Paleoenvironments and Paleoecology of the Vertebrate Fauna from a Late Cretaceous Marine Bonebed, Canada

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Abstract

Bonebeds – concentrations of bioclastic debris of vertebrates in geological strata – can accumulate under a variety of conditions. They are common in marine deposits of the Late Cretaceous Western Interior Seaway of North America, and are often characterized as lag deposits. In general, these deposits represent unknown periods of accumulation and contain a mélange of taxa, possibly transported from a variety of habitats. As such, the contents of these marine bonebeds are often considered less useful for studies of paleoecology and paleoenvironments than are fossils recovered from rock units that represent continuous sedimentary deposition within one or more contiguous paleoenvironments. We examined the fossil contents of one particularly rich marine bonebed of "middle" Cenomanian age to determine if useful conclusions can be drawn with respect to the habitats and probable interactions of its pre-depositional fauna. This bonebed occurs as discontinuous lenses in shales of the upper part of the Belle Fourche Member of the Ashville Formation in the Pasquia Hills of Saskatchewan, Canada.

Acid preparation of these lenses revealed an assemblage containing: 20 chondrichthyan taxa: a chimaeriform, hybodontiforms, diverse lamniforms and rare rajiforms; 15 actinopterygian taxa: a caturid, pycnodonts, an aspidorhynchid, a pachycormid, a plethodid, ichthyodectids, pachyrhizodontids, an albulid, a putative salmoniform, enchodontids, and an acanthomorph; and nine tetrapods including turtles, pliosaurs and elasmosaurs, four marine bird taxa, a terrestrial bird, and a lizard. Evaluation of probable habitats of the fish fossils reveals many pelagic forms, but a sparse nectobenthic fauna. Only one or two genera of those identified are considered to be euryhaline, and there are no obligate freshwater forms. The overwhelming majority of taxa identified are fully marine. Inferred feeding strategies for fish taxa include several durophagous forms including *Ptychodus*, a pycnodont and an albulid, with most other taxa, including the most abundant shark species (lamniforms) and osteichthyans *(Enchodus)* appearing to have been active predators with piercing dentitions. There are also predators/scavengers with cutting dentitions (anacoracid sharks) and a probable planktivore *(Cretomanta)*. Interpretation of the taphonomy and faunal content indicates that the bonebed accumulated near shore over a period up to tens of thousands of years and was largely composed of bioclastic detritus from shallow, contiguous habitats, with some input from a deeper, anoxic shelf assemblage.

Introduction

The Western Interior Seaway (WIS) was an epicontinental sea that covered the middle of North America during the last 35 million years of the Cretaceous, linking the proto-Atlantic/Tethys seas to the south with the paleo-Arctic Ocean to the north (Fig. 1). Vertebrates were diverse in the seaway by the "mid"-Cenomanian, with more than 70 taxa known from fossil localities in Canada and the United States (RUSSELL 1988, CUMBAA et al. 2010).

Most marine vertebrate remains of this age in North America occur in bonebeds, typically transgressive lag deposits, which are relatively common in the "mid"-Late Cenomanian. However, in sediment-starved portions of the basin, such as the eastern margin, bonebeds often occur as the result of winnowing during basin-wide sea-level lowstands and/or storm deposits (SCHRÖDER-ADAMS et al. 2001). The eastern mar-

gin of the seaway received dramatically less siliciclastic sedimentation than the Rocky Mountain foredeep on the western side of the basin (MCNEIL & CALDWELL 1981, CHRISTOPHER et al. 2006), a physical factor that facilitated the concentration of biogenic components in the sediment. The bonebed discussed here, from the Pasquia Hills of Saskatchewan, is thought to have been formed by winnowing on a shallow seafloor, probably near shore, above storm wave base and under tidal influence (SCHRÖDER-ADAMS et al. 2001, CUMBAA et al. 2006).

Material and methods

The vertebrate fossil material reported here was discovered along the Bainbridge River in the Pasquia Hills of Saskatchewan, Canada, during field work led by the senior author, under a Saskatchewan Heritage Palaeontological Resource Investigation permit. The bulk of the material was collected by the authors in 2006, and is catalogued in the Earth Sciences collections of the Royal Saskatchewan Museum, Regina.

The intact bonebed lenses were brought back to the laboratories of the Canadian Museum of Nature, and were cleaned and then immersed in deep trays of water for several days, at which time a meter was used to record baseline pH. The trays were then drained, and the lenses re-immersed in buffered 5–10 percent acetic acid. After repeated acid changes over many weeks, the disaggregated material was removed, rinsed, and placed in regularly changed tap water until the pH matched the baseline. The specimens were wet sieved and separated by size for ease of sorting using a standard stacking graduated mesh series to 0.5 mm, retaining the fines that passed through the last screen. One large lens from the locality had been exposed to the elements for several years; it had disaggregated naturally, and was collected in place. The dried matrix was sorted under magnification, using a binocular microscope. All residue 1 mm or larger was sorted. After cursory examination of several samples of the finer sieved fractions under a binocular microscope yielded no new taxa, we picked through only a representative sample.
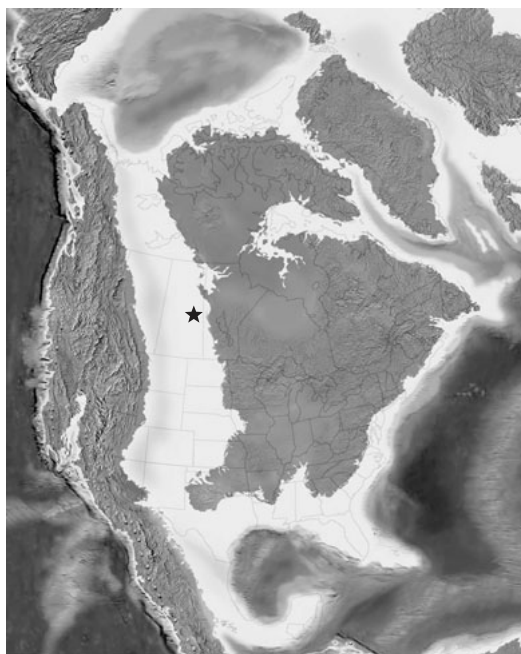

Fig. 1.
Paleogeographic map of the Late Cretaceous Western Interior Seaway, 85 Ma. The star indicates the approximate position of the Bainbridge River locality. The margins and extent of the seaway would have been different in the Cenomanian, some 10 million years earlier than this projection. Modified from BLAKEY (2011).

