 124286).

are from taxodiaceous conifers. Fossilized conifer wood is present as coalified wood in the Expedition Fiord sediments and permineralized wood in the Kanguk Formation; growth rings are evident in both types of samples. Several fossil wood specimens from the marine sediments are conspicuously bored and at least some of these traces can be classified as *Teredolites* (Figure 7*a*).

The angiosperm palynomorphs support a Campanian age. The presence of *Translucentipollis plicatilis* near the upper part of the Kanguk Formation exposure at Eidsbotn graben and *Wodehouseia edmontonicola* in the Expedition Fiord Formation at Viks Fiord graben can be correlated with the occurrence of these palynomorphs in the uppermost Campanian of Alberta (most probable age ranges 73–76 and 72–73.5 MYR ago, respectively; Lerbekmo & Braman 2002; Braman & Koppelhus 2005; Eberth 2005).

4. Discussion

(a) Paleoenvironment and taphonomic setting

Upper Cretaceous sediments on Devon Island represent a regressive marine sequence that progressed from distal mudstones to more proximal greensands and coastal terrestrial sediments. The thickness of the greensand sediments is somewhat surprising. Studies suggest that glauconitization of granular substrates occurs in open marine environments at the sediment/water interface under conditions of low sedimentation; this process is estimated to take 10^3–10^6 years. Fecal pellets are the most common substrates for glaucony forming in modern environments, but porous planktonic tests or mineral grains may also serve as foci for the development of green marine clays (Odin & Fullager 1988). These
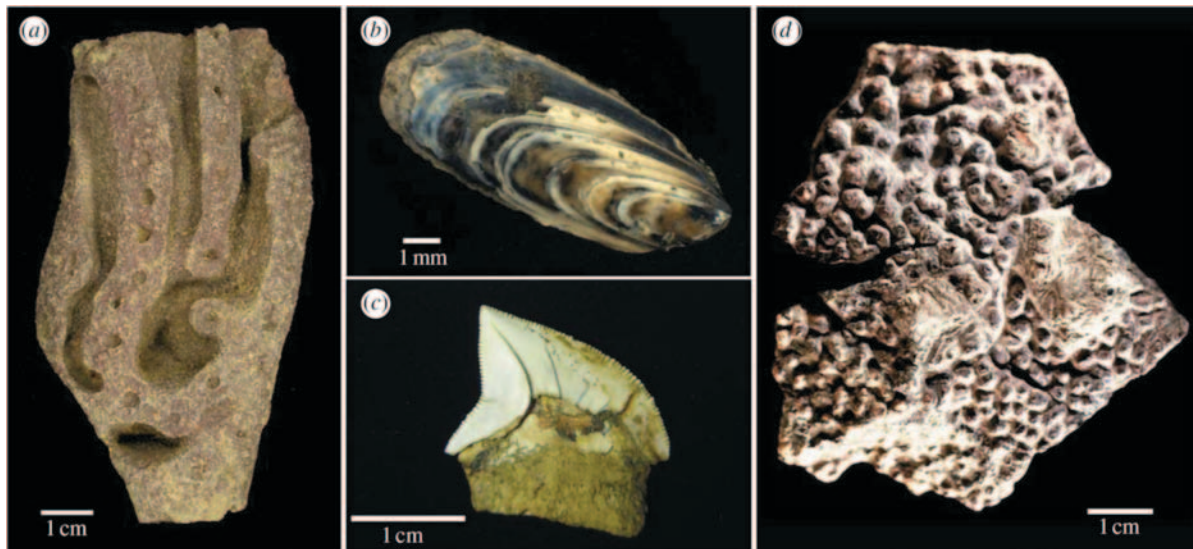
Figure 5. Invertebrate and vertebrate fossils from the study areas. (*a*) *Nunavutospongia irregulara* hexactinellid sponge from Eidsbotn (paratype, NUIF 176). (*b*) Lingulid brachiopod from Eidsbotn. (*c*) *Squalicorax pristodontus* shark tooth, Viks Fiord (NUFV 336). (*d*) Dermal plate from an unidentified bony fish, Eidsbotn (CMNFV 52783).
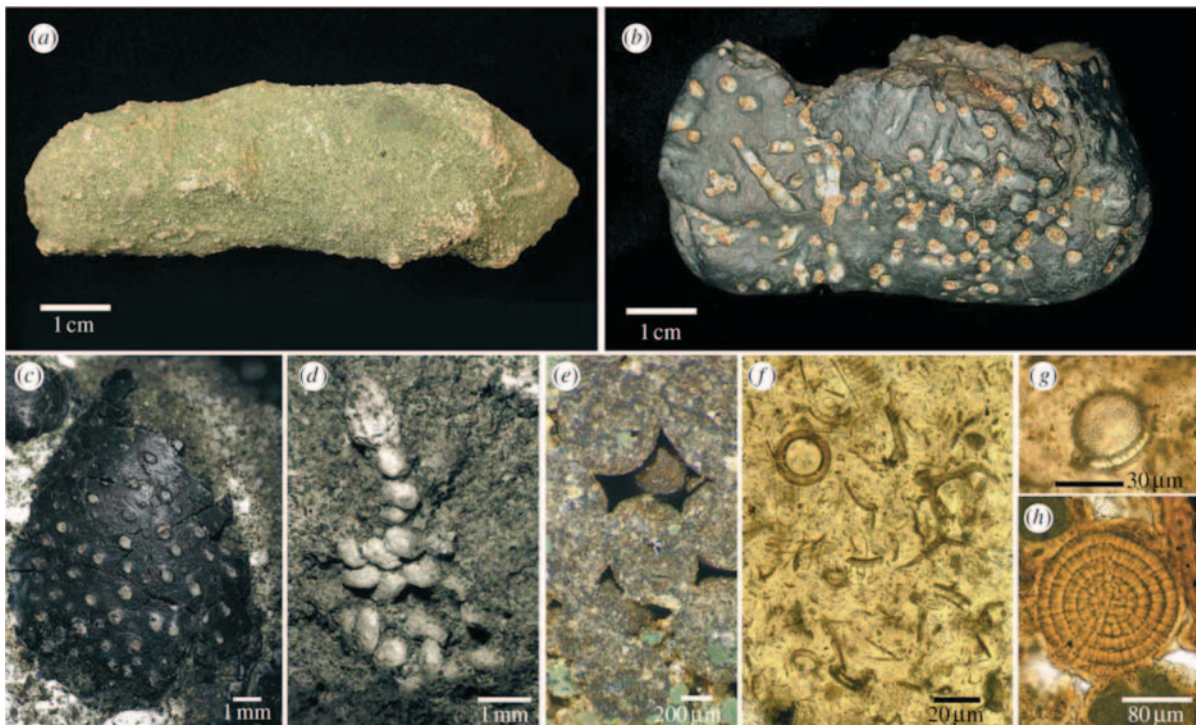

