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

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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

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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 PALAEONTOLOGY

Order ICHTHYODECTIFORMES Bardack and Sprinkle, 1969
Family ICHTHYODECTIDAE Patterson and Rosen 1977
Genus *Xiphactinus* Leidy 1870
Xiphactinus audax Leidy 1870
Figure 2

Referred Material: TMP 1973.011.3081, the anterior portion of articulated left and right dentaries.

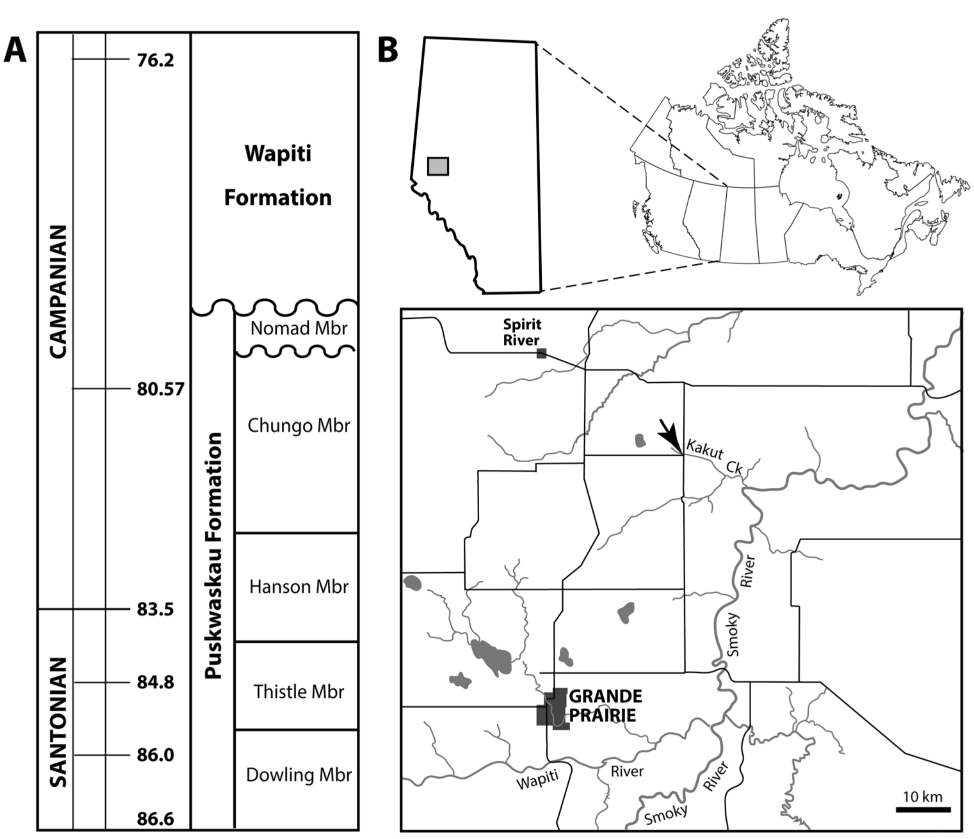

Figure 1. A) Summary stratigraphic chart for the Santonian to early Campanian of northwestern Alberta. B) Maps showing, counter-clockwise from top right: location of Alberta within Canada; location of regional map of Grande Prairie area within Alberta; location of fossil site along Kakut Creek, northeast of Grande Prairie. Location of TMP 1973.011.3081 is marked with an arrow.