Geological setting

The locality, in the Pasquia Hills of east-central Saskatchewan, the northernmost upland in the Manitoba Escarpment (Fig. 2), is a 22 m high cliff, exposed at the edge of the Bainbridge River. In the "mid" Cenomanian, its latitude would have been approximately 55° N (SCOTESE 2001). The locality preserves about ten million years of marine sedimentary accumulation, including two unconformities of unknown but limited duration above the level of the bonebed (SCHRÖDER-ADAMS et al. 2001). The bonebed lenses occur roughly two meters below a thick bentonite layer (CUMBAA & BRYANT 2001) thought to be the "X" bentonite of the late middle Cenomanian, which has yielded an age of 95.87 ± 0.10 Ma elsewere (BARKER et al. 2011). The interval containing the lenses occurs 2–3 m above the base of the exposure, and roughly five cm above a regional stratigraphic marker, the *Ostrea beloiti* beds, in the upper part of the Belle Fourche Member of the Ashville Formation (MCNEIL & CALDWELL 1981, CUMBAA & BRYANT 2001). This marker bed at the locality is composed of disarticulated single valves of this oyster, in random orientation with occasional vertebrate inclusions.

The lenses are bounded above and below by nonbioturbated, non-calcareous black shale, rich in algal cysts. Foraminifera are sparse, with *Verneuilinoides perplexus* and *Saccammina lathrami* in the lowest part of the section (SCHRÖDER-ADAMS et al. 2001).
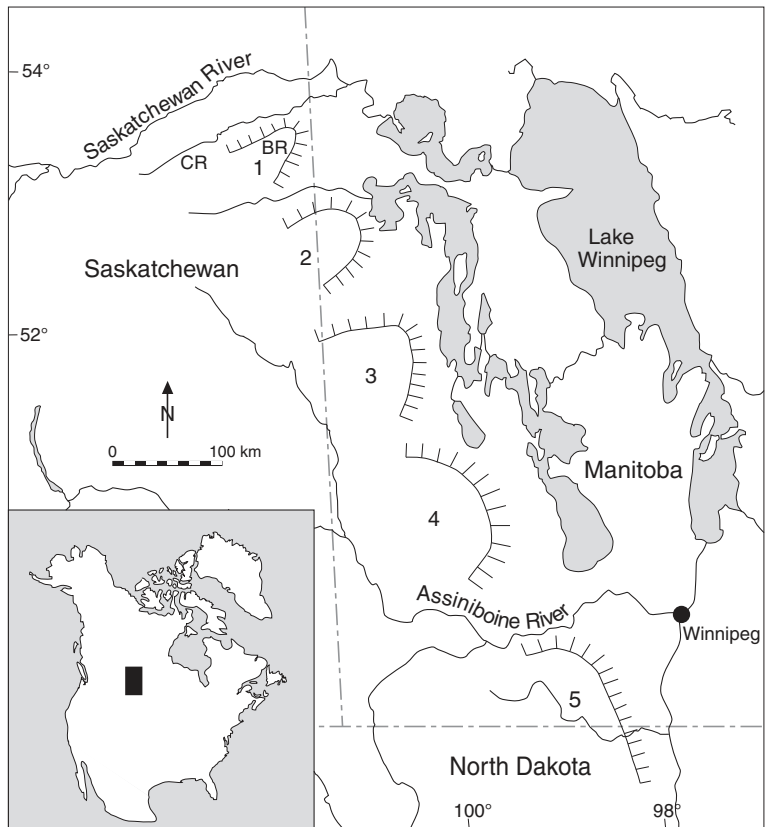
Fig. 2.
Map of the Manitoba Escarpment and the Bainbridge River bonebed locality, marked by BR. The uplands comprising the escarpment include: 1) the Pasquia Hills; 2) the Porcupine Hills; 3) Duck Mountain; 4) Riding Mountain; and 5) Pembina Mountain. These uplands form the eastern erosional edge of the Canadian Western Interior Basin.

Some larger lenses (~60 cm by 20 cm) of the Bainbridge River bonebed were found in situ a few metres apart, within the same bedding plane and filling the troughs or rippled surfaces (CUMBAA & BRYANT 2001). The individual lenses taper at each end and show layering, with deposition of coarse bioclastic material sandwiching thin mudrock interbeds (PHILLIPS 2008). Ripple marks on the upper surface of some of the bonebed lenses indicate wave influence, and mud drapes at the bottom of others show tidal influence during bed formation (SCHRÖDER-ADAMS et al. 2001). Large calcite-lined vugs encasing bentonitic clay are common within the lenses, most likely indicating chunks of bentonite having been ripped up from the seafloor during a storm, ultimately becoming part of the lenses as bioclast-studded mud balls. The calcitic matrix includes a small percentage of inoceramid-derived prismatic calcite, often as single prisms but occasionally in bundles (SCHRÖDER-ADAMS et al. 2001). Rarely, a larger portion of a single inoceramid valve is incorporated into a lens. The bonebed lenses are characterized by obvious vertebrate fossils, primarily teeth, coprolites and disarticulated bones, which are highly concentrated, vary considerably in size, and are for the most part randomly oriented (Fig. 3).

Bonebed taphonomy and depositional setting

Although bonebeds have been extensively examined, the vast majority of studies have focused on bone concentrations in non-marine palaeoenvironments. A taphonomic study was conducted of the bonebed discussed here and others of its age in the Manitoba Escarpment of eastern Saskatchewan and western Manitoba (PHILLIPS 2008). This bonebed formed in thin layers and lenses, which contain more than 55 % phosphatic bioclasts (PHILLIPS 2008); an earlier study characterized samples as containing 48–70 % bone and phosphatic nodules, many of the latter clearly being coprolites (SCHRÖDER-ADAMS et al. 2001).

There was little or no terrigenous sedimentation along most of the eastern shore of the Seaway during the "mid" Cenomanian, resulting in condensed sections. Observations along the entire Manitoba Escarpment

demonstrate that lands bordering the eastern margin of the WIS were flat to low-lying, with little gradient to rivers and streams emptying into the sea (McNEIL & CALDWELL 1981). The lack of sediment from terrestrial erosion is confirmed by detailed analysis of the bonebed; argillaceous material and siliciclastic grains are rare to absent, with the phosphatic clasts suspended in a matrix of sparry calcite cement. Less than three percent inoceramid-derived prismatic calcite is observable in point count analysis, but is readily seen in SEM microphotographs (PHILLIPS 2008).

Element shape would seem to be the main predictor of good preservation within the bonebed. Chondrichthyan elements, almost exclusively teeth, exhibit very little wear and breakage attributable to post-depositional processes. Osteichthyan remains include elements from the entire body, but only teeth and vertebrae are well preserved. Flat, blade-like and brittle elements such as the bones of the skull and the opercular series are almost always broken, usually beyond identifiability. Scales are present, but rarely so, and are almost always broken. Long and cylindrical elements such as teeth, on the other hand, fare very well, but are only occasionally preserved in place in tooth-bearing elements. The spines and processes of vertebrae are generally missing, but the spindle or barrel-shaped centra are very well preserved. Bird teeth and bones representing the entire body, with the exception of the relatively flat and thin sternum, are present and exhibit relatively little abrasion (SANCHEZ 2010). Some large tetrapod elements, such as those of plesiosaurs, can show considerable abrasion, while others, such as small flipper elements, are very well preserved. Overall, the breakage, abrasion and disarticulation of the vertebrate fossils indicate a significant level of transport and/or winnowing, but comparatively less so than in many other bonebeds in the region (PHILLIPS 2008).

