**Xiphactinus audax** Leidy 1870 from the Puskwaskau Formation (Santonian to Campanian) of northwestern Alberta, Canada and the distribution of *Xiphactinus* in North America

Matthew J. Vavrek¹, Alison M. Murray² and Phil R. Bell³

¹Royal Ontario Museum, Department of Natural History, 100 Queen's Park, Toronto, ON M5S 2C6, Canada, matthew@matthewvavrek.com
²Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada, ammurray@ualberta.ca
³Department of Environmental and Rural Science, University of New England, Armidale, NSW 2351, Australia, pbell@une.edu.au

Abstract: *Xiphactinus* is the largest teleost fish known from the Late Cretaceous of North America, and has been found across much of the Western Interior Basin. Despite extensive Late Cretaceous marine deposits occurring in Alberta, there has previously been only two possible records of *Xiphactinus* from the province, neither of which has been diagnosable to the species level. We describe here a portion of the lower jaws, including teeth, of *Xiphactinus audax* from northeast of Grande Prairie, Alberta. The fossil has large, thecodont teeth that are circular in cross section and lack any carinae, and are highly variable in their overall size. This fossil is the first diagnostic material of *X. audax* from Alberta, and extends the range of the species by over a thousand kilometres. During the Late Cretaceous, the area the fossil was found in was near the Arctic Circle, and represents an important datapoint within the poorly known, northern portion of the Western Interior Basin.

Key Words: Ichthyodectiformes; Late Cretaceous; marine; Teleostei; Western Interior Basin

INTRODUCTION

The ichthyodectid *Xiphactinus* is the largest teleost fish known from the Late Cretaceous of North America (Bardack 1965; Schwimmer et al. 1997; Shimada et al. 2006). Specimens of *Xiphactinus* have been found from Cenomanian (Cumbaa et al. 2006) through Campanian (DeMar and Breithaupt 2006) deposits throughout much of the southern Western Interior Basin, from central Saskatchewan (Cumbaa and Tokaryk 1999; Cumbaa et al. 2006) south to Texas (Bardack 1965), as well as Campanian to Maastrichtian beds along the Atlantic coast in New Jersey (Grandstaff et al. 1992), North Carolina, Georgia and Alabama (Schwimmer et al. 1997). Although known from a variety of formations, the most spectacular specimens of *Xiphactinus* come from the Niobrara Formation of Kansas, where well-preserved, virtually complete skeletons were being excavated as early as the 1870s (Cope 1872; Bardack 1965). Some of these nearly complete specimens are close to 5 m in total length, although isolated elements from even larger individuals are also known (Bardack 1965; Shimada and Everhart 2004).

Despite extensive marine deposits in Alberta, to date only two other questionable records of *Xiphactinus* have been reported from the province. The first record is from “east of Lesser Slave Lake” noted by Bardack (1965). However, he listed no referred material and gave no description of any specimen, with the record consisting only of a personal communication from Wann Langston. A search of likely museum collections where any such fossils would have been accessioned has yielded nothing. The general lack of appropriate-aged fossil bearing deposits from that area, as well as the lack of referable or figured specimens, makes this record dubious. A second Albertan record consists of two isolated scales from the Kaskapau Formation near Watino, Alberta (Wilson and Chalifa 1989), although those authors note that the scales do not conform in every aspect with those of *Xiphactinus* and so referred the specimens to “cf. Xiphactinus”.

The specimen we describe here, TMP 1973.011.3081, was first mentioned in an unpublished PhD thesis by Christopher Collom (2001), and later mentioned again by Bell et al. (2014). However, the specimen itself was never...
described and was only assigned to the genus *Xiphactinus*. Further study of the specimen has revealed a number of characteristics that allow the assignment of the specimen more precisely to *Xiphactinus audax*, expanding the range of this species considerably. The specimen itself is notable for its relatively northern location within the Western Interior Seaway, and also confirms and fully documents the presence of *Xiphactinus* in Alberta.

**Institutional Abbreviations:** CMN, Canadian Museum of Nature, Ottawa, Ontario, Canada; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; UALVP, University of Alberta Laboratory for Vertebrate Palaeontology, Edmonton, Alberta, Canada.

