

THE ICE AGE GIANT BEAVER

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Samenvatting

Reuzenbevers (geslacht *Castoroides*) zo groot als beren bewoonden gedurende het hele Pleistoceen moerassen en meren in Noord-Amerika. Maar wat aten ze? En bouwden ze net als moderne bevers dammen? Isotopenonderzoek aan collageen uit fossiel botmateriaal leert dat deze grote bevers voor hun voedsel voornamelijk op waterplanten aangewezen waren en niet aan bomen knaagde. Ze bezetten dus een andere voedselniche dan hun verre neven uit het geslacht *Castor*, zoals onze Europese bever, die voor hun dieet vooral afhankelijk zijn van bladeren en boomschors. Het gebit van de Noord-Amerikaanse reuzenbever is heel kenmerkend: hun snijtanden zijn niet glad maar zijn overlangs gegroefd, net als de hoektanden van het huidige nijlpaard, en hun kiezen bleven waarschijnlijk gedurende hun hele leven doorgroeien, met typerende gevouwen lobben op het kauwvlak. De verschillen in dieet en levenswijze betekenden dat beide typen bever naast elkaar konden bestaan in het Noord-Amerika van de ijstijd. Wel zullen de twee bevergeslachten met elkaar hebben geconcentreerd bij het zoeken van goede plekken om te wonen. Aan het eind van het Pleistoceen werd hun woonomgeving te droog en te warm voor de reuzenbevers om nog te kunnen voortbestaan. Vroege mensen hebben voor zover wij weten niet aan hun ondergang bijgedragen.



Figure 1. Right) Life-sized artistic rendition of the Ice Age giant beaver (Castoroides ohioensis) displayed outside the Yukon Beringia Interpretive Centre, Whitehorse, Yukon Territory. The sculpture stands over four feet tall!

Left) Close up view of the giant beaver's impressive incisors. Note the distinctive longitudinally ridged enamel coating the front teeth.

Rechts) Levensgrote artistieke weergave van de pleistocene reuzenbever (Castoroides ohioensis), tentoongesteld buiten het Yukon Beringia Interpretive Centre, Whitehorse, Yukon Territory. Het standbeeld is meer dan 1,20 meter hoog!

Links) Close-up van de indrukwekkende snijtanden van de reuzenbever. Let op het kenmerkende overlangs gegroefde email dat de tanden bedekt.





For over a million years, giant beavers (genus *Castoroides*) the size of bears roamed the North American landscape. They inhabited swamps and lakes throughout the Ice Age (Swinehart & Richards, 2001; McDonald & Glotzhofer, 2008) and were the largest of their kind ever to exist.

Now extinct, fossils from the iconic Pleistocene giant beaver are found across North America, from Florida to Alaska (Cahn, 1932; Martin, 1969; Hulbert et al., 2014). The giant beaver grew up to several feet long, weighing 100 kg with a long ropey tail similar to that of a modern muskrat (Fig. 1 to 3). While cumbersome on land, the giant beaver was well-adapted for life in the water, with large rudder-like hind feet and eyes perched on top of its head – ideal for surveying the shore for potential predators.

But what did this rodent of unusual size eat to sustain itself? And did the giant beaver build equally massive dams, altering the flow of Ice Age rivers?

Stable isotopes were used to untangle these questions about the Ice Age giant beaver. From a stable isotope perspective, you are what you eat (DeNiro & Epstein, 1978; 1981). Simply put, the isotopic composition of the food that you eat is incorporated by metabolic processes into your bodily tissues. Unlike the radioisotope ^{14}C , these stable isotope signatures remain constant over time (barring taphonomic decomposition processes). This means that many well-preserved Pleistocene fossils (particularly from cold, dry permafrost regions) retain their original stable isotope composition and can