Coprolites, almost certainly of piscine origin due to their size, number, and similarity in form and content to intestinal molds (cololites) that we have observed in articulated fossil fishes in localities of Early Turonian age within the region, are a significant component of the bonebed. It is likely that most of the rounded calcium phosphate nodules in the bonebed are of coprolitic origin. These range in size from about 3–20 mm in greatest dimension, and many have obvious fish vertebrae and scale inclusions. The sheer number of what appear to be fully formed and undistorted coprolites, distributed throughout all lenses, indicates the accumulation of a continuous rain of biotic debris on and into a soft bottom, where the coprolites stayed long enough to harden. This suggests depositional conditions in relatively quiet water with little initial disturbance or transport, and lack of a significant detritivore fauna. This is indicative of a relatively inhospitable initial depositional environment, such as anoxic bottom waters postulated for these levels in the description of the Ashville Formation (McNEIL & CALDWELL 1981) and for the layer containing the bonebed lenses at the Bainbridge locality (SCHRÖDER-ADAMS et al. 2001).

Many mechanisms could result in the accumulation of biotic debris, including deposition in place, storm deposits, erosional deposits, or a time-averaged accumulation as the result of a transgressive lag, with incoming waters "rolling up" bones and teeth exposed for possibly considerable and certainly variable periods of time after initial deposition (WALKER & BAMBACH 1971, KIDWELL & BOSENCE 1991, ROGERS & KIDWELL 2000). Deposition in place ("within-habitat" of KIDWELL & BOSENCE 1991) can be eliminated as a mechanism by the evidence of the coprolites, and probably by the large size of the faunal community of differing habitats. Storm deposition – a single event – also appears unlikely due to the high concentration of almost exclusively vertebrate remains and the virtually complete lack of articulated specimens. ROGERS & KIDWELL (2000) examined Late Cretaceous (Campanian) vertebrate deposits, including those from the transgressive advance of the Bearpaw Sea, the last major expansion of the WIS. They found that vertebrate remains seem to 'behave' differently from shell deposits, and postulated shoreface on shoreface erosional deposits – erosion of older shoreline deposits by wave and current action – to explain the accumulation of vertebrate remains. Although those deposits from the western edge of the WIS represent a similar assemblage to that of the eastern deposit discussed here, detailed stratigraphic study of the Bainbridge locality (SCHRÖDER-ADAMS et al. 2001) reveals no sign of the kind of erosion described by ROGERS & KIDWELL (2000).

Fauna and their potential paleoenvironments

The taphonomy of the bonebed suggests variation in the bottom conditions under which the bioclasts were deposited, including depth and degree of transport. In a hypothetical transect from a shelf-like, quiet and anoxic environment (SCHRÖDER-ADAMS et al. 2001, SIMONS et al. 2003) to a more active and oxygenated shoreline, more than one potential paleoenvironment and a variety of habitats are likely to have been

Fig. 3.
Bainbridge River bonebed. **A,** thin-section through a bonebed lens. Note random element concentration and orientation in the upper two-thirds of the thin-section versus a stronger alignment of elongated elements and slightly coarser, more compacted matrix in the lower third, hinting at variable uni-directional current action throughout the deposition of the bonebed. **B,** Partially acid-prepared surface of a bonebed lens from the locality. Representative specimens include: **1**, one of several coprolites and oblong to rounded calcium phosphate pebbles; **2**, osteichthyan vertebrae; **3**, *Enchodus* palatine; and **4**, *Archaeolamna* tooth. Teeth of sharks and bony fishes are the most common identifiable elements represented, followed by osteichthyan vertebrae and coprolites.

present, eventually contributing fauna to the bonebed. Table 1 lists the vertebrates identified from the bonebed, the relative abundance of each taxon, and its presumed 'usual' habitat or paleoenvironment(s). Question marks reflect uncertainty; for example, ptychodontid sharks had nectobenthic feeding habits and so frequented bottom environments, but vertebral form and wide distribution of some species indicate they were probably pelagic swimmers as well, like most other sharks. There are many examples of extant fishes that are pelagic in nature, yet feed seasonally or regularly on benthic faunas and may breed or live as young in very shallow, nearshore waters; in fact, there are few if any absolute correlations between species and specific environments in living fishes. Nevertheless, brief descriptions are provided here for environments and environmental parameters at the Bainbridge locality for which we have at least indirect evidence.

Offshore, shallow shelf

Offshore during "mid"-Cenomanian time, the dominance of organic-rich mudstones and the paucity of benthic faunas suggest that bottom waters of the WIS, particularly in the northern portion, were stratified and frequently anoxic or dysoxic (PRATT et al. 1993). Biomarker analysis of Cenomanian/Turonian shales at the Bainbridge River locality indicates a poorly mixed water column and periods of euxinia (SIMONS et al. 2003). The excellent preservation of algal cysts, low-diversity assemblage of benthic Foraminifera, lack of bioturbation, and the presence of isorenieratene (a pigment biosynthesized by the brown strain of a green sulfur bacterium) in the samples above and below the bonebed layer all indicate frequently depleted oxygen conditions in a restricted basin (SCHRÖDER-ADAMS et al. 2001).

Despite these conditions, with the resulting low diversity of benthic invertebrates and the absence of reef-builders in much of the WIS, colonies of large to giant (1–2 m) inoceramid bivalves, with encrusting oysters and other organisms, extended well into the Arctic (DHONDT 1992, KAUFFMANN et al. 2007), thriving through chemosymbiosis in chemically toxic benthic environments. These colonies may have served as reef-like habitat on a shelly substrate raised only slightly above the sea floor, providing shelter and loci for food for both vertebrates and invertebrates, possibly to some extent mitigating the frequent-to-constant dysoxic conditions (KAUFFMAN et al. 2007).

However, inoceramids are also known from a wide range of facies and marine environments ranging from black shales to nearshore sands (HARRIES et al. 1996). A thousand kilometers to the south of the Bainbridge River locality, in the Upper Cretaceous (Late Coniacian–Santonian) Niobrara Chalk of Kansas, large (>1 m) inoceramids living in the quiet bottom waters at depths of 30–150 m (HATTIN 1982) apparently served as refuge for schools of small acanthomorph fishes (STEWART 1990, 1996) which almost certainly did not live in highly anoxic environments. The WIS Turonian locality at Lac des Bois, NWT, Canada, produced an interesting association: a partially articulated caturid lying on an inside valve of an inoceramid (CUMBAA & MURRAY 2008), much like the acanthomorph association described by STEWART (1990, 1996). In the Belle Fourche Member at the Bainbridge River locality, the soft mudrock shows strong evidence of quiet-water conditions, but lacks abundant evidence of substantive inoceramid colonies like those of other Manitoba Escarpment localities of roughly the same age. For example, the matrix of a bonebed near Riding Mountain (Fig. 2) is composed mainly of inoceramid prisms, but at the Bainbridge locality, less than three percent of the bonebed is composed of calcite prisms from broken-up inoceramids shells (PHILLIPS 2008), and even partial valves are rare. Table 1 lists both caturids and one or more acanthomorphs from the bonebed, but each is also known from other, non-inoceramid paleoenvironments.