**GEOLOGICAL SETTING**

The Puskwaskau Formation is a marine, mudstone-dominated wedge up to 350 m in thickness, that was deposited in relatively shallow waters of the Western Interior Seaway (Hu and Plint 2009). The Puskwaskau was deposited during the Niobrara Cycle (Kauffman 1977), and is Santonian to early Campanian in age (Hu and Plint 2009; Fig. 1). The Puskwaskau is divided into five members, which are, in ascending order, Dowling, Thistle, Hanson, Chungo and Nomad (Stott 1963, 1967; Hu and Plint 2009). Collom (2001) suggested that the Santonian/Campanian boundary is within the upper part of the Hanson Member, placing the Chungo and Nomad members within the lower Campanian. Although the exact stratigraphic position of the fossil is unknown, the matrix still attached to the fossil is similar in nature to a number of other marine vertebrate specimens found in the area, particularly those discussed by Bell et al. (2014). The majority of the specimens discussed in that paper were inferred to have come from the upper portions of the Puskwaskau Formation, likely the Chungo or Nomad members (Bell et al. 2014). This is further corroborated by the location where TMP 1973.011.3081 was found, on a relatively small, shallow creek that drains a limited area. Geologic maps of the region indicate that the creek drains an area that is mainly part of the upper portions of the Puskwaskau Formation, concordant with the idea that the fossil comes from one of the upper members of the formation. Assuming TMP 1973.011.3081 is from one of these upper members, it would be early Campanian in age.

**SYSTEMATIC PALAEOONTOLOGY**

Order *ICHTHYODECTIFORMES* Bardack and Sprinkle, 1969

Family *ICHTHYODECTIDAE* Patterson and Rosen 1977

Genus *Xiphactinus* Leidy 1870

*Xiphactinus audax* Leidy 1870

**Referred Material:** TMP 1973.011.3081, the anterior portion of articulated left and right dentaries.
Locality and Horizon: The fossil was likely collected sometime in the 1950s or 1960s, based on the personal collection records of George Robinson, the original collector. The notes associated with the fossil in the TMP collections state that the specimen was “from the Bad Heart River near bridge.” However, in Robinson’s original collections ledger, he noted that he found the fossil along “Kakut Ck near bridge on Wanham Rd” and that it came from the “Bad Heart Sst.” Another note he made, beside the entry for several invertebrate specimens collected from the same location, states that the bridge had been replaced by a culvert. His description, and comparison with historical maps of the area and modern maps, shows that the fossil came from exposures near Kakut Creek where the present day Secondary Highway 733 crosses it, at approximately 55.61°N 118.39°W. The exact horizon the fossil came from is unknown, and it was likely found ex situ, as the unprepared portions of matrix still attached appear to have been water worn, likely from sitting in the creek itself for some time.

Description: TMP 1973.011.3081 preserves approximately the anterior one-third of the left and right dentaries, and measures 16 cm long. The dentary symphysis forms a sigmoidal curve in lateral view with a tooth positioned on each side right beside the symphysis. The pores for the mandibular canal are not clearly visible as this area of the jaw is somewhat distorted and very worn. The symphysis measures 9.2 cm in a straight line from the lower edge to the upper, which is close to the average length for *X. audax* [8.7 cm with a range of 6.0–13.85 based on measurements of 81 specimens (Bardack 1965)]. The dorsal surfaces of the dentaries undulate, being deepest under the largest tooth.

There are six right and six left tooth positions preserved, some of which contain almost complete teeth while others are represented only by the tooth base. The two anterior-most teeth on either side of the symphysis are fairly large, and would have reached an estimated 3 cm above the dentary bone. The third tooth on each side are the largest of the preserved teeth. The third tooth on the left side is almost
Xiphactinus, the two other large Cretaceous ichthyodectid fishes known from North America, both have teeth that are much smaller and of more uniform size than those of Xiphactinus (e.g., Bardack, 1965). Species of Xiphactinus have much larger teeth and display heterodonty in their size. Therefore, this specimen clearly belongs to Xiphactinus. Additionally, Schwimmer et al. (1997) noted the characteristic thecodont dentition of Xiphactinus — this is well exemplified in the Alberta specimen by the tooth exposed by preparation so that the whole root, reaching to the ventral edge of the jaw, is visible. This identification is also supported by the undulating alveolar margin of the jaw (Bardack 1965) and the slight sigmoidal curve of the symphysis; both the alveolar margin and symphysis are relatively straight in the other two genera.