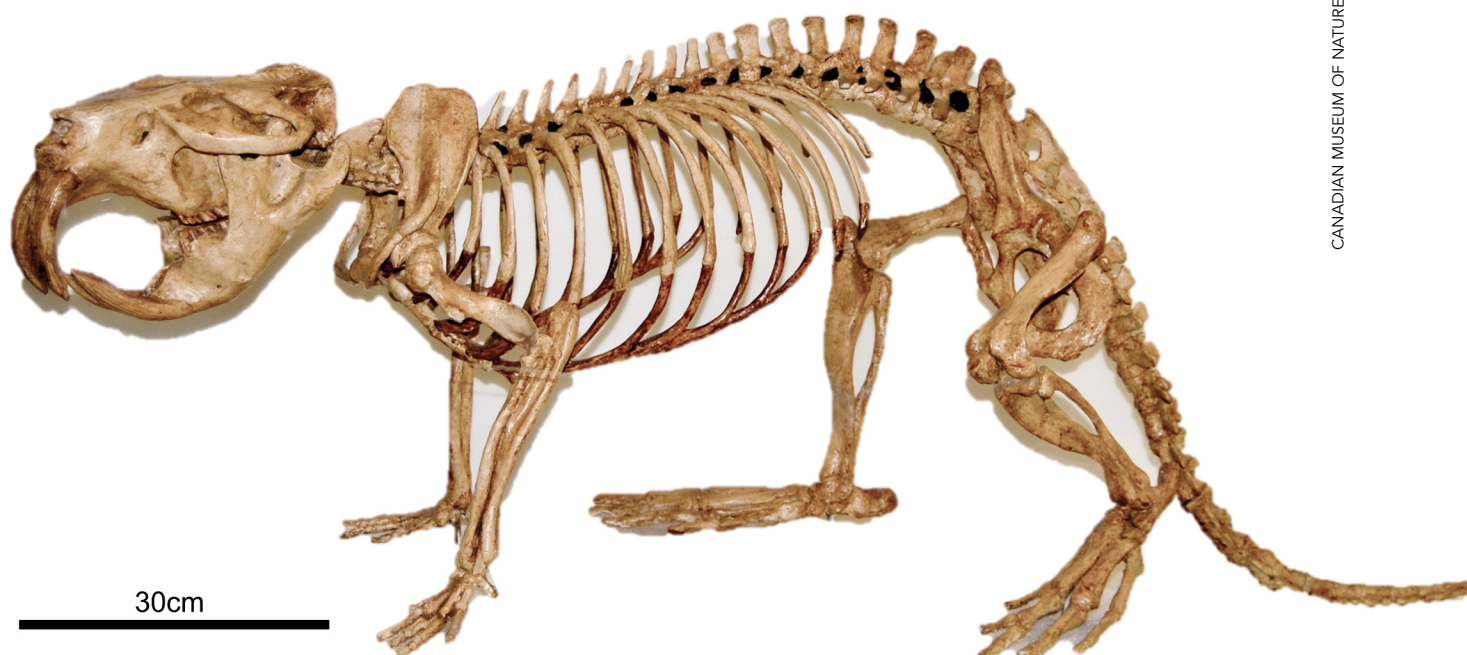
be used to reconstruct the diet and ecology of these long extinct animals (e.g., Schwartz-Narbonne et al., 2019).

DID GIANT BEAVERS FELL TREES?

The stable carbon and nitrogen isotope composition of collagen protein preserved in ancient giant beaver bones shows that they consumed a diet of aquatic plants (Plint et al., 2019). The giant beaver was particularly fond of plants that grew around the edges of wetlands, and plants that grew fully submerged underwater. A diet like this meant the giant beaver would have spent much of its time on the shore or diving to the bottom of lakes and ponds to graze.

This new dietary evidence does not support the idea that giant beaver ever cut down trees or built dams akin to the modern beaver (*Castor canadensis* and *Castor fiber*) (Rosell, 2022).

The extant modern beaver (*Castor*) is a large (15 to 40 kg) Holarctic rodent, and is a renowned ecosystem engineer, second only to humans for purposefully modifying the landscape to suit its needs (Fig. 4 and 5). Its habit of cutting down trees to build lodges and to dam flowing water has a profound effect on the surrounding ecosystem, creating new wetland habitat and increasing local biodiversity (Rosell, 2022). The modern beaver also consumes aquatic plants but relies heavily on fresh leafy foliage and the soft inner layers of tree bark. If the giant beaver also cut and consumed trees for food, we would have instead expected to see the stable isotope composition of its bone to resemble that of *Castor*



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Figure 2. A cast of a giant beaver (*Castoroides ohioensis*) skeleton originating from Minnesota.
Afgietsel van het skelet van een reuzenbever (*Castoroides ohioensis*) afkomstig uit Minnesota.