Caturids, for example, are known from nearshore, shallow-water WIS deposits suggestive of the proximity of biohermal or even fluvial paleoenvironments in the Lower Cretaceous Trinity Group of Texas (RUSSELL 1988), but are also well known from offshore mudstones in the Jurassic (e.g. MARTILL 1991). Acanthomorph fishes today occupy a variety of environments, and can be found in almost any aquatic environment (FRIEDMAN 2010). "Mid"-Cretaceous acanthomorphs were much more restricted in the range of habitats occupied, but marine paleoenvironments include a specimen from the Greenhorn Limestone in Kansas from oxygenated waters of normal salinity, directly associated with inoceramids at a depth of 30–90 m (ARRATIA & CHORN 1998), and several taxa from shallower waters at Namoura, Lebanon (FOREY et al. 2003). The Namoura locality has also produced abundant land plants (mostly angiosperms), an enantiornithine (terrestrial) bird, and a theropod dinosaur in addition to marine vertebrates, leading FOREY et al. (2003) to suggest deposition on a shallow marine platform abutting islands in the Tethys Sea. Although *Xenillion*, an acanthomorph from Early Cenomanian WIS deposits in Alberta was found in anoxic black shales, it was argued that it lived in shallower, more oxygenated waters, and that postmortem, the carcass settled to the bottom (WILSON & MURRAY 1996).

Table 1. Taxa, habitat and relative abundance[1] of BR3 bonebed vertebrates. Habitat abbreviations: **Pel**, Pelagic; **Mar**, marine; **Litt**, littoral/estuarine; **Eu**, euryhaline; **Terr**, terrestrial; **?**, uncertain. Estimated size (mass) is expressed in kilograms. Identification (I.D.) basis: **pal**, palatine; **t**, teeth; **vo**, vomer; **pmax**, premaxillary; **den**, dentary; **ros**, rostrum; **hyp**, hypural; **vrt**, vertebrae; **phar**, pharyngeal; **sp**, spine; **car**, carapace (frag); **dn**, dentary; **mult**, multiple elements; **hum**, humerus; **tmt**, tarsometatarsus. Phylogenetic origin generally follows NELSON (2006), ARRATIA (2008) and UNDERWOOD & CUMBAA (2010).

Taxa		Pel	Necto-benthic	Mar	Litt	Eu	Terr	Rel. Abun.	Est. Size	I.D. Basis
CHONDRICHTHYES										
Edaphodontidae	*Edaphodon* sp.		X	X				rare	<1	pal
Hybodontidae	*Meristodonoides rajkovichi*	X		X	?			maj	10–30	t
Ptychodontidae	*Ptychodus* ex. gr. *decurrens*	?	X	X	?			rare	20–50	t
	Ptychodus occidentalis	?	X	X	?			rare	20–50	t
	Ptychodus rhombodus	?	X	X	?			mod	5–20	t
Orectolobiformes inc. fam.	*Cretorectolobus robustus*		X	X				rare	1–5	t
	Orectoloboides angulatus		X	X				rare	<1	t
Odontaspididae	*Eostriatolamia paucicorrugata*	X		X	X			mod	5–20	t
	Roulletia canadensis	X		X	X			dom	10–50	t
Archaeolamnidae	*Archaeolamna* ex. gr. *kopingensis*	X		X	X			dom	10–30	t
	Telodontaspis agassizensis	X		X	X			min	5–15	t
Cretoxyrhinidae	*Cretoxyrhina denticulata*	X		X				rare	<100	t
	Cretodus semiplicatus	X		X	X			rare	<100	t
Otodontidae	*Cretalamna* cf. *C. appendiculata*	X		X	X			rare	20–50	t
	Cretalamna sp.	X		X	X			rare	20–50	t
Anacoracidae	*Squalicorax curvatus*	X		X	X			maj	10–50	t
	Paleoanacorax pawpawensis	X		X	X			dom	5–15	t
Rhinobatidae	*Rhinobatos* cf. *R. incertus*		X	X	X			rare	1–10+	t
?Batomorphii incertae sedis	*Cretomanta canadensis*		?	X	?			min	?	t
OSTEICHTHYES										
Pycnodontidae	*Micropycnodon kansasensis*		X	X	X	X		min	<1	vo
	cf. *Paleobalistum* sp.		X	X	X	X		min	<1	vo
Caturidae	Caturidae indet.	X		X	?			min	<0.5	pmax
Aspidorhynchidae	*Belonostomus* sp.	X			X	X		rare	<1	dn
Pachycormidae	*Protosphyraena* sp.	X		X				rare	20–40	t
Plethodidae	Plethodidae indet.	X		X				rare	<10	ros
Pachyrhizodontidae	*Elopopsis* sp.	X		X	X			min	2–5	t
	Pachyrhizodus minimus	X		X	X			rare	1–2	hyp
Ichthyodectidae	*Ichthyodectes* cf. *I. ctenodon*	X		X	X			rare	10–15	t,vrt
	Xiphactinus audax	X		X	?			rare	>100	t
Albulidae	cf. Albulidae		X		X			min	0.5–1.5	phar
Protacanthopterygii inc. sed.	?Salmoniformes indet.	X		X	X	?		mod	3–4	vrt
Enchodontidae	*Enchodus* cf. *E. gladiolus*	X		X	X			mod	2	pal
	Enchodus cf. *E. shumardi*	X		X	X			mod	2	pal
	Enchodus sp.	X		X	X			dom	2	pal
Acanthomorpha incertae sedis	Acanthomorpha indet.	X	X	X	?			rare	<0.5	sp,vrt
TETRAPODA										
Reptilia (non-avian taxa)										
Testudines incertae sedis	Testudines indet.	X		X	X			rare	3–5	car
Lepidosauria incertae sedis	Squamata indet.						X	rare	<0.5	dn
Plesiosauria	Elasmosauridae indet.	X		X				rare	350+	t
	Pliosauridae indet	X		X				min	150+	t
Aves										
Hesperornithiformes	*Pasquiaornis hardiei*	X		X	X			min	<1.5	mult
	Pasquiaornis tankei	X		X	X			min	3–5	mult
Ichthyornithiformes	*Ichthyornis* sp.			X	X			rare	<0.5	hum
Enantiornithiformes inc. sed.	Enantiornithes indet.						X	rare	<0.5	tmt

[1] Relative abundance for number of specimens: rare, <50; min, <100; mod, <250; maj, <2500; dom, >2500.

