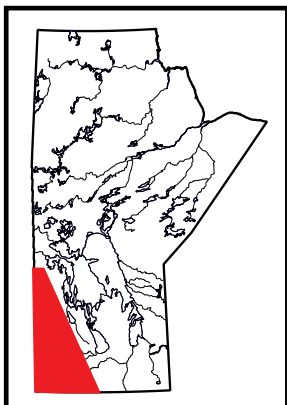


In Brief:

- Surveys were conducted at Canadian institutions housing Manitoba escarpment vertebrate fossil collections, and several collection biases were identified
- Fossils of sharks and birds are most abundant in current collections, and fossils of reptiles and fish are least abundant
- Collection biases can be counteracted with future work that targets poorly known lithostratigraphic units and the collection of microvertebrate fossils

Citation:

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**Summary**

An ongoing study examining the stratigraphic distribution and composition of the Late Cretaceous vertebrate faunal associations of the Western Interior Seaway (WIS) of Manitoba has revealed several historical collection biases in current institution collections of vertebrate fossils from the Manitoba escarpment of southwestern Manitoba to east-central Saskatchewan. These biases have led to the unequal representation of some taxonomic groups in certain time periods, such as mid-Cenomanian chondrichthyans and early Campanian marine reptiles when compared to fish from all Cretaceous members. The identification and presentation of historical collection biases is necessary before analyses of faunal provinciality, habitat preferences and faunal changes through time can be undertaken, as these biases can skew interpretations of Cretaceous paleoecology of the WIS. Data-supported recommendations for future work are provided to address and reduce biases in future vertebrate fossil collection.

Introduction

Late Cretaceous (100.5–66 Ma) sedimentary strata in Manitoba were deposited in a shallow marine setting near the eastern margin of the WIS, which hosted a diverse marine vertebrate community of fish, sharks, reptiles and birds (Bardack, 1968). Exposures of Late Cretaceous deposits in Manitoba range in age from the Cenomanian to Maastrichtian and are mainly restricted to the Manitoba escarpment, a northwest-trending ridge consisting of five topographic highs and about 675 km in total length, from the Manitoba–North Dakota border near Walhalla, North Dakota, to the Manitoba–Saskatchewan border near Hudson Bay, Saskatchewan (Bamburak and Nicolas, 2013). New stratigraphic information on Cretaceous deposits of the WIS in Manitoba, including an updated lithostratigraphic framework (Bamburak and Nicolas, 2009), radiometric ages of bentonites (Bamburak et al., 2013, 2016) and defined foraminiferal zones (Nielsen et al., 2008; Schröder-Adams, 2014), made available over the last two decades has improved historically challenging regional correlations with coeval deposits in Saskatchewan and Alberta (Christopher et al., 2006; Nielsen et al., 2008) and North Dakota (McNeil and Caldwell, 1981). However, vertebrate biostratigraphy and biogeography data are currently lacking.

Institution fossil collections are essential for identifying the composition of faunal assemblages and are invaluable for examining temporal and biogeographic trends due to their large sample sizes and accessibility. For example, Nicholls and Russell (1990) described spatial differences between time-transgressive, early Campanian WIS communities on a continental scale using institution collections. However, when considering more detailed paleoecological analyses, institution collections have limitations. As the majority of Manitoba escarpment institution specimens are limited to genus-level in terms of taxonomic identification and lithostratigraphic member in terms of stratigraphic information, it can be difficult to discern small-scale changes between fossil associations through time.

Previous descriptions of vertebrate fossil collection biases in Manitoba are limited to the early Campanian Pembina Member of the Pierre Shale (Nicholls, 1989; Nicholls and Russell, 1990). Nicholls (1989) described collection biases known to affect the Pembina Member fossil collection between 1972 and 1985. These biases included time-limited access and expedited collection of specimens discovered in bentonite strip mining operations, inconsistent collecting methods and duration of collecting between localities and preferred collection of large and semi- to fully articulated specimens. Preservation biases included taphonomic factors and alteration by post-depositional crystallization of gypsum. For example, Nicholls (1989) demonstrated the number of catalogued fish specimens from the Pembina Member faunal assemblage is not indicative of their

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true abundance since only articulated fish remains and no isolated fish elements were collected prior to the study, resulting in significant underrepresentation of fish in the Pembina Member collection.