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Figure 3. Giant beaver (*Castoroides*) cranium and mandible casts.
Afgietsels van cranium en onderkaak van de reuzenbever (*Castoroides*).

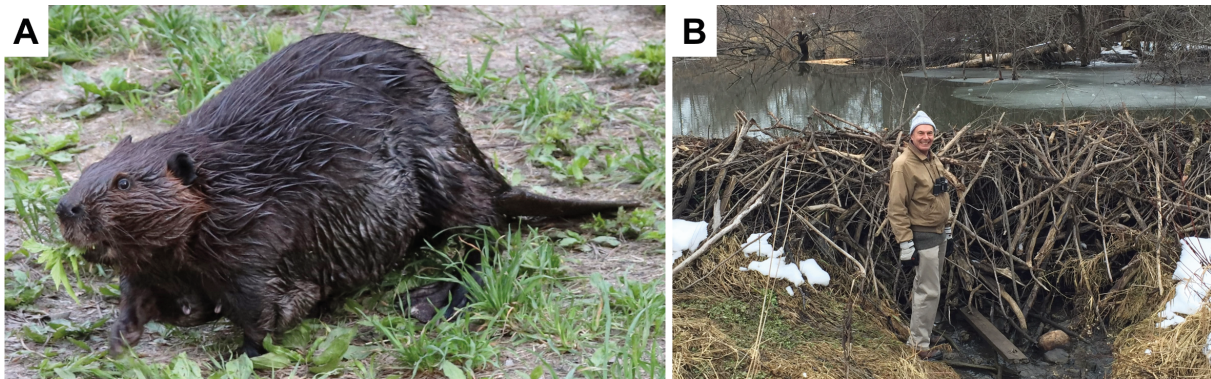
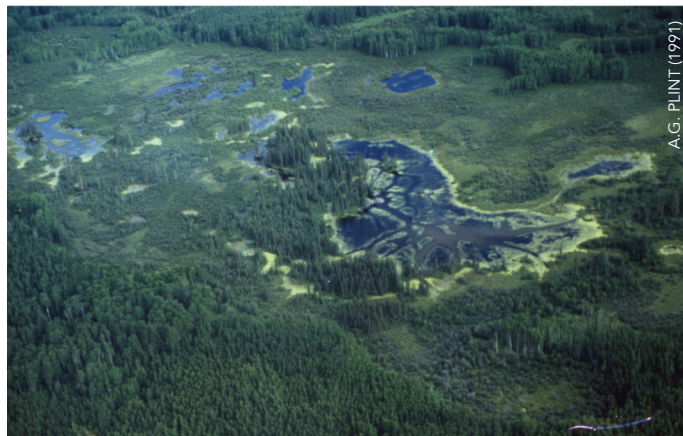


Figure 4. A) Female beaver (*Castor canadensis*) from southwestern Ontario (2020).
B) Beaver dam in southwestern Ontario – author family member for scale! (2021).
A) Vrouwelijke bever (*Castor canadensis*) uit het zuidwesten van Ontario (2020).
B) Beverdam in het zuidwesten van Ontario – met een familielid van de auteur voor de schaal! (2021).



A.G. PLINT (1991)

Figure 5. Aerial view of a landscape flooded by extensive beaver (*Castor canadensis*) dam building in north-western Alberta, Canada.
Luchtfoto van een landschap overstroomd ten gevolge van uitgebreide dambouw door bevers (*Castor canadensis*) in het noordwesten van Alberta, Canada.

and to reflect the stable isotopic signature of terrestrial trees and shrubs (Plint et al., 2019).