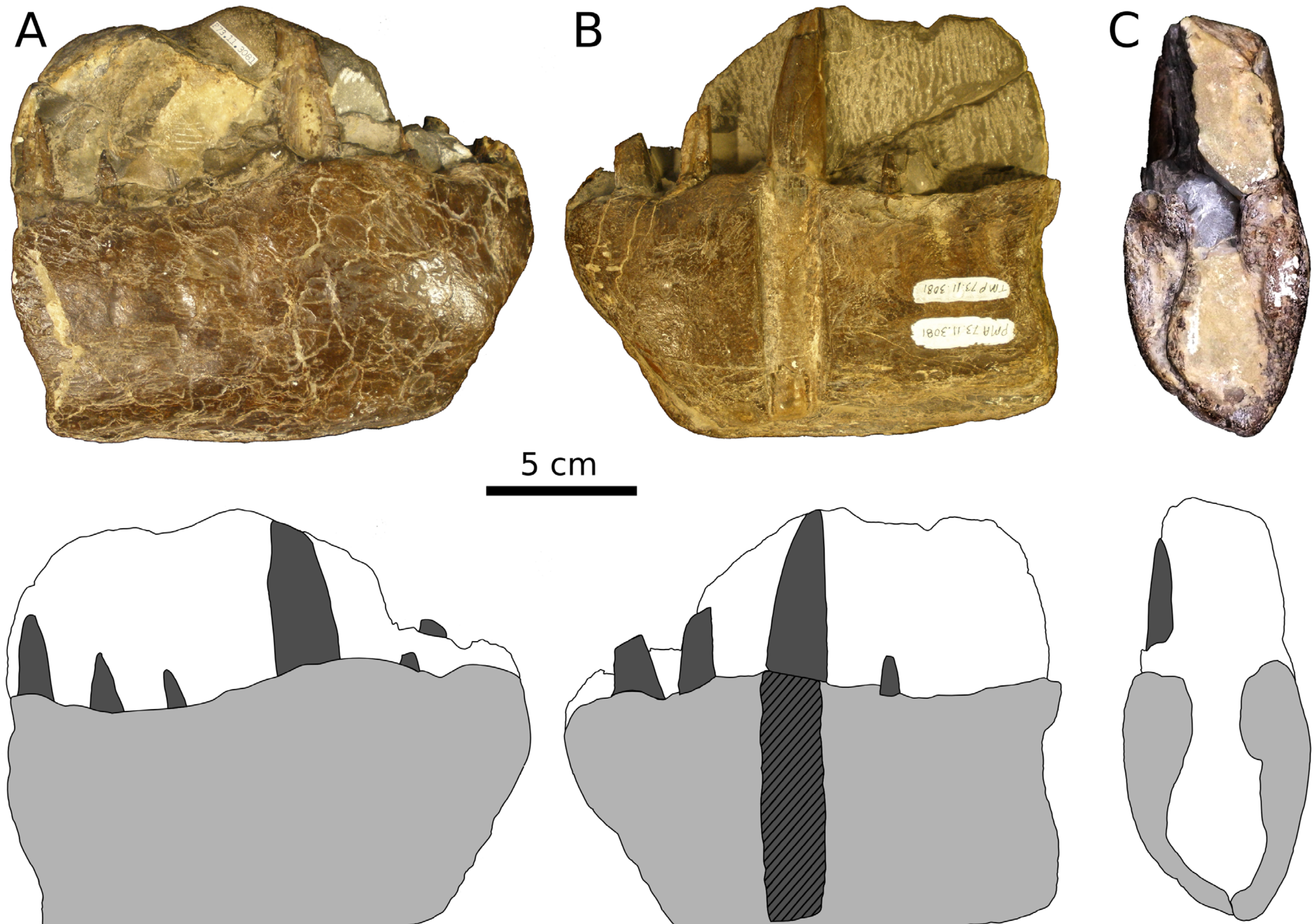

Figure 2. TMP 1973.011.3081, partial jaws of *Xiphactinus audax* Leidy 1870. A) Right lateral view. B) Left lateral view. C) Posterior view. For all line drawings matrix is shaded white, bone is shaded light grey, teeth are shaded dark grey, and cross-hatching indicates areas of exposed tooth root.

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 C^k 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 complete, missing only a small portion at the labial side of the tip, and reaches 5.5 cm above the dentary bone. The dentary in this area had been prepared away so that the tooth root is visible (Fig. 2B). The tooth is clearly thecodont as the root reaches all the way to the ventral margin of the jaw, making the complete tooth just short of 13 cm long. The fourth tooth, visible on both sides, is the smallest present, and quite slender. The almost complete left fourth tooth is 1.2 cm high, and would have been only slightly taller when complete. Only the bases of the fifth and sixth teeth on the left dentary are preserved. On the right dentary, the tip of the fifth tooth is present, and this tooth is 1.8 cm above the margin of the bone. The sixth tooth is almost as large as the anterior teeth, at about 2.8 cm tall.

The root of the largest tooth on the left side, where the jaw bone has been removed, can be seen clearly, and it is round in cross section. The tooth bases of the fifth and sixth positions on the left dentary are also round in cross section. None of the preserved teeth possess carinae.