Two North American species of Xiphactinus are currently considered valid (see discussion below). The teeth of X. audax lack carinae, while those of X. vetus are somewhat laterally compressed and recurved, and bear an anterior or anterolingual carina and sometimes a posterior carina (Schwimmer et al., 1997). The teeth of the Alberta specimen closely resemble those of X. audax, and therefore, this specimen can be confidently assigned to this species. The relative size of the Albertan fish can be estimated based on the size of the jaw fragment. Bardack (1965) noted that the mean length of the symphysis in X. audax is 8.7 cm, with a range of 6.0–13.85 based on measurements of 81 specimens. The symphysis of the Alberta specimen was about 9.2 cm, indicating the fish that this dentary came from was of an intermediate size, possibly around 3 m in total length.

**Additional Material:** A second specimen (Fig. 3), in the collections of the Canadian Museum of Nature (specimen number CMN 51273), likely came from the same area as TMP 1973.011.3081. The label states it is from Bad Heart, Alberta, collected in 1961 by Robert Cochrane, and identified as cf. Xiphactinus by ‘CMS’ (which would be C.M. Sternberg). CMN 51273 preserves the symphysis and partial left and right dentaries, along with other elements that could benefit from more preparation. The heterodont, thecodont dentition, sigmoidal curve of the symphysis and the undulating dorsal edge of the dentary confirm the identification of Xiphactinus. The teeth have no carinae and circular cross section (pers. obs.), and so we consider this specimen to also belong to X. audax. The CMN specimen is from a slightly smaller fish than the TMP specimen.

**DISCUSSION**

The most comprehensive review of Xiphactinus was by Bardack (1965), as part of a larger treatise on the taxonomy of chirocentrid fishes. The understanding of the relationship of chirocentrids and ichthyodectids has changed considerably since that publication [see Nelson (1973) and Patterson and Rosen (1977) for a more thorough review of Ichthyodectiformes taxonomy]; however, Bardack’s revisions to the generic taxonomy of Xiphactinus have largely stood unchanged. Bardack (1965) retained four species in the genus Xiphactinus, but did so based on their distribution in time and space rather than for morphological
reasons. *Xiphactinus gaultinus* and *Xiphactinus mantelli* are known from Europe, while *Xiphactinus australis* is from Australia. Specimens of these three species are quite fragmentary (Bardack 1965) making them difficult to distinguish from *X. audax*. All the North American species known at that time were considered synonyms of *X. audax* by Bardack (1965). New records of *Xiphactinus* sp. have since been recovered from South America (Carrillo-Briceño et al. 2012), and a separate species of *Xiphactinus* from North America, *X. vetus*, was re-erected by Schwimmer et al. (1997). This second species of North American *Xiphactinus* can be relatively easily distinguished from *X. audax* by the morphology of the teeth (see Remarks above).

The two North American species show a large amount of overlap in their distributions (Fig. 4; Tab. 1). *Xiphactinus audax* has been found from northern Alberta through the Western Interior Basin and along the Atlantic Coastal plain. Remains of *X. vetus* are most commonly found along the Atlantic Coastal plain (Schwimmer et al. 1997), although recent finds in Wyoming have significantly extended its range (DeMar and Breithaupt 2006). The relative rarity of *X. vetus* in the Western Interior or *X. audax* along the eastern seaboard may have more to do with the lack of appropriate aged marine deposits, rather than any true range boundary (Schwimmer et al. 1997). Although the two species are found within geographically overlapping strata, they do not appear to have co-existed. Definitive remains of *X. audax* have been recovered from Cenomanian through to early Campanian deposits, with a possible occurrence from the upper Albian of Kansas (Williston 1894), while *X. vetus* is only known from younger, middle Campanian through to lower Maastrichtian deposits (Schwimmer et al. 1997; DeMar and Breithaupt 2006).

Although presently far south of the Arctic Circle, the locality where TMP 1973.011.3081 was found would have been close to 65°N during the early Campanian (Irving et al. 1993; Smith et al. 1994; Bell et al. 2014; Vavrek et al. 2014a). Excluding the two records of indeterminate *Xiphactinus* and *Xiphactinus*-like taxa from Arctic Canada, this represents the northernmost record of *X. audax*. During an expedition in 1965 to the early Campanian (Hills et al. 1999) Smoking Hills Formation along the Anderson River, Northwest Territories, Russell (1967) found and uncovered the tail and posterior abdominal portion of a very large fish he referred to as *?Xiphactinus*. However, due to a number of factors the specimen was not collected, and so its identity cannot be confirmed.