Many of the coprolites incorporated into the Bainbridge bonebed were likely originally deposited as fecal material by pelagic fishes, dropping into the deeper, quiet, soft, anoxic and relatively inhospitable bottom sediment favored by inoceramid pelecypods. Through chemical interaction within the substrate, the fecal material was able to harden before being washed into the wave-rippled, tidal, shallow-water environment in which the bonebed formed. Bones and teeth of many of the pelagic and nectobenthic vertebrates could have been deposited there, dropped down from above after death, but only a small portion of the vertebrates listed in Table 1 likely made regular incursions into this inhospitable benthic environment. The upper, more aerated waters of normal salinity, and the shallower areas where the turnover of wave action assisted biotic productivity, were likely more often frequented by most of the vertebrates identified. The presence of wave ripples on the upper surface of some of the bonebed lenses as well as preserved mud drapes throughout the bed, and gutter casts on the lower surface of other lenses suggest the bonebed took its final form under shallow-water conditions, while the contents were still in a plastic state.

Oyster beds

A common macroinvertebrate within the stratigraphic context of the bonebed is the oyster *Ostrea beloiti*. Disarticulated single valves and small bioturbated sandstone lenses consisting predominantly of oysters are scattered throughout a meter or so of the black shales encompassing the bonebed (SCHRÖDER-ADAMS et al. 2001). Less than five cm below the bonebed, the randomly-oriented valves, virtually all left, or the non-attached valves, form a layer recognized regionally as a stratigraphic marker, the *Ostrea beloiti* beds, in the upper part of the Belle Fourche Member, Ashville Formation (McNEIL & CALDWELL 1981). The development of this oyster calcarenite is thought to signal the transition from intermediate to peak periods of marine transgression (McNEIL 1984). CHRISTOPHER et al. (2006) refer to this sequence as the *Ostrea beloiti* Zone. HATTIN (1965) and HATTIN & SIEMERS (1987) describe similar accumulations of these oysters in the contemporaneous Graneros Shale of Kansas, forming biostrome-like beds of current or storm-accumulated shell hash with occasional vertebrate elements, set in a calcarenite matrix. A number of factors led HATTIN (1965) to conclude that these oyster accumulations occurred during conditions of rising sea levels, in waters of normal salinity.

In the *Ostrea beloiti* zone at the Bainbridge River locality, bioturbation within the scattered laminae of sand, in addition to large numbers of disarticulated oyster valves, indicates a more oxygenated and probably shallower environment, susceptible to some current flow (SCHRÖDER-ADAMS et al. 2001). On the basis of similar fauna and lithology, HATTIN (1965) suggested deposition of this unit at a depth of 30 m or less. Extant oysters, also benthic suspension feeders, will grow in a variety of conditions, including exposure of beds at low tide, but experiments show that the optimum conditions for growth and reproduction occur near the top of oyster reefs, in depths of about six metres, in areas of water flow with minimized sedimentation (LENIHAN 1999).

All of the vertebrates in Table 1, pelagic and nectobenthic as well, would have inhabited, frequented, or passed through this nearshore productive zone. Nectobenthic, durophagous osteichthyan taxa such as the pycnodonts *Micropycnodon* and *Paleobalistum* most likely fed on oysters or their epibionts, either taxa that encrusted large inoceramids offshore in an anoxic environment or those that formed beds in shallower water, although POYATO-ARIZA (2005) suggested that pycnodonts as a group were generalists in their durophagous feeding strategy, inhabiting marine, brackish and for a few taxa, even freshwater environments (e. g., CIONE & PEREIRA 1985); however, none were adapted to either strong currents or to open pelagic waters. Both pycnodont genera from the Bainbridge River bonebed are known from relatively shallow marine environments elsewhere in the WIS (CUMBAA et al. 2010). Although durophagous, the albulid, like extant bonefishes, probably lived on a varied diet of crustaceans, squid, pelecypods and fishes in or near this shallow-water environment (HILDEBRAND 1963).

Other coastal environments

We suggest that the bonebed likely accumulated in shallow water, possibly within sight of the shoreline. Although there is no direct evidence of bays, streams feeding into the coastline, or specific shoreline habitat or conditions, there is at least some indirect evidence in addition to the wave-rippled upper surface of some of the bonebed lenses. Terrigenous sediment was not a factor in the accumulation of sediment at the locality (SCHRÖDER-ADAMS et al. 2001); generally, the land on the eastern margin of the WIS was flat-lying with a low-energy coastline (McNEIL & CALDWELL 1981). Thin-sectioned bonebed samples from the locality show some current alignment (SCHRÖDER-ADAMS et al. 2001), but it was neither strong nor

continuous, indicating a weak along-shore current or perhaps a nearby stream input of variable intensity. The faunal list (Table 1) gives little evidence from either numbers of taxa or specimens that these nearshore or littoral habitats contributed much in the way of skeletal material to the development of the bonebed. The terrestrial bird and lizard could indicate proximity to either nearshore or estuarine habitat, or alternatively, could represent 'bloat and float' specimens that drifted out via a coastal stream. No obligate freshwater fish taxa have been identified from the bonebed, and the only fishes considered to have been euryhaline are the aspidorhynchid, *Belonostomus*, the pycnodonts and possibly the putative salmoniform.

Most of the vertebrates listed in Table 1 are not linked to a restricted environment or habitat. STAHL (1999) discussed the difficulty of placing holocephalians within a specific marine environment, suggesting that larger chimaeriform species such as *Edaphodon* (rare in our samples) belonged to the benthic community, but were drawn to the shallows to feed and to release egg cases. The very common hybodont shark in our samples, *Meristodonoides*, was most likely a shallow marine and brackish water predator, judging by descriptions of the many deposits in Texas where hybodont teeth are common (WELTON & FARISH 1993); some species may even have entered fresh water. We discussed earlier the difficulty of assigning a specific paleoenvironment to the ptychodontid sharks, even though they are acknowledged benthic feeders (CAPPETTA 1987, COMPAGNO 2001). Orectolobid sharks, rare in our samples, are also considered to be benthic species (CAPPETTA 1987, COMPAGNO 2001). The other neoselachian sharks in our samples, for the most part generalist pelagic predators, would have moved between nearshore and shelf environments in search of prey. These include the most common shark families in our samples, the odontaspids, archaeolamnids, and anacoracids – each with more than 2500 specimens – as well as rare cretoxyrhinids and otodontids. The very rare rhinobatids are also considered to be shallow-water benthic feeders (CAPPETTA 1987, COMPAGNO 2003).

Other than those already mentioned, the osteichthyans in Table 1, with the exception of the ubiquitous *Enchodus*, a somewhat common but as yet unidentified probable salmoniform, and a less common pachyrhizodontid, *Elopopsis*, were rare. The large pachycormid *Protosphyraena,* one or more plethodid taxa, and the giant ichthyodectid, *Xiphactinus* (all very rare), are the only ones that would have maintained a pelagic lifestyle, and would probably not have ventured into shallow waters. The others, all pelagic feeders, would probably have moved back and forth between deeper and relatively shallow marine environments. Whether or not the putative salmoniform (sensu NELSON 2006) was anadromous or at least euryhaline is a question that should be pursued further through isotopic or REE analyses. The earliest definitive Salmoniformes (CAVIN et al. 2006) are from "middle" Cenomanian deposits in Lebanon; the Bainbridge material is quite distinct from these *(Gaudryella*, *Ginsburgia*, and *Gharboria)*, and bears further examination to ascertain its affinities.