This strong preference for submerged aquatic plants rendered the giant beaver highly dependent on wetland habitat for sustenance and survival. This ecological dependence on plentiful wetlands for food and shelter from predators was devastating for the giant beaver during the rapidly changing environmental conditions of the late Pleistocene. The loss of both wetland habitat in lowland regions and the associated open mixed-conifer forests coincided with the regional disappearance of giant beaver populations in many areas across North America throughout the Pleistocene (Plint et al., 2019).

The stable isotope dietary evidence strongly suggests that the giant beaver and the extant beaver occupied complementary dietary niches during the Pleistocene. These two rodents probably competed for habitat; however, their dietary niches were sufficiently different to allow the two genera to co-exist across North America during the Pleistocene.

The modern beaver's ability to engineer the landscape to create new wetland habitat space, combined with an increasing abundance and diversity of leafy deciduous tree species in North America probably gave it a distinct advantage over the giant beaver. The giant beaver eventually dwindled to a population spread out along the southern margin of the Great Lakes (then fuelled by the retreating continental ice sheets), when the climate eventually became too warm and arid to support the habitat needed for survival (Stuart-Williams & Schwarcz, 1997; McDonald & Bryson, 2010).

The giant beaver went extinct towards the end of the late Pleistocene megafaunal extinction event, alongside giant ground sloths and mastodons that shared similar forested habitat (Faith & Surovell, 2009; Stuart, 2015). The youngest known giant beaver fossil ^{14}C date is currently 10,150 BP (Feranec & Kozłowski, 2010). While the megafauna of the Great Lakes region (including the giant beaver) likely overlapped temporally with early human populations in the north-east for nearly a thousand years, there is currently no zooarchaeological evidence that humans hunted or otherwise used the giant beaver as a resource (Boulanger & Lyman, 2014).

THE GIANT BEAVER FAMILY TREE

The modern beaver (genus *Castor*) is not a direct descendant of the extinct giant beaver (*Castoroides*). They last shared a common ancestor around 20 million years ago during the late Miocene (Rybczynski, 2007; Plint et al., 2020; Xenikoudakis et al., 2020). A semi-aquatic clade of the beaver lineage diverged from the burrowing clade in a single evolutionary transition from terrestrial to aquatic lifestyle. This semi-aquatic clade subsequently gave rise to the extinct Miocene European beaver *Steneofiber eseri*, the extant Holarctic beaver (*Castor*), the extinct Pliocene beaver (*Dipoides*), and the extinct North American Pleistocene giant beaver (*Castoroides*) (Rybczynski, 2007; 2008; Flynn, 2009; Plint et al., 2020).

Occasionally referred to as the "Eurasian giant beaver", *Trogotherium cuvieri* was once widespread throughout the

Pliocene and Pleistocene, with fossils recovered from France to China. Despite the nickname, *T. cuvieri* and *Castoroides* were not closely related. Although *Castoroides* was significantly larger than *T. cuvieri*, they shared similar morphological traits (a long ropey tail and longitudinally ridged incisor enamel) and may have shared some similarities in diet (Fostowicz-Frelik, 2008; Yang et al., 2021).

GIANT BEAVER FOSSIL IDENTIFICATION

Today, giant beaver fossils are most frequently preserved and unearthed in the United States in the region south of the Great Lakes. Other regions that yield well preserved giant beaver fossils are peninsular Florida, and the Old Crow Basin in Yukon Territory. The action of glacial advance and retreat, and a lack of ideal preservation conditions mean giant beaver fossils are rarely unearthed in most parts of Canada, although discoveries have been made in Manitoba, southern Ontario, and New Brunswick (Miller et al., 2000; Karrow, 2007; Manitoba Museum, 2017).

Giant beaver teeth are highly distinctive. Adult giant beaver incisors are several inches long and nearly an inch in diameter. These incisors lack the chisel-like edge and smooth enamel seen in extant beavers (Fig. 6); instead, giant beaver incisors possess longitudinally ridged enamel (Fig. 1 and 3) that is very similar in appearance to the canines of extant *Hippopotamus amphibius*.