A second specimen of a possible *Xiphactinus* from the Arctic was reported by Hills et al. (1999), from the Kanguk

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**Figure 4.** Map of confirmed or possible *Xiphactinus* occurrences from Canada and the United States. Grey shading indicates non-marine regions. Coastline shown is approximately that of the early Turonian, adapted from Kauffman (1984). In cases where multiple localities are in very close proximity, some localities have been omitted for clarity. For a more comprehensive list of localities, please consult the supplementary materials, as well as Bardack (1965) and Schwimmer et al. (1997).
Table 1. Partial list of occurrences of *Xiphactinus* from North America. Note that several of the Kansas occurrences of *X. audax* from Table 3 in Bardack (1965) have been omitted due to their close proximity to one another both stratigraphically and geographically.

| Name            | Material                                      | Latitude N | Longitude W | Locality           | Province/State, Formation | Age                      | Geologic Reference | Taxonomic Reference |
|-----------------|-----------------------------------------------|------------|-------------|--------------------|---------------------------|-------------------------|--------------------|---------------------|
| *Xiphactinus*   | not stated                                     | 79.75      | 85.6        | Fosheim Peninsula  | NU, Kanguk                | Latest Cenomanian/Turonian–Campanian | 1                   | 1                   |
| ?*Xiphactinus*  | uncollected, posterior portion of body         | 69.3       | 128.3       | Anderson River     | NT, Smoking Hills         | early Campanian          | 1, 2, 3            |
| *X. audax*      | partial left and right dentaries               | 55.61      | 118.39      | Kakut Creek        | AB, Puskwaskau             | Santonian–Campanian     | 4                   | 4                   |
| cf. *Xiphactinus* | scales                                        | 55.72      | 117.63      | Watino             | AB, Kaskapau               | early Turonian            | 6                   | 6                   |
| *X. audax*      | teeth                                          | 53.48      | 102.24      | SMNH Locality 63E09-0003 (Bainbridge River) oyster beds | SK, Belle Fourche Mb, Ashville Fm | middle Cenomanian | 7                   | 8                   |
| *Xiphactinus*   | scales or teeth                                | 53.48      | 102.24      | SMNH Locality 63E09-0003 (Bainbridge River) white-speckled shales | SK, Favel (Second White Specks Marker) | early Turonian | 7                   | 9                   |
| *X. audax*      | scales or teeth                                | 53.21      | 103.52      | SMNH Locality 63E03-0001 (Carrot River) | SK, Belle Fourche Mb, Ashville Fm | middle Cenomanian | 7                   | 8, 9                |
| *Xiphactinus*   | complete                                       | 53.21      | 103.52      | SMNH Locality 63E04-0001 (Carrot River) | SK, Favel (Keld Mb) | early Turonian | 7                   | 9                   |
| *Xiphactinus*   | single scale                                   | 52.8       | 102.4       | SMNH Locality 63D09-0002 (Etomami River) | SK, Pierre Shale | early Campanian–early late Campanian | 10                  | 9                   |
| *X. audax*      | articulated and disarticulated material        | 49.1       | 98.3        | Morden             | MB, Pembina Mb, Pierre Fm | lower Campanian          | 1                   | 3, 11, 12            |
| Name             | Material                  | Latitude | Longitude | Locality                | Province/State, Formation             | Age          | Geologic Reference | Taxonomic Reference |
|------------------|---------------------------|----------|-----------|-------------------------|---------------------------------------|--------------|-------------------|---------------------|
| X. audax         | complete skeleton         | 43.31    | 103.39    | SE of Hot Springs       | SD, Niobrara                          | Santonian    | 13                | 13                  |
| X. vetus         | isolated teeth            | 44.13    | 107.78    | Old Number One (UW V-81036) | WY, Mesaverde                        | upper Campanian | 14                | 14                  |
| X. vetus         | isolated teeth            | 44.12    | 107.78    | Old Number Four (UW V-81038) | WY, Mesaverde                        | upper Campanian | 14                | 14                  |
| X. vetus         | isolated teeth            | 44.1     | 107.76    | Sunset to Dawn Two (UW V-81076) | WY, Mesaverde                        | upper Campanian | 14                | 14                  |
| Xiphactinus sp.  | spines                    | 41.5     | 91.6      | Riverside               | IA, Graneros Shale                   | Cenomanian   | 15                | 15                  |
| X. audax         | 2 teeth                   | 40.1     | 97.2      | Highway 15 Roadcut      | NJ, Greenhorn Limestone               | Turonian     | 16                | 16                  |
| X. audax         | single tooth              | 37       | 102.7     | Comanche National Grassland | NJ, Greenhorn Limestone               | middle Cenomanian | 17              | 17                  |
| X. audax         | not stated                | 39.89    | 98.03     | Lovewell Reservoir      | KS, Carlile Shale                    | middle Turonian | 18               | 18                  |
| ?X. audax        | 4 teeth                   | 39       | 98.92     | NW Russell County       | KS, Greenhorn Limestone (FHSM)        | middle Cenomanian | 19              | 19                  |
| X. audax         | not stated                | 38.72    | 100.7     | Hell's Bar              | KS, Niobrara                          | Santonian    | 20                | 20                  |