In order to update the work of Nicholls and Russell (1990) and to describe the diversity of Late Cretaceous WIS vertebrate faunal associations through time, surveys of several institutions (museum and university collections; Table GS2021-6-1) housing fossil specimens collected from the Manitoba escarpment in Manitoba and Saskatchewan were conducted in 2020 and 2021. As a result of these surveys, several collection biases were identified, building on the initial biases discussed by Nicholls (1989). For the purpose of this study, collection biases are defined as fossil collecting methods or practices that have led to disproportionate representation of certain taxonomic groups within a faunal assemblage or certain lithostratigraphic units relative to others, in existing institution collections. The identification and presentation of historical collection biases is imperative for a proper understanding of the distribution of Cretaceous vertebrates in Manitoba and to test hypotheses of faunal provinciality, habitat preferences and temporal and spatial changes in faunal assemblages through time.

Results

Representative fossil specimens from either the most or second-most abundant taxon of each lithostratigraphic member collected from the Manitoba escarpment are shown in Figure GS2021-6-1. The majority of Manitoba escarpment institution specimens are fragmentary marine reptile and hesperornithiform bird (Figure GS2021-6-1g) remains from the Pembina Member, Pierre Shale, collected from bentonite mining operations in the Morden-Miami area from 1939 to 1990 (Bamburak and Nicolas, 2013). However, in terms of individual

specimens, the most sampled lithostratigraphic unit of the Manitoba escarpment is the early to late Cenomanian Belle Fourche Member, Ashville Formation, particularly in the Carrot River and Bainbridge River bone beds in Saskatchewan (Cumbaa and Bryant, 2001; Schröder-Adams et al., 2001; Cumbaa et al., 2006, 2010, 2013; Underwood and Cumbaa, 2010; Figure GS2021-6-2a, b). These microvertebrate bone beds were consistently sampled over multiple years and the samples were prepared with an acid-digestion technique resulting in a relatively large and disproportionate number of recovered specimens relative to other Manitoba escarpment units and horizons.

The two Manitoba escarpment lithostratigraphic members with the least fossil representation in institution collections are the Morden Member, Carlile Formation, and the Odanah Member, Pierre Shale. The Morden Member has produced a partial actinopterygian dentary assigned to *Enchodus shumardi* and 75 chondrichthyan dermal denticles (e.g., Manitoba Museum specimen MM V-2689 and in University of Manitoba, Department of Earth Sciences [UM] Teaching Collection; Figure GS2021-6-1d), including two identified as *Cretomanta canadensis*. The Odanah Member has produced one isolated yet complete and well-preserved actinopterygian scale (Figure GS2021-6-1i).

Vertebrate specimens collected from the Manitoba escarpment are unevenly distributed in terms of both represented taxa and lithostratigraphic members. Avian specimens are mostly represented by isolated limb elements mainly consisting of tibiae, fibulae and femora (Figure GS2021-6-1g), the majority of which were collected from the Belle Fourche Member and are housed at the Royal Saskatchewan Museum (RSM), whereas those collected from the younger Pembina Member are housed at the Canadian Fossil Discovery Cen-

Table GS2021-6-1: List of institution collections surveyed for this study.