Because the jaw is broken at the posterior end, the cross-sectional shape of the two dentaries can be seen. The alveolar surface is much wider than the ventral part of the dentary. The cross section is comma shaped, with the ventral tail of the comma curving medially (Fig. 2C).

Remarks: *Ichthyodectes* and *Gillicus*, 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.

Figure 3. CMN 51273, partial jaws of *Xiphactinus audax* Leidy 1870, in right lateral view.

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

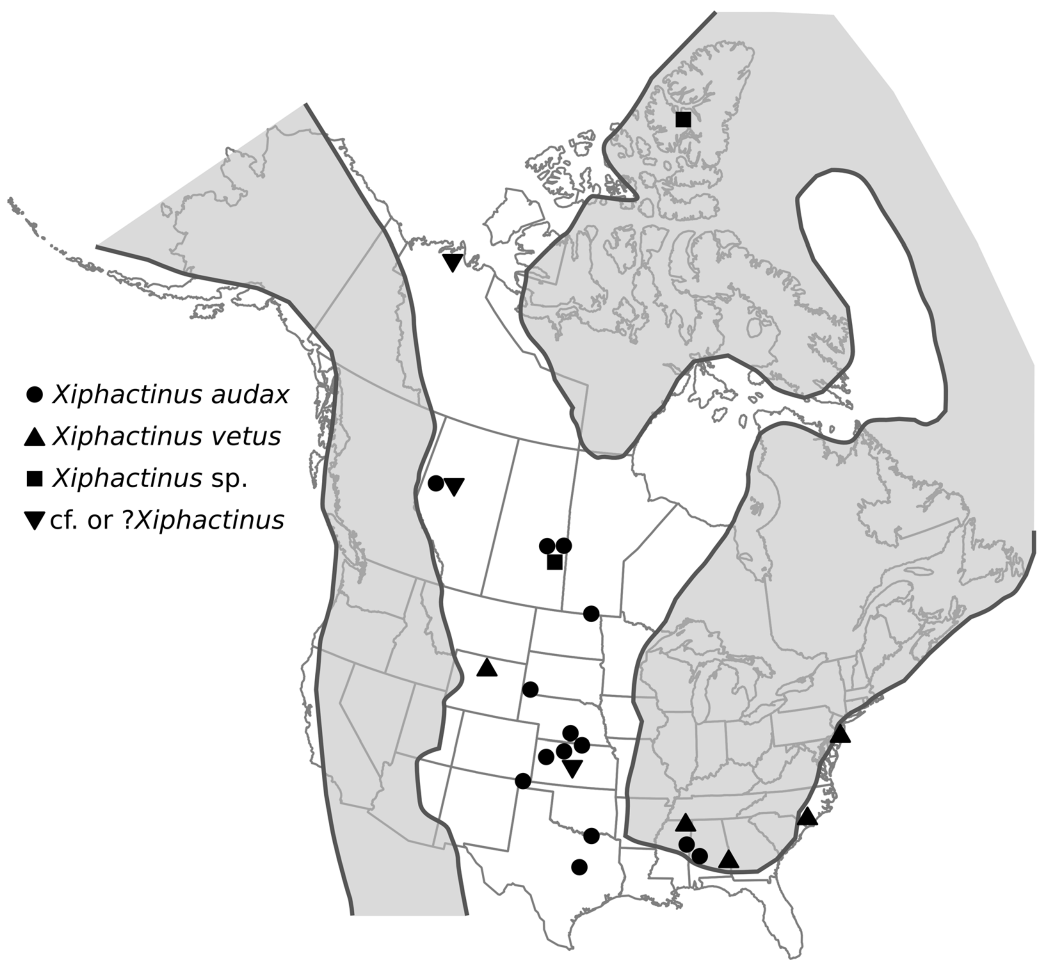

Figure 4. Map of confirmed or possible *Xiphactinus* occurrences from Canada and the United States. Grey shading indicates non-marine regions. Coastline shown is approximately that of the early Turonian, adapted from Kauffman (1984). In cases where multiple localities are in very close proximity, some 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	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 N	Longitude W	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 (FHSM)	KS, Greenhorn Limestone	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 N	Longitude 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		32.16	85.03	Hannahatchee Creek	GA, Blufftown Formation	middle Campanian	26	26, 35
X. audax	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

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30. Leidy 1856
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32. Stephenson 1912
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34. England 2003
35. Case and Schwimmer 1988
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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.

ACKNOWLEDGEMENTS

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