Figure 6. Coprolites and coprolite inclusions from the Kanguk Formation, Devon Island. (*a*) Greensand coprolite with patches of invertebrate pellets clustered on the surface (UL59/NUVF 75). (*b*) Dark phosphatic coprolite from Eidsbotn graben showing extensive burrowing (UL52/NUVF 75). (*c*) Decapod crustacean exoskeleton within a coprolite (UL94/NUVF 75). (*d*) Invertebrate fecal pellets on the surface of a greensand coprolite (RLO29/NUVF 70). (*e*) Invertebrate fecal pellets inside a greensand coprolite. Voids between pellets indicate mineral replacement rather than void-filling concretionary growth (UL98-1/CMN 52000). (*f*) Abundant siliceous microfossils inside a phosphatic coprolite (UL52c/NUVF 75). (*g*) *Costopyxis* sp. diatom within a greensand coprolite (UL98-2/CMN 52001). (*h*) Radiolarian within a greensand coprolite (UL98-1/CMN 52000).

generalized conditions for glaucony formation and the observations of glauconitized radiolarian tests suggest that the thick Kanguk Formation greensands reflect a robust and protracted rain of planktonic tests and feces in a syndepositionally subsiding basin, providing a relatively stable soft-sediment habitat on the continental shelf. Abundant greensand grains in the coprolites indicate that the process of glauconitization did not post-date the marine community.