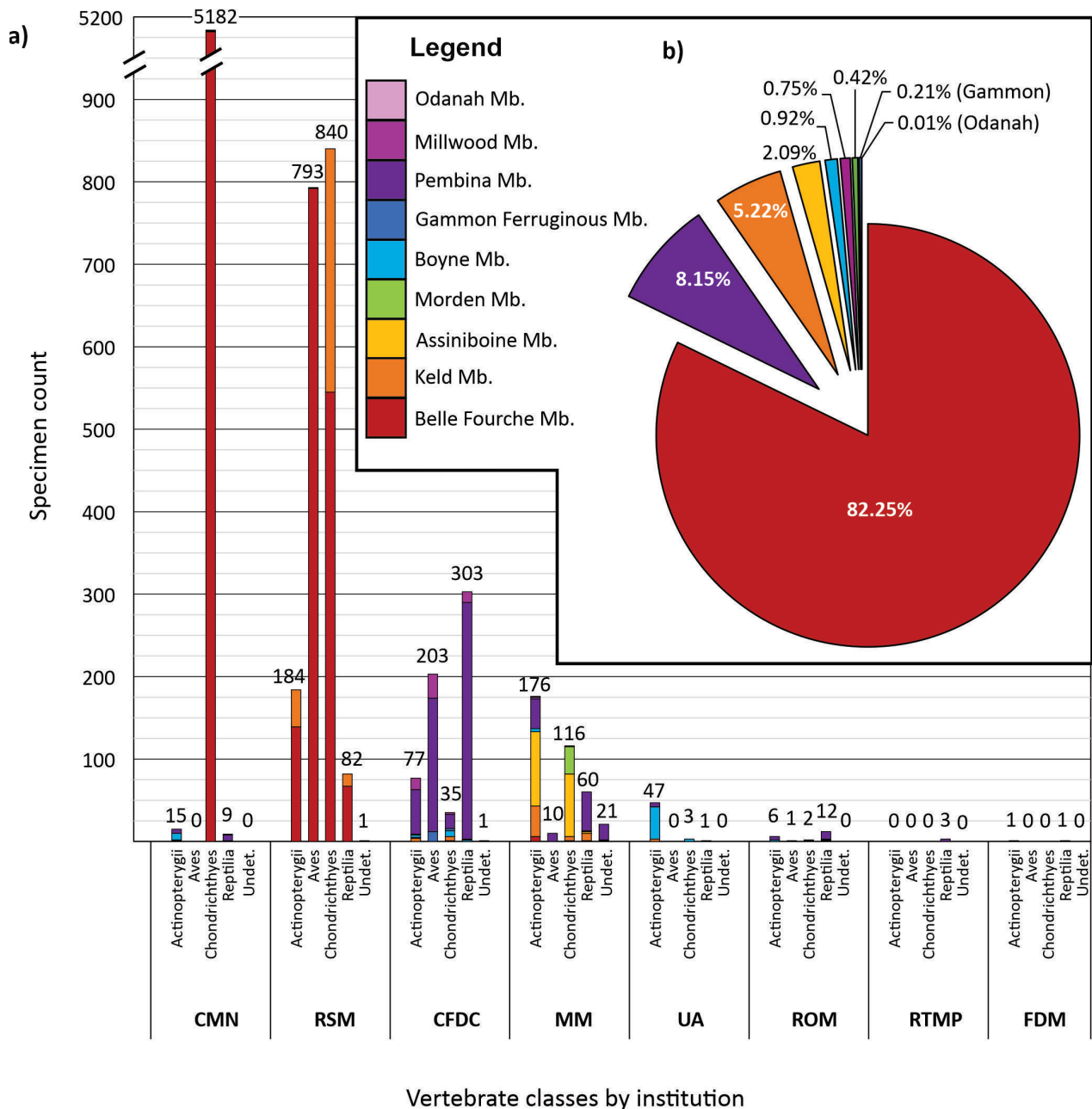
Abbreviation	Institution	Location
CFDC	Canadian Fossil Discovery Centre (previously Morden and District Museum)	Morden, Manitoba
CMN	Canadian Museum of Nature (previously National Museum of Canada)	Ottawa, Ontario
FDM	Fort Dauphin Museum	Dauphin, Manitoba
MM	Manitoba Museum (previously Manitoba Museum of Man and Nature)	Winnipeg, Manitoba
ROM	Royal Ontario Museum	Toronto, Ontario
RSM	Royal Saskatchewan Museum (previously Saskatchewan Museum of Natural History)	Regina, Saskatchewan
RTMP	Royal Tyrrell Museum of Palaeontology	Drumheller, Alberta
UA	University of Alberta, Department of Biological Sciences	Edmonton, Alberta
UM	University of Manitoba, Department of Earth Sciences (previously Department of Geological Sciences)	Winnipeg, Manitoba