| X. audax         | multiple partial skeletons | 39.08    | 99.24     | KUVP Ellis-5            | KS, Fairport Mb, Carlile Shale       | Turonian     | 21                | 21                  |
| X. audax         | complete skeleton         | 38.91    | 101.24    | south side, Smoky Hill River, west of Russell Springs | KS, Smoky Hill Chalk, Niobrara | late Santonian | 22               | 22                  |
| X. audax         | teeth                     | 38.9     | 98.6      | Near Wilson Lake, eastern Russell County | KS, Dakota Sandstone | middle Cenomanian | 23       | 23                  |
| ?Xiphactinus     | vertebra                  | 37.2     | 99.8      | vicinity of Ashland     | KS, “Neocomian or Comanche Cretaceous” | ?Neocomian (possibly Albian) | 24           | 24                  |
| X. audax         | complete skeleton         | 31.53    | 97.21     | Bosque Farm             | TX, Eagle Ford                        | Turonian     | 13                | 13                  |
| X. audax         | complete skeleton         | 33.37    | 96.72     | Celina                  | TX, Austin Chalk                      | Coniacian–lower Santonian | 13          | 13                  |
| Name             | Material                                | Latitude Longitude N W | Locality | Province/State, Formation | Age                        | Geologic Reference | Taxonomic Reference |
|------------------|-----------------------------------------|------------------------|----------|---------------------------|----------------------------|--------------------|---------------------|
| X. audax         | complete skeleton                       | 33.53 96.36            | Savoy    | TX, Austin Chalk          | Coniacian–lower Santonian  | 13                 | 13                  |
| X. vetus         | not stated, likely tooth                 | 40.3 74.3              | Ellisdale Site | NJ, Marshalltown          | late Campanian             | 25, 26             | 25, 26              |
| ?Xiphactinus     | not stated                               | 39.78 75.17            | Inversand Company marl pit (Navesink) | NJ, Navesink              | early Maastrichtian       | 26, 27             | 27                  |
| X. vetus         | isolated lateral teeth                   | 40.26 74.27            | Big Brook | NJ, Marshalltown/ Wenonah/Mount Laurel/Navesink | upper Campanian–lower Maastrichtian | 26, 28 | 26, 28, 29 |
| X. vetus         | type of Polygonodon vetus                | 39.86 74.69            | Burlington County | NJ, Navesink or Hornerstown | upper Campanian–lower Maastrichtian | 26, 26, 30 |
| X. vetus         | 2 teeth                                 | 39.56 75.65            | Chesapeake and Delaware Canal | DE ?Marshalltown     | upper Campanian             | 26, 31             | 26, 31              |
| X. vetus         | teeth                                   | 34.57 78.5             | Cape Fear River | NC, Snow Hill Marl Mb, Black Creek Fm | upper Campanian             | 13, 26, 32 | 13, 26, 32 |
| X. vetus         | isolated teeth                           | 34.55 78.45            | Phoebus Landing | NC, Snow Hill Marl Mb Black Creek Fm | upper Campanian             | 36                | 26, 33              |
| Xiphactinus      | not stated                               | 34.1 79.5              | Pee Dee River | SC, ?Peedee              | Campanian to Maastrichtian | 34                 | 34                  |
| X. vetus         | skull fragments, vertebrae, fin spines   | 32.41 87.2             | G. S. Moore Farm | AL, Mooreville Chalk      | upper Santonian             | 36                 | 36                  |
| X. audax         | five vertebrae                           | 32.61 87.67            | Crawford Farm | AL, Mooreville Chalk      | upper Santonian             | 36                 | 36                  |
| X. audax         | skull fragments and vertebrae            | 32.76 88.02            | Hewlett Farm | AL, Mooreville Chalk      | upper Santonian             | 36                 | 36                  |
| X. audax         | vertebrae and lower jaw fragments        | 32.96 88.13            | West Greene, NW | AL, Mooreville Chalk      | upper Santonian             | 36                 | 36                  |
| X. audax         | palatoquadrate                           | 32.42 87.2             | Harrell Station | AL, Mooreville Chalk      | upper Santonian             | 36                 | 36                  |
| Name   | Material                                      | Latitude N | Longitude W | Locality | Province/State, Formation | Age             | Geologic Reference | Taxonomic Reference |
|-------|-----------------------------------------------|------------|-------------|----------|---------------------------|-----------------|-------------------|---------------------|
| *X. audax* | vertebrae, fragmentary skull                   | 32.94      | 88.06       | Hale’s Farm | AL, Mooreville Chalk      | upper Santonian  | 36                | 36                  |
| *X. vetus*   | teeth and vertebrae                           | 31.99      | 85.14       | Cowikee Creek | AL, Blufftown         | middle Campanian | 26                | 26, 35              |
| *X. audax*   | not stated                                     | 33.52      | 88.4        | Tombigbee Sand | MS, Eutaw            | late Santonian   | 37                | 37                  |
| *X. vetus*   | teeth                                         | 34.58      | 88.63       | Frankstown  | MS, Demopolis           | upper Campanian  | 26                | 26, 38              |
| *X. audax*   | skull bones, fin rays, teeth, vertebrae        | 33.8       | 94.1        | Ben Lomond, AR | AR, Brownstown Marl | early Campanian  | 39                | 39                  |
| *X. audax*   | jaw fragment                                   | 34         | 93.5        | Delight, AR | AR, Brownstown Marl      | early Campanian  | 39                | 39                  |