Because seawater is undersaturated with respect to silicic acid, preservation of diatomaceous sediments in coastal regions is an indicator of high primary productivity (Nelson *et al.* 1995). Thus, the thick biogenic mudstones along with the considerable greensands and dinoflagellate cysts at the Devon Island sites indicate vigorous productivity that required access to ample nutrients. This suggests basic differences in nutrient supply from those in the modern Arc-
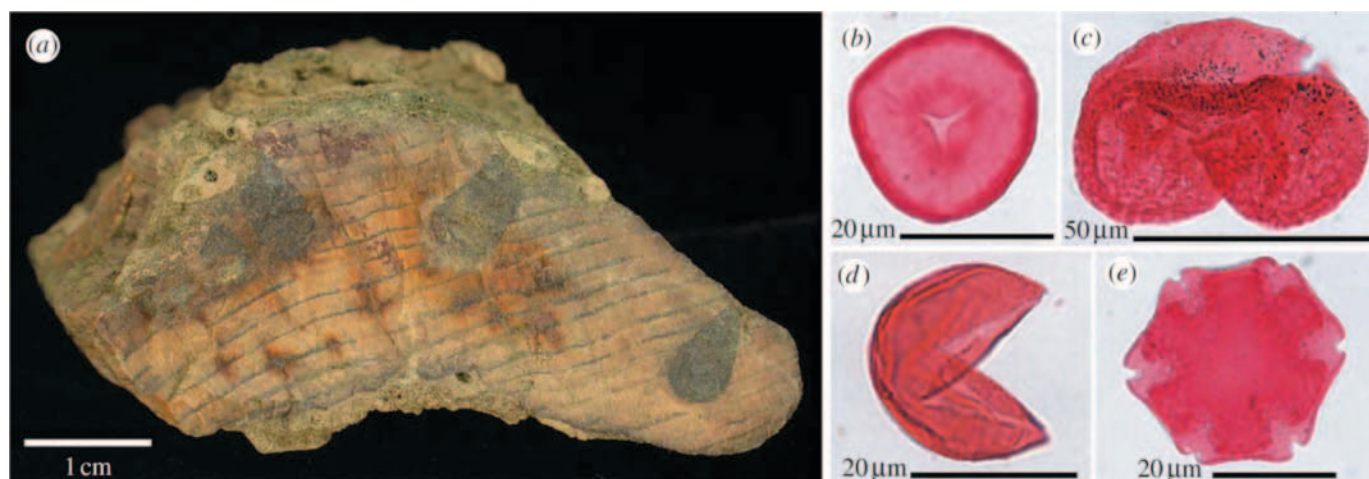
Figure 7. Terrestrial plant fossils from the Expedition Fiord and Kanguk Formations on Devon Island. (*a*) Permineralized conifer wood from Eidsbotn showing growth rings and pear-shaped *Teredolites* borings (RLO1/NUPB 7). (*b*) *Stereisporites* sp. sphagnum spore (EF0503; GSC type no. 124287). (*c*) Bisaccate conifer pollen grain (VF0111; GSC type no. 124288). (*d*) Taxodiaceous conifer pollen grain (VF0301; GSC type no. 124289). (*e*) *Clanculatus ignotus* angiosperm pollen grain (VF0109; GSC type no. 124290).

tic. With the exception of areas influenced by deep ocean upwelling (e.g. Bering, Chukchi, and Barents seas), nutrient concentrations are relatively low in much of the modern Arctic, and phytoplankton respond to nutrients released during sea ice break up (Fogg 1998; Sakshaug 2004). Tectonic reconstructions suggest that deep water connections between the Arctic Basin and other oceans were not present in the Late Cretaceous (Lawver *et al*. 1990). Therefore, it is unlikely that the Sverdrup Sub-basin (including the Devon Island sites; Embry & Osadetz 1988) experienced deep water upwelling. As such, riverine inputs and shallow, wind-driven upwelling must have delivered significant nutrient supplies to the ancient Devon Island environment.