The marine reptiles – turtles and short- and long-necked plesiosaurs – would have inhabited pelagic to nearshore environments; the turtles must have come ashore to deposit eggs. The hesperornithiform birds, active feeders on fishes in the nearshore pelagic environment, would have also spent time on shore, at least during nesting season. The tern-like bird *Ichthyornis* would have been a surface feeder in both offshore and nearshore environments, but would have been shore-based for nesting and possibly for resting, as the morphology of the bones shows no swimming adaptations (CLARKE 2004).

Environmental 'pooling'

A reasonable model to explain the mix of environmental preferences of vertebrates identified from the bonebed is some sort of time-averaged transgressive lag. The Bainbridge River algal cysts, pollen, Foraminifera, and vertebrate fauna are all in agreement indicating a "middle"-Late Cenomanian age for the bonebed. Although we do not have precise temporal resolution of the strata immediately surrounding the bonebed, it is unlikely that the fauna represents a significantly "biostratigraphically condensed" assemblage with mixed geological ranges (KIDWELL & BOSENCE 1991), but rather a variant of an "environmentally condensed" assemblage model, which invokes marine transgression on a sediment-starved outer shelf. FÜRSICH & KAUFFMAN (1984) define this as faunas representing different environments in time that are "telescoped into one stratigraphic horizon". Simply put, vertebrate remains from paleoenvironments from the beach to the outer shelf could be exposed by a gradual sea level fall, then rolled up with the incoming waters of a transgressive advance to form an assemblage: in this case, a bonebed representing faunal contributions from both an anoxic shelf environment and much shallower waters, including bays and possibly estuaries. Time estimates for the accumulation of such lags in coastal and shelf environments range from hundreds of years to tens of thousands of years, based on dated shell assemblages (KIDWELL

& BOSENCE 1991). KELLER et al. (2004) suggested the major marine transgression associated with OAE 2 at the end of the Cenomanian took place over a period of about 90 000 years, and noted a similar rapid rise in δ13C and sea levels in underlying "mid"-Cenomanian deposits. On the eastern margin of the WIS, the much lower sediment loads, shallower depth and very gradual slope (McNEIL & CALDWELL 1981, CHRISTOPHER et al. 2006) would have been significant factors in the duration of accumulation and the composition of transgressive lags.

Once the disarticulated elements comprising the bonebed had come together in shallow water, frequent lifting, mixing and winnowing of the soft sediment by waves, with the lightest and most hydrodynamically susceptible elements drifting away and/or being broken up, would seem to be the model that best fits the evidence for formation of the bonebed (SCHRÖDER-ADAMS et al. 2001). The resulting mélange settled into troughs or other topographic lows, slowly solidifying and ultimately undergoing compaction before the waters and sediment of the WIS deepened, and the shoreline moved farther to the east.

Environmental parameters

Regardless of the source paleoenvironment or habitat, the samples discussed here represent a fauna or faunas that lived in the WIS during the "mid"-Cretaceous climatic optimum, when sea temperatures were warmer than those of today. PUCÉAT et al. (2007), using δ18O from fossil fish teeth as a proxy for ocean temperatures, developed a thermal gradient indicating average yearly ocean temperatures of approximately 22 °C at the paleolatitude of the Bainbridge River locality. As a comparison, this is roughly equivalent to average yearly sea surface temperatures today along the Atlantic coast from Savannah, Georgia to Daytona Beach, Florida in eastern North America (SHEARMAN & LENTZ 2010), roughly 25 degrees of latitude south of the paleolatitude of the bonebed locality. Climate on the eastern margin was humid and wet in the mid Cretaceous, with freshwater runoff contributing to salinity and temperature stratification (WHITE et al. 2001).

Farther south, samples from the Cenomanian-Turonian Bridge Creek Limestone Member of the Greenhorn Formation indicate that highly saline bottom waters probably reached 29 °C (WRIGHT 1987). Paleosalinity is thought to have been variable in the WIS, but generally ranged from normal to brackish in the upper layers (WRIGHT 1987). Although more data are needed from the shallow eastern margin of the WIS, available information points toward reduced-salinity surface waters overlying warmer, more saline and denser bottom layer waters, with a layer of normal salinity in between; generally warm waters and stratification caused by salinity differences created widespread stagnant conditions (WRIGHT 1987). Other than the variably dysoxic and inhospitable bottom water conditions offshore, the available evidence does not point to any real barriers or restrictions to the productivity of marine life along the eastern margin of the WIS in the Cenomanian.

Paleoecology

There are two remarkable paleoecological aspects of the Bainbridge River bonebed fauna: an astonishingly high predator to prey ratio and domination by a half-dozen species, all predators. Figure 5 shows representative vertebrate taxa, grouped according to presumed feeding strategy. Figure 4 shows the relationships between abundance (numbers of identified specimens), size (as expressed by estimated weight), and presumed feeding strategy of the major taxonomic groups. It summarizes the information presented in Table 1 and information on the paleoecology of each group as presented here.

Concentrating on the 41 taxa in Table 1 that lived in the shallow marine shelf to shallow littoral or sublittoral paleoenvironments, only a few were not piscivorous. These few taxa include rare fossils of the chimaeriform *Edaphodon*, which probably scavenged and fed on hard-shelled benthic invertebrates (NESSOV & AVERIANOV 1996), and three species of the shark *Ptychodus*, which are generally thought to have fed on hard-shelled invertebrates such as inoceramids (KAUFFMAN 1972). However, the teeth of *Ptychodus* from the bonebed rarely show wear, so it is possible the food sources of these sharks were not the same, or as hard-shelled, as favored by *Ptychodus* elsewhere (UNDERWOOD & CUMBAA 2010). Other non-piscivorous taxa include: the ray *Rhinobatos*, very rare in our samples, which probably also fed on crustaceans and molluscs (WELTON & FARISH 1993); the ?batomorph *Cretomanta canadensis*, which was probably a planktivore (UNDERWOOD & CUMBAA 2010); two pycnodonts in the genera *Micropycnodon* and cf. *Paleobalistum*, which fed largely on hard-shelled invertebrates, including molluscs and echinoids (NURSALL 1996); and an albulid, which like extant bonefishes, probably fed on benthic or nectobenthic

Fig. 4.
Approximate size range and relative abundance of the different vertebrate groups inhabiting particular trophic niches, based on fossils recovered. Note the dominance of pelagic predators within all of the vertebrate groups present. Very small taxa are likely to be underrepresented due to taphonomic factors; invertebrates occupying similar niches (such as squid) are not represented.
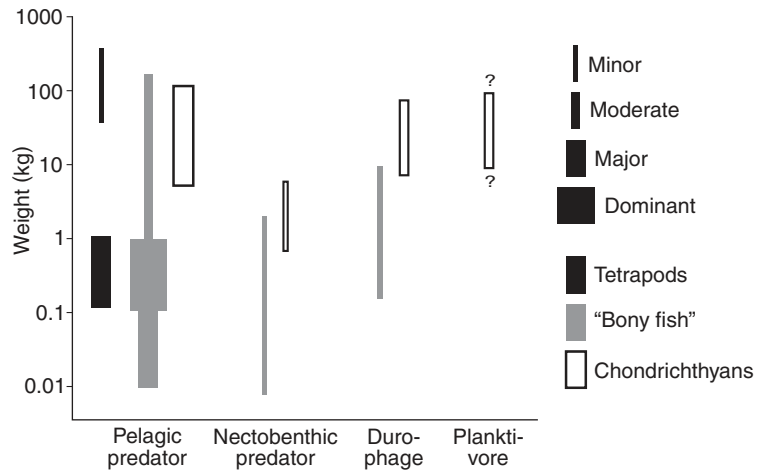
invertebrates (HILDEBRAND 1963). Of the marine tetrapods, only the turtles were not piscivorous; the turtle remains were of juveniles, which likely fed on invertebrates.