Giant beaver cheek teeth are open-rooted and are assumed to have grown continuously throughout the animal's life. Their occlusal surface displays distinct folded lophs (Fig. 7). *Castoroides dilophidus*, the giant beaver species predominant in the fossil record of the American southeast, frequently exhibits a divided loph in their premolars and molars (Hulbert et al., 2014). Baby giant beaver teeth are wedge-shaped in profile, with a complex occlusal surface of folded enamel. The teeth flare towards the base as the newest enamel layers keep pace with the growth of the skull (Fig. 8).

Ice Age palaeontology educational programs and collections should note that replicate casts of giant beaver skulls may not be faithful to the original fossil material. Due to their fragility, the zygomatic arches of fossil skulls are frequently partially or entirely broken away. A popular giant beaver skull cast frequently purchased for teaching collections was constructed from an incomplete specimen and the zygomatic arches appear to be based on those of *Castor canadensis* (Fig. 9). This oversight has distorted the overall proportions and size of the skull cast (Fig. 10).

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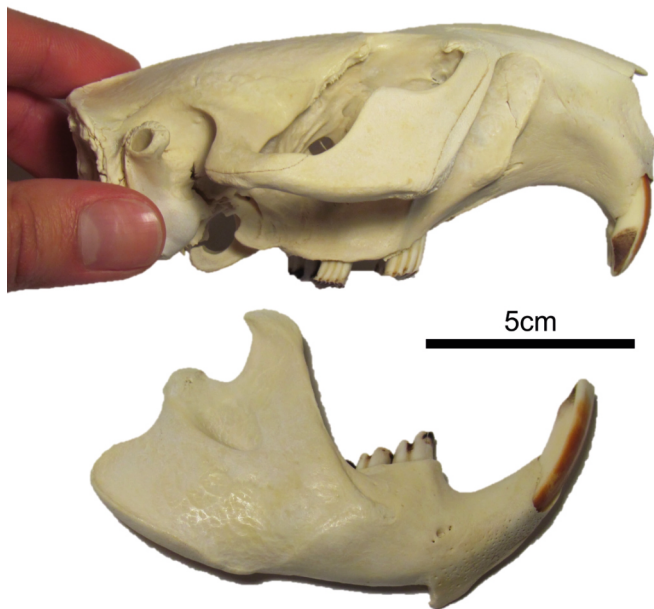


Figure 6. Extant North American beaver (*Castor canadensis*) cranium and mandible.

Cranium en onderkaak van de huidige Noord-Amerikaanse bever (*Castor canadensis*).

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Figure 7. A) Occlusal surface of a giant beaver (*Castoroides ohioensis*) mandibular cheek tooth displaying distinct folded enamel lophs. B) Longitudinal view of a giant beaver (*Castoroides ohioensis*) maxillary cheek tooth. Specimens collected from the Old Crow Basin, Yukon Territory.

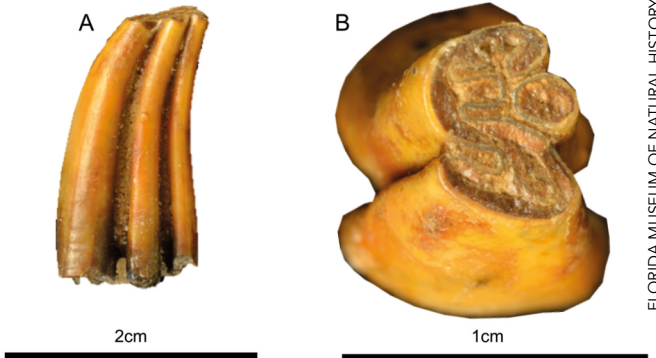
A) Kauwvlak van een onderkaakse kies van een reuzenbever (*Castoroides ohioensis*) met gevouwen email-lobben. B) Lengte-aanzicht van een bovenkaakse kies van een reuzenbever (*Castoroides ohioensis*). Specimens verzameld in het Old Crow Basin, Yukon Territory.



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Figure 8. Giant beaver (*Castoroides*) cheek teeth from a very young animal. A) Profile view, with occlusal surface pointing up. B) Occlusal surface of juvenile giant beaver cheek tooth. Specimens collected in Florida.

Kiezen van een heel jonge reuzenbever (*Castoroides*). A) Profielaanzicht, met het kauwvlak naar boven wijzend. B) Kauwvlak van een kies van een jong