The Devon Island assemblages display several distinctive characteristics in addition to the high diversity and abundance of microfossils. Whereas palynomorphs, wood, and siliceous and phosphatic body fossils have been recovered, no calcareous skeletons are preserved. This taphonomic feature suggests dissolution of aragonitic fossils due to low pH in nearshore sediments (Aller 1982), that is often associated with high productivity (Brett 1995). Although no soft-bodied metazoans are evident, burrows and fecal pellets reflect the activity of non- to lightly mineralized benthic invertebrates. Little transport and low wave energy are indicated by the condition of fossil lingulids at Eidsbotn graben. These tiny inarticulate brachiopods have relatively thin valves, yet most are still paired, intact and retain a glossy periostracum (Figure 5*b*). Finally, one of the most conspicuous taphonomic features of the greensand deposits is the disproportionately large number of coprolites relative to body fossils from possible fecal producers. This does not reflect a chemical preservation bias, as the fossil bones, teeth, lingulids and coprolites from the site are all phosphatic.

The thick siliceous mudstones and greensands suggest that the Devon Island sediments represent somewhat condensed stratigraphic sections characterized by prolonged periods of low sedimentation. On the whole, the relative lithological homogeneity and inferred low sedimentation rates suggest that the thick greensand deposits hosted members of one temporally persistent community, or a "within-habitat time-averaged assemblage" (Walker & Bambach 1971; Kidwell 1998).

As such, the Devon Island fossils probably present a reasonable representation of common phosphatic and siliceous macrofaunal inhabitants of the site in the Late Cretaceous. Yet the preponderance of coprolites in comparison with vertebrate fossils is somewhat surprising, given that taphonomic conditions allowed preservation of both, and because fishes and reptiles continually shed ever-replacing teeth. One scenario explaining this imbalance is that the abundant coprolites were produced by largely non-resident visitors that exploited the area's resources on a seasonal basis. In the modern Arctic, a variety of vertebrates migrate to polar waters to exploit summer resources (Ainley & DeMaster 1990), and some Cretaceous Arctic vertebrates may have also migrated with the seasons (Russell 1990). The dense, if patchy, coprolite deposits certainly provide evidence for extensive habitat use that would not be inferred from body fossils alone.