Figure GS2021-6-1: Representative fossil specimens from each Late Cretaceous Manitoba lithostratigraphic member: **a)** *Archaeolamna kopingenensis* tooth in labial view (Royal Saskatchewan Museum (RSM) P2466.8), Belle Fourche Member, scale bar = 1 cm; **b)** *Squalicorax curvatus* tooth in lingual view (University of Manitoba, Department of Earth Sciences [UM], Teaching Collection), Keld Member, scale bar = 0.25 cm; **c)** *Enchodus* sp. undetermined tooth (UM Teaching Collection), Marco Calcarenite, Assiniboine Member, scale bar = 0.25 cm; **d)** undetermined chondrichthyan dermal denticle (UM Teaching Collection), Morden Member, scale bar = 0.025 cm; **e)** *Enchodus* sp. undetermined skull in dorsal view (University of Alberta, Department of Biological Sciences, UALVP 15064), Boyne Member, scale bar = 1 cm; **f)** *Archaeolamna* sp. tooth in lingual view (Canadian Fossil Discovery Centre [CFDC] S.2013.03.13), Gammon Ferruginous Member, scale bar = 1 cm; **g)** *Hesperornis regalis* right femur in anterior view (Manitoba Museum [MM] V-137), Pembina Member, scale bar = 5 cm; **h)** *Enchodus ferox*(?) tooth (CFDC F.2007.06.23), Millwood Member, scale bar = 1 cm; **i)** undetermined actinopterygian scale (MM V-68), Odanah Member, scale bar = 0.5 cm.

tre (CFDC), MM and Royal Ontario Museum (ROM). Since no avian specimens from the Assiniboine, Morden and Boyne members are represented in the collections, a significant gap in known avian specimens of approximately 11 million years exists between early Turonian and early Campanian time. Chondrichthyan specimens are almost entirely represented by

teeth (Figure GS2021-6-1a, b, f) and those housed at the MM and CFDC were collected from most of the Late Cretaceous members of the Manitoba escarpment, except the Odanah Member. Chondrichthyan specimens housed at the RSM were collected from the Belle Fourche and Keld members, though the majority (over 5000 teeth) have been collected from



Vertebrate classes by institution

Figure GS2021-6-2: Distribution and abundance of Late Cretaceous vertebrate specimens collected from the Manitoba escarpment and housed in Canadian institution collections, organized by **a)** traditional vertebrate classes represented by each collection, with specimen counts by represented individuals and represented proportions of lithostratigraphic members shown as coloured stacks; and **b)** distribution of specimens by lithostratigraphic member with proportions calculated from a total of 8185 specimens. Specimen totals for the Manitoba Museum (MM) include those specimens from the University of Manitoba, Department of Earth Sciences, Teaching Collection that will be deposited at the MM in late 2021. Abbreviations: CFDC, Canadian Fossil Discovery Centre; CMN, Canadian Museum of Nature; FDM, Fort Dauphin Museum; ROM, Royal Ontario Museum; RSM, Royal Saskatchewan Museum; RTMP, Royal Tyrrell Museum of Palaeontology; UA, University of Alberta, Department of Biological Sciences; Undet., undetermined class.

the Carrot River bone bed within the mid-Cenomanian Belle Fourche Member and are housed at the Canadian Museum of Nature (CMN). Actinopterygians are represented in nearly all institution collections and from nearly every Cretaceous member of the Manitoba escarpment (Figure GS2021-6-1c, e, h, i). The abundance of actinopterygian specimens per lithostratigraphic member has the most uneven distribution relative to other taxonomic classes, with 145 specimens from the Belle

Fourche Member, 91 from the Keld Member, 91 from the Assiniboine Member, 1 from the Morden Member, 56 from the Boyne Member, 1 from the Gammon Ferruginous Member, 104 from the Pembina Member, 16 from the Millwood Member and 1 from the Odanah Member. Most Pembina Member actinopterygian specimens are housed at the MM and CFDC, whereas most Belle Fourche Member actinopterygian specimens are housed at the RSM. Keld Member actinopterygian

specimens are housed at the RSM, MM, CFDC, University of Alberta, Department of Biological Sciences (UA) and the Fort Dauphin Museum (FDM).