**Taxonomic and Geologic References for Table 1**

1. Hills et al. 1999
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4. Collom 2001
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30. Leidy 1856
31. Lauginiger 1984
32. Stephenson 1912
33. Robb 1989
34. England 2003
35. Case and Schwimmer 1988
36. Applegate 1970
37. Phillips and Loftis 1999
38. Manning and Dockery 1992
39. Irwin and Fielitz 2013
Formation on Ellesmere Island. The specimen was collected but not described, and at this time cannot be relocated, so it is presently unknown even what element(s) is/are represented. This locality was dated as early to middle Campanian based on palynomorphs recovered from the same section. Additional material (in the CMN collections) identified by S.L. Cumbaa as belonging to cf. *Xiphactinus* and *Xiphactinus audax* was collected from Cretaceous deposits of Devon Island by the field parties of J. Eberle and K. Chin in 1998 and 2003. The geographic location of some of these finds is interesting, as during the Late Cretaceous, these Arctic localities may have actually been closer to Europe than many of the locations within the Western Interior Basin (e.g., see map in Vavrek et al. 2014a). Regardless of the exact taxonomic affiliation of these Arctic finds, *Xiphactinus audax* still possesses an incredibly large geographic range, stretching for thousands of kilometres within the Western Interior Basin. Although this additional record of *Xiphactinus audax* adds to our growing knowledge of marine vertebrates from the northern part of the Western Interior Basin (e.g., Cumbaa and Tokaryk 2009; Cumbaa et al. 2006; Cook et al. 2008, 2010, 2012; Bell et al. 2014; Vavrek et al. 2014b) the region still remains understudied compared to more southerly regions (Cook et al. 2008, Vavrek et al. 2014b). Further work in northern areas is required so as to better understand the true ranges and biogeography of marine vertebrates during the Late Cretaceous.

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