The fortuitous preservation of conformable terrestrial sediments at the top of the glaucony facies provides insights on terrigenous inputs into the marine system. Palynomorphs and sizeable wood fossils indicate that warmer temperatures in the Late Cretaceous Devon Island region helped sustain coastal forests or woodlands. Other Cretaceous Arctic sites show similar fossil evidence for polar forests (Núñez-Betelu & Hills 1992*b*; Spicer 2003; Falcon-Lang *et al*. 2004), often dominated by taxodiaceous conifers (Falcon-Lang *et al*. 2004). Reconstructions of Arctic taxodiaceous forests during the warm Eocene indicate lush, deciduous, productive forests (Jahren 2007) with standing leaf biomass estimated at 2.1–3.2 Mg ha^{-1} (Williams *et al*. 2003*a*,*b*). The Late Cretaceous Devon Island coastal forests may have been comparably productive, shedding large quantities of leaves at the end of the growing season. Indeed, palynological data and Rock-Eval characterization of sediment kerogens indicate considerable terrigenous organic input to the marine environment during the Cretaceous. The ubiquity of terrestrial debris is
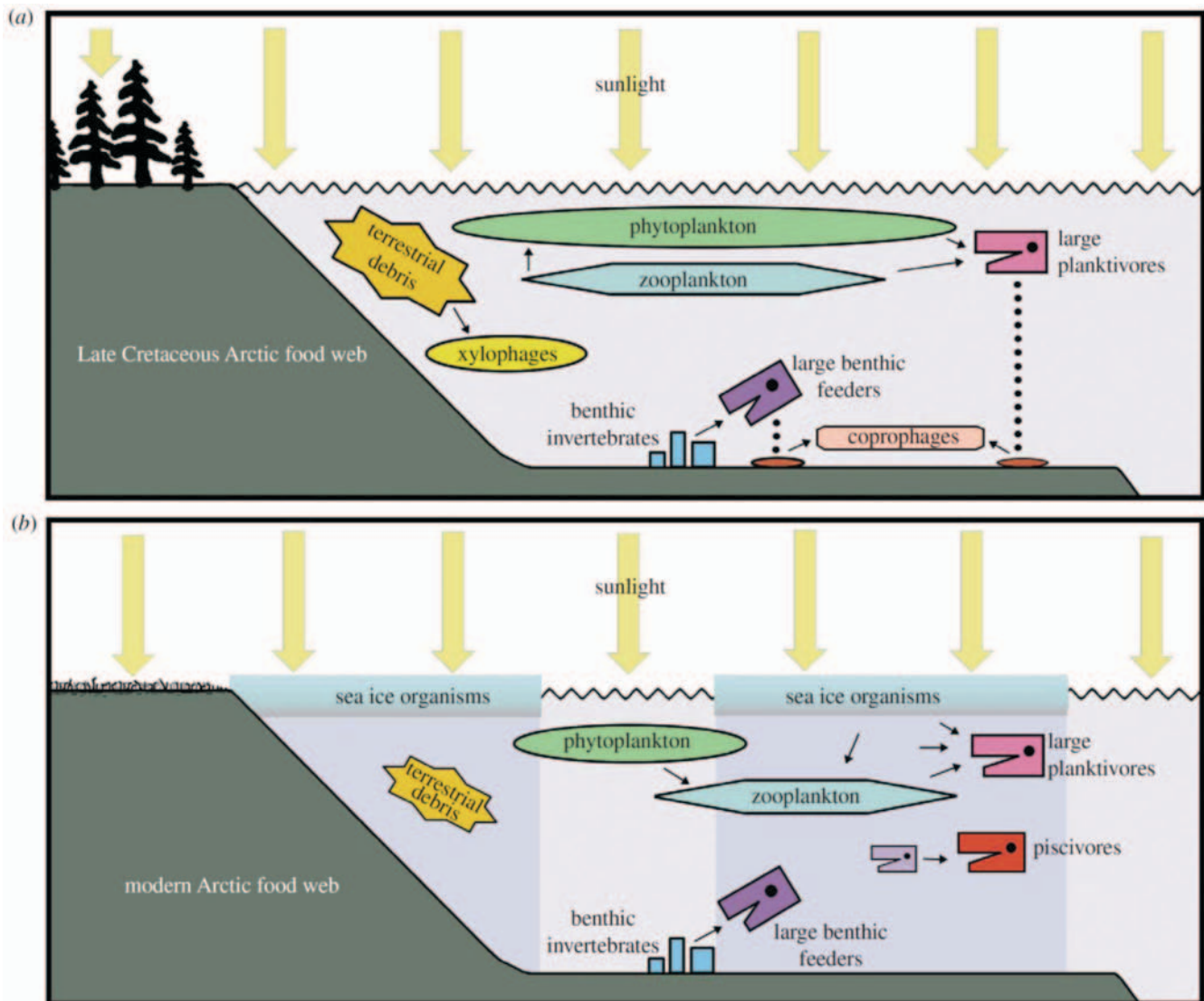
Figure 8. Schematic of food webs in the (*a*) Late Cretaceous Devon Island ecosystem and (*b*) a generalized modern Arctic ecosystem. The most conspicuous physical differences are the absence of sea ice and the presence of terrestrial forests in the ancient system. In the Cretaceous, large planktivores were probably large fishes with trophic niches comparable to modern Arctic baleen whales. The Cretaceous large benthic predators were probably plesiosaurs with feeding habits similar to extant walruses. Note that coprophagous animals are probably also active in the modern Arctic, but large vertebrate feces may not reach the benthos.

also demonstrated by the occurrence of wood chunks and terrestrial macerals in coprolites. These observations are consistent with the fact that riverine run-off from the polar forests would have delivered significant fluxes of terrigenous particulate and dissolved organic carbon to the marine environment, especially during periods of synchronous leaf drop and heightened fluvial run-off.