Reptile specimens are mainly from the Pembina Member with at least 287 specimens at the CFDC, 47 at the MM, 9 at the ROM, 7 at the CMN and 3 at the Royal Tyrrell Museum of Palaeontology (RTMP). There are also 67 RSM specimens from the Belle Fourche Member; 9 MM specimens and 15 RSM specimens from the Keld Member; 13 CFDC specimens from the Millwood Member; and one to two specimens from the other members among the surveyed collections. *Terminonaris robusta* is the only known crocodile species from the Manitoba escarpment and is represented by two specimens, both collected from the Keld Member. A 30–40% complete, semi-articulated postcranial skeleton of *Terminonaris robusta* is housed at the FDM (specimen FDM MD-1055-1; Hatcher and Jancic, 2010) and a nearly complete, fully articulated skeleton is housed at the RSM (specimen RSM P2411.1; Wu et al., 2001). The known quantity of reptile specimens from strata between early Turonian and early Campanian age is relatively low, with 2 MM specimens and 1 ROM specimen from the Assiniboine Member; none from the Morden Member; and 2 CFDC specimens, 1 MM, 1 ROM, 1 UA and 1 CMN specimen from the Boyne Member. In terms of reptilian representation from other lithostratigraphic members, a total of 68 reptilian specimens, mostly partial, postcranial elements belonging to plesiosaurs, are known from the Belle Fourche Member and 14 from the Millwood Member, mainly partial teeth, jaw elements and vertebrae belonging to mosasaurs.

Discussion and recommendations for future work

The results of this survey identified several biases, including a significant size bias between Manitoba escarpment macrovertebrate fossils and microvertebrate fossils in institution collections. The two marine vertebrate bone bed faunal assemblages of the Belle Fourche Member, the Carrot River and Bainbridge River bone beds, are the most sampled horizons of the Manitoba escarpment, yielding nearly 7000 microvertebrate fossils to date. In terms of macrovertebrate specimens, the lower Pembina Member is the most sampled unit, yielding nearly 700 macrovertebrate fossils to date. This can be problematic when examining diversity between assemblages, as uneven sampling between macro- and microvertebrate can skew paleoecological interpretations. Methods for evaluating diversity coverage of sampled microvertebrate assemblages and determining the appropriate quantity of bulk sample to collect for sufficient diversity coverage are discussed in Jamniczky et al. (2003) and Close et al. (2018). Additionally, modelling and statistical methods can be used to counter uneven sampling (e.g., Brocklehurst, 2015).

In order to offset biases in microvertebrate fossil collections, surface prospecting plus bulk sampling of microverte-

brate fossil horizons from lithostratigraphic units other than the Belle Fourche Member is recommended. Processing the bulk samples by screen washing in water, or acid digestion in 10–20% acetic acid, should increase yields. In Manitoba, well-preserved microvertebrate fossil specimens have been successfully recovered from the Laurier Limestone Beds of the Keld Member (specimen MM V-2733), the Marco Calcarenite of the Assiniboine Member (specimens MM V-2555, V-2556, V-2557, V-2587), Morden Member (specimen MM V-2689), Boyne Member (specimen MM V-2520), Pembina Member (specimen MM V-2519), Millwood Member (UM Teaching Collection, specimen EPD 20020729) and have been observed but not known to be collected from the Gammon Ferruginous Member. The excellent degree of fossil preservation and 10–40% microvertebrate fossil content observed within the Marco Calcarenite near the top of the Assiniboine Member indicate its faunal assemblage would be most comparable with those of the Belle Fourche Member bone beds and would warrant further bulk sampling and acid preparation.