Most fishes, including the most abundant osteichthyans *(Enchodus)* and shark species (lamniforms), appear to have been active predators with clutching or piercing dentitions, although predators or scavengers with cutting dentitions (anacoracid sharks) also form a significant percentage of the fauna. The sharks with clutching or piercing dentitions represented in the bonebed include: the very common hybodont *Meristodonoides*; the rare orectolobiforms *Cretorectolobus* and *Orectoloboides*; two odontaspids, including the common *Eostriatolamia* and the dominant *Roulletia*; two archaeolamnids, including the dominant *Archaeolamna* and the much less common *Telodontaspis*; two rare cretoxyrhinids, *Cretoxyrhina* and *Cretodus*; and what appear to be two rare species of the otodondid, *Cretalamna* (UNDERWOOD & CUMBAA 2010). The anacoracid sharks *Squalicorax* and *Paleoanacorax* had cutting dentitions and thus could feed on prey of relatively large size such as fishes (including other sharks), turtles and other marine reptiles and birds, and almost certainly were scavengers; distinctive marks from the serrated teeth of *Squalicorax* have been found on the bones of many large marine vertebrates, and even on the bones of dinosaurs that had drifted out into offshore waters (SCHWIMMER et al. 1997).

Osteichthyan predators with piercing dentition include a small, uncommon caturid and the small, rare aspidorhynchid, *Belonostomus*. Remains of the large pachycormid *Protosphyraena* are rare in the bonebed, as are fossils of a plethodid. Tselfatiiforms show several specializations with regard to feeding apparatus; lacking diagnostic fossils, we can only cite suggested predation on soft-bodied invertebrates or possibly filter-feeding as possibilities (CAVIN & FOREY 2008). Fossils of ichthyodectids, the large *Ichthyodectes* and the giant *Xiphactinus*, are also uncommon. The ichthyodectids are well-known predators, with museum specimens often displaying entire fish in the stomach cavity (WALKER & BRETT 2002). Pachyrhizodontids are somewhat more common, with fossils of *Elopopsis* being somewhat more common than the rare *Pachyrhizodus minimus*. With well-developed teeth and streamlined bodies, these fishes were almost certainly piscivores. Fossils of the as yet unidentified ?salmoniform are relatively common; as a medium-sized predator in coastal and estuarine waters, prey was most likely smaller fishes and soft-bodied invertebrates. Thousands of the disproportionately large teeth, and smaller numbers of vertebrae and bones of the head of two or more species of the enchodontid *Enchodus* are extremely common. *Enchodus* almost certainly preyed on other fishes (FIELITZ 2004). The high numbers of this modest-sized predator that must have been present underscore the dearth of identified prey species. The feeding mode of the rare, small acanthomorph(s) is unknown; it could have been a grazer (BELLWOOD 2003).

Of the marine tetrapods, the plesiosaurs, both the long-necked elasmosaurs and the short-necked pliosaurs, were most likely omnivorous, feeding primarily on pelagic fishes and cephalopods (CICIMURRI & EVERHART 2001). However, the discovery of two Early Cretaceous elasmosaurs with stomach contents dominated by benthic invertebrates, including bivalves, gastropods and crustaceans, forces us to think more broadly with respect to their feeding strategies (MCHENRY et al. 2005). The three taxa of marine birds all had teeth, and almost certainly fed on fishes and possibly soft-bodied invertebrates. The two
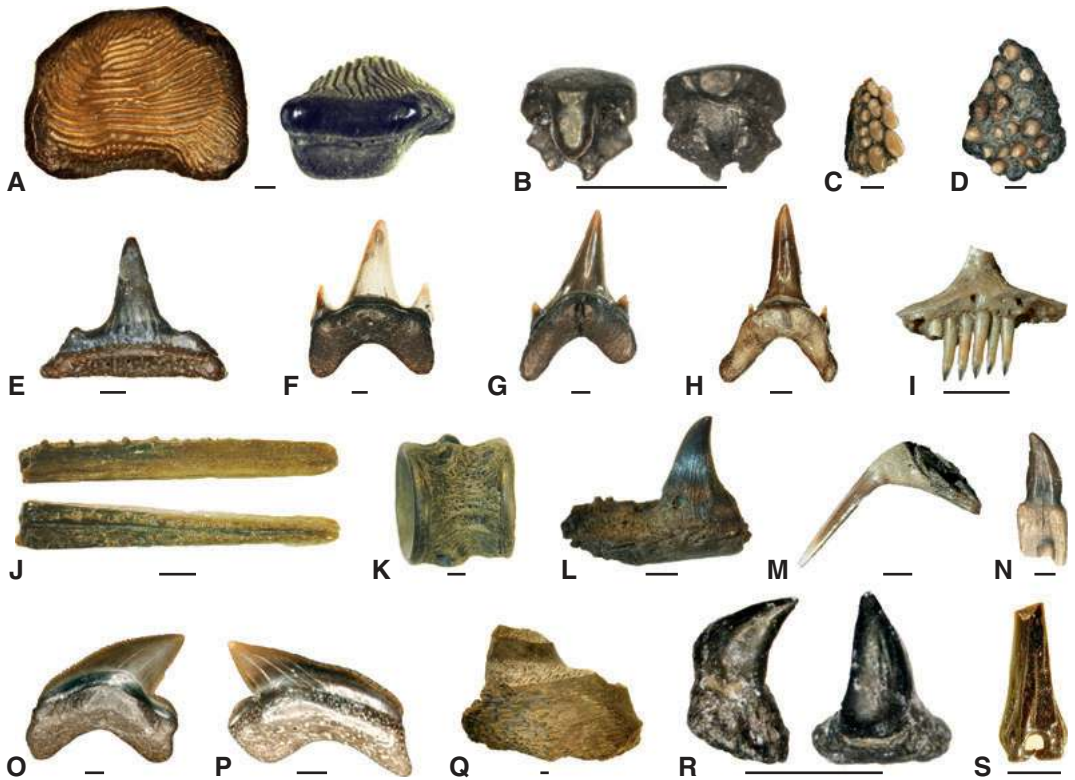
Fig. 5.