Rivers supply new (Jickells *et al.* 1991) and regenerated (Dittmar & Kattner 2003) nutrients to marine systems, although there is debate about the impacts of dissolved and particulate terrestrial carbon on marine life. Some conclude that riverine inputs are refractory and contribute little to marine productivity (Dittmar & Kattner 2003), whereas others suggest that marine organisms use more terrigenous carbon than previously suspected (Dunton *et al.* 2006). Although modern Arctic rivers currently contribute large amounts of organic matter to the ocean (Rachold *et al.* 2004), Weller *et al.* (1995) predicted that warming temperatures in the modern Arctic will accelerate soil oxidation processes and increase

nutrient run-off. Thus, in the warmer Late Cretaceous, the combination of increased terrigenous inputs and intensified microbial activity should have enhanced terrigenous nutrient contributions to the marine system. Local, wind-driven upwelling probably also played an important role in nutrient delivery, possibly serving to re-suspend riverine and regenerated nutrients. The relatively low TOC levels in the mudstones (0.11 to 3.34%) indicate that the terrigenous carbon was not sequestered in anoxic sediments, suggesting that it was either incorporated into the marine ecosystem and/or exported to deeper waters. It is worth noting that Late Cretaceous high productivity is also indicated in offshore Arctic Basin environments (Alpha Ridge) by ocean cores that show diatomaceous sediments (Kitchell & Clark 1982; Dell'Agnese & Clark 1994; A. Davies 2006, unpublished doctoral dissertation) or diatom biomarkers in mudstones with terrigenous debris (Jenkyns *et al.* 2004).

Organic matter in the form of large woody debris can be directly incorporated into temperate or tropical marine sys-

tems through the feeding activities of teredinid bivalves (shipworms). The xylophagous habit of these mollusks is facilitated by nitrogen-fixing microbial symbionts (Distel 2003), and populations of extant teredinids can be very dense (as many as 10000 burrows m⁻²; Tuente *et al.* 2002). The presence of *Teredolites* borings at both Devon Island sites demonstrates that a percentage of wood resources entering the ancient temperate marine environment was directly integrated into the marine system.

(b) Trophic relationships

Taphonomic observations suggest that the fossil assemblages from Eidsbotn and Viks Fiord grabens offer biased views of total community diversity. Coprolite evidence is also biased, as all feces from large marine animals do not reach the benthos—some are easily dissipated (e.g. Best *et al.* 1995). Nevertheless, the taxonomic and coprolitic evidence reveals several resource-based guilds, including phyto- and zooplankters, large planktivores, filter feeders, bioturbating predators, coprophages and xylophages (Figure 8).

The co-occurrence of diatoms and radiolarians points to exploitation of phytoplankton by heterotrophic protists; larger soft-bodied and lightly skeletonized zooplankton probably also used this resource. The abundance of microfossils and paucity of bone in over 30 per cent of the collected coprolites indicate that sizeable nektonic organisms in turn fed on the phyto- and zooplankton complex, and that planktivory by large animals was a common feeding strategy. Furthermore, these coprolites appear to be the product of late spring to summer feeding activity, when light levels fostered autotrophic blooms. Some of the phosphatic coprolites have an interior structure that suggests that the fecal producers were sharks with scroll-type intestinal valves.