In addition to the unequal representation of microvertebrate fossils from the Belle Fourche Member bone beds, opportunistic collection of avian, chondrichthyan and reptilian macrovertebrate fossils from the Keld and Pembina members has resulted in the disproportionate representation of these members in institution collections relative to the other Manitoba escarpment members (Figure GS2021-6-2b). Prospecting that targets currently underrepresented lithostratigraphic members and horizons will help reduce the existing biases in institution collections and gain a truer representation of the original WIS fauna. Increasing representation of the Boyne and Millwood members in institution collections in particular would prove valuable for temporal comparisons of Manitoba escarpment faunal assemblages, and also for spatial comparisons with well-sampled coeval units from other WIS localities including the Coniacian to early Campanian Smoky Hill Chalk Member of Kansas (e.g., Shimada and Fielitz, 2006) and the mid-Campanian Bearpaw Formation of Alberta (e.g., Cook et al., 2017).

In order to conduct successful surface fossil prospecting, factors determining which lithostratigraphic unit to prospect should include known fossil content abundance, degree of fossil preservation, outcrop exposure surface area and outcrop accessibility. The lithostratigraphic members and units that meet these criteria and are currently underrepresented in institution collections are recommended for future fossil prospecting in Manitoba. They include, from oldest to youngest, the Laurier Limestone Beds (Keld Member), Assiniboine Member (including the Marco Calcarenite), Boyne Member, Gammon Ferruginous Member and Millwood Member. Donation, or providing notice, of discovered fossil specimens to an institution with a publicly accessible specimen database and equipped to properly recover in situ fossils would also help in increasing representation. Publicly accessible, roadside

outcrop locations of Upper Cretaceous units in southwestern Manitoba that are available for surface prospecting are provided by Bamburak and Nicolas (2013). Fossil collection should only be undertaken with possession of a heritage permit, land-owner permission and appropriate training in the collection of in situ fossils.

Conclusions

Collection biases identified in institution collections of Late Cretaceous Manitoba escarpment vertebrates include 1) opportunistic sampling and acid preparation of select microvertebrate bone beds; 2) preferred collection of semi- to fully articulated macrovertebrate specimens; and 3) dependency on economic activities to facilitate fossil collection, mainly bentonite mining within the lower Pembina Member. Due to the dominant historical collection biases of opportunistic and preferred collection of chondrichthyan and avian microvertebrate specimens from the Belle Fourche Member and reptilian and avian macrovertebrate specimens from the Pembina Member, other lithostratigraphic members and taxonomic groups are significantly underrepresented in institution collections. Overall, taxonomic classes with unequal representation in existing institution collections are chondrichthyans and avians and those with underrepresentation are actinopterygians and reptilians. Lithostratigraphic members with the most representation in institution collections, in order from highest to lowest abundance, are the Belle Fourche, Pembina and Keld members. Lithostratigraphic members with the least representation, from highest to lowest abundance, are the Assiniboine, Boyne, Millwood, Gammon Ferruginous, Morden and Odanah members. Future collection should target the Laurier Limestone Beds (Keld Member), Assiniboine Member (including the Marco Calcarenite), Boyne Member, Gammon Ferruginous Member and Millwood Member to offset historical institution collection biases. This information is crucial for a better approximation of Cretaceous vertebrate diversity and understanding the paleoecology and evolutionary changes in WIS faunas over time.

Economic considerations

Fossil collections, and the information extracted from them, provide context to the lithostratigraphic units that host them. This context includes taxonomic, climatic, geographic and temporal information critical to understanding the variability and change in the geological environments through both time and space. Fossil information provides the ability to correlate stratigraphic units globally, predict and pinpoint where economic accumulations of mineral resources are most likely to occur and, just as importantly, where they do not occur. Fossil information is important for the targeting of resources, including petroleum, bentonite, brick clay and high-calcium limestone. Fully recovered, informative and excellently preserved specimens deposited in conservation-suitable

institution collections in Manitoba will ultimately benefit the province's tourism sector, the global paleontology community and the general public by protecting and showcasing examples of the province's paleontological heritage and furthering the understanding of ancient life history.

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