Representative fossil vertebrate taxa from the locality, grouped by inferred feeding strategy.

Group 1, durophagous feeders: **A** *Ptychodus rhombodus* RSM P2989.52, lower symphyseal tooth in occlusal and lateral views. **B,** '*Rhinobatos*' cf. *incertus* RSM P2989.182, tooth, lingual and labial views. **C,** cf. *Paleobalistum* tooth plate. **D,** cf. Albulidae tooth plate.

Group 2, active nectobenthic and pelagic predators: **E,** *Meristodonoides rajkovichi* RSM P2989.49, lower anterior tooth in labial view. **F,** *Archaeolamna* ex. gr. *kopingensis* RSM P2989.130, fourth lower lateral tooth in lingual view. **G,** *Roulletia canadensis* RSM P2989.106, first lower lateral tooth in lingual view. **H,** *Eostriatolamia paucicorrugata* RSM P2989.85, ?second lower anterior tooth in lingual view. **I,** Caturidae indet. RSM P2983.58, premaxilla with teeth, ventral/lingual view. **J,** *Belonostomus* sp. RSM P2983.59, paired dentary with teeth. **K,** ?Salmoniformes indet. RSM P2626.24, vertebral centrum in lateral view. **L,** *Elopopsis* sp. RSM P2626.23, right dentary with tooth, lateral view. **M,** *Enchodus* sp., right palatine with tooth. **N,** *Pasquiaornis* cf. *P. tankei*, left lower tooth.

Group 3, scavengers: **O,** *Squalicorax curvatus* RSM P2989.156, ?upper anterolateral tooth, lingual view. **P,** *Paleoanacorax pawpawensis* RSM P2989.169, lateral tooth in lingual view. **Q,** Chimaeroidea indet. RSM P2626.21, partial mandible.

Group 4, planktivores: **R,** *Cretomanta canadensis* RSM P2989.184, tooth in lateral, labial views. **S,** Acanthomorpha indet. RSM P2626.25, fin spine. The feeding strategy of the acanthomorph is unknown.

Scale bars = 1 mm. For additional views of some elements and for illustrations of specimens of other taxa, see UNDERWOOD & CUMBAA (2010) and CUMBAA et al. (2010).

hesperornithiforms were foot-propelled divers able to feed at the surface or pursue pelagic prey (REES & LINDGREN 2005). At least one partial hesperornithiform vertebra was recovered, its surface etched by the digestive acids of a predator or scavenger. *Ichthyornis* was a tern-like bird that would have plucked fish and occasional invertebrates from the surface (CLARKE 2004).

Comparison to other "mid"-Cretaceous faunas

There is convincing evidence for strong palaeolatitudinal variation in the faunas of the WIS, with relatively few species being common to both the northern and southern parts of the seaway (e. g. RUSSELL 1988, UNDERWOOD & CUMBAA 2010, CUMBAA et al. 2010). While the Bainbridge bonebed has produced a more Boreal fauna than that present within the southern part of the WIS, there is equally little similarity between the Bainbridge fauna and coeval northern faunas from Europe. In the chalk facies of Europe, the Cenomanian chondrichthyan fauna contains a very high diversity of small to medium sized nectobenthic taxa (e. g., UNDERWOOD & WARD 2008) with very abundant specimens of scyliorhinids, orectolobids, *Synechodus*, *Squatina* and especially the squaliform *Protosqualus*. Whilst there are diverse lamniforms, including common examples of *Archaeolamna*, many of the species are different and an additional pelagic predator, the hexanchid *Gladioserratus*, is also present. This dissimilarity between two faunas from adjacent continents and at a similar palaeolatitude again indicates that the northern part of the WIS was rather different from other marine habitats of the time.

Summary

Examination of Table 1, and especially of Figure 4, shows that the faunal composition of the bonebed does not represent "normal" accumulation of biotic debris from a single, static paleoenvironment, even over a period of time ranging from decades to thousands of years, but rather a mix of habitats. For example, inoceramid colonies, and in shallower water, oyster beds were present and must have attracted durophagous and other fish species, much as reefs do today. The bonebed fauna includes large numbers of pelagic predators, most quite small, and low numbers of generally small nectobenthic predators. Durophagous and planktivorous organisms were generally larger in size, but modest in number. Obviously some predators ate smaller predators, but large numbers of obvious prey species are either lacking or unrecognized in the fauna.

At least some of the material accumulated in a quiet, shelf environment with anoxic bottom waters. This is attested to by the presence of fragments of inoceramids, and of thousands of fully-formed coprolites, which had time to harden in the absence of detritivores. The biotic elements were concentrated further by winnowing in place, with the lighter fraction drifting away; linear-shaped elements sometimes are aligned, indicating a weak current pattern. Available evidence suggests the bonebed developed its final form in shallow water, draping and filling in scours, troughs of rippled surfaces and other low spots on the bottom, and rippled by wave action on the top. At the time of deposition, sedimentation was still almost negligible, but waters rose quickly on the shallow eastern margin in this transgressive phase of the WIS. The bonebed appears to have solidified in shallow water, as evidenced by surface ripples, but was soon below storm wave base where it was protected and soon covered by the gradual accumulation of a soft, muddy anoxic layer.

The taphonomic evidence of many rounded shapes and broken spines and processes shows that the highly concentrated faunal components of the bonebed were abraded in place by frequent winnowing, and/or were transported shoreward at least some distance, most likely by incoming transgressive waters following a basin-wide lowstand of unknown duration (SCHRÖDER-ADAMS et al. 2001, PHILLIPS 2008). By definition, this process means that the deposit is time-averaged, and as well, contains fauna from several contiguous habitats or paleoenvironments. In this respect, Table 1 is not an accurate 'snapshot' of marine life on a particular "mid"-Cenomanian day at a particular point on the eastern margin of the WIS. However, this bonebed fauna, in spite of obvious gaps (i. e., identifiable small prey species), likely represents a substantive portion of the vertebrate species inhabiting one or more contiguous paleoenvironments from shoreline to shelf roughly 95 Ma ago. The sedimentology and biostratigraphy of the Bainbridge locality suggests accumulation of the lag over a geologically brief (<0.1 Ma) period of time.

Strata of the same age along the eastern margin of the WIS that produce articulated vertebrate fossils have yet to be discovered, so these bonebeds are our best source of paleobiological information. Comparison of this bonebed fauna with those of similar age confirms there was strong paleolatitudinal variation within the WIS (CUMBAA et al. 2010, UNDERWOOD & CUMBAA 2010) and that the Bainbridge fauna is overall a boreal one, but with little similarity to coeval northern faunas from Europe (UNDERWOOD & CUMBAA 2010). The examination of probable habitats, relative abundance and feeding modes of the Bainbridge fauna presented here should be enhanced by isotopic analyses to better isolate paleoenvironments and an increased effort to recover identifiable elements from very small prey species.

Acknowledgements

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