A portion of the planktonic bounty filtered down to the sea floor where it was available to benthic feeders. The greensand coprolites reflect exploitation of the benthos by sizeable animals that probably ingested sediment as they targeted invertebrates such as the crustaceans and mollusks found in the coprolites. Specimens with little recognizable skeletal debris probably indicate feeding on soft-bodied fauna whose remains did not survive digestion and diagenesis. Candidates for the coprolite-producing benthic feeders include elasmosaurid plesiosaurs; numerous benthic organisms have been discovered in the gut region of Australian Cretaceous elasmosaurs (McHenry *et al.* 2005). Diatoms are common to abundant in most of the greensand coprolites, suggesting that as with the phosphatic coprolites, feeding was coincident with plankton blooms. The numerous burrows and fecal pellets in the coprolites also indicate vigorous benthic activity.

5. Conclusions

Santonian to Campanian deposits on Devon Island reveal a surprisingly productive and persistent ancient coastal marine ecosystem adapted to temperate polar conditions. Fossil evidence indicates both similarities and differences between this ancient system and the modern Arctic. Whereas most primary production in the Arctic now occurs in patchy, ephemeral blooms tied to marginal ice zones and polynyas, the Late Cretaceous Devon Island site hosted an apparently ice-free, productive, stationary ecosystem that was not driven by deep ocean upwelling.

The evidence for abundant terrigenous matter in the Devon Island sediments supports the presumption that the Cretaceous Arctic forests generated considerable vegetative debris. Because warmer temperatures would have accelerated microbial activity, we infer that the persistent primary productivity of the ancient marine system was probably supported by terrigenous nutrient and organic carbon inputs from ancient Arctic forests.

Although the spatial supply of nutrients in the modern and ancient systems differs, the vertical flux of carbon appears to have been similar, where primary production in the water column is coupled with productive benthic ecosystems. Such pelagic–benthic coupling (Grebmeier *et al.* 1988) is particularly pronounced during strong seasonal phytoplankton blooms when zooplankton populations cannot fully exploit rapidly reproducing phytoplankton, and unused plankton resources sink to the ocean bottom (Sakshaug 2004). In the modern Arctic, benthic crustaceans, bivalves, echinoderms and polychaetes use this resource (Grebmeier *et al.* 1988; Dayton 1990). Some of these taxa are represented in the ancient system, and others may have been similarly important, even though taphonomic biases preclude their presence in the fossil assemblage. Higher trophic levels also reflect pelagic–benthic coupling. The Kanguk Formation coprolites record trophic interactions that bear similarities to the typically short food chains in today's Arctic, where apex predators often feed directly on plankton or benthic invertebrates (Ainley & DeMaster 1990).

In general, the Cretaceous suite of resource-based guilds appears to have been broadly analogous to that of the modern Arctic. Nevertheless, the combination of warmer temperatures and Late Cretaceous evolutionary context presented a setting that supported a number of organisms atypical of the modern Arctic. Invertebrates such as wood-boring bivalves and extinct hexactinellid sponges (Rigby *et al.* 2007) were present in the ancient system. Plesiosaurs and large extinct fishes apparently filled niches comparable to extant Arctic marine mammals such as whales and seals.

This study focused on Arctic systems, but comparisons between high- and low-latitude Late Cretaceous nearshore marine ecosystems are also instructive. One analysis of two different Late Cretaceous diatom assemblages revealed more resting spores at an Arctic locality (Alpha Ridge) than a mid-latitude site, suggesting that pronounced seasonality contributed to "bloom and bust" patterns (A. Davies 2006, unpublished doctoral dissertation). In vertebrates, a survey of marine taxa from sediments of the Cretaceous Western Interior Seaway suggests lower overall diversity at higher latitudes, with more plesiosaurs and hesperornithiform birds in the north and more sharks and turtles further south (Nicholls & Russell 1990). More detailed comparisons will be useful, but the significance of photoperiodic constraints on polar ecosystems is underscored by the fact that the Devon Island assemblages and other temperate Cretaceous Arctic sites show special characteristics such as seasonality, low vertebrate diversity and/or short food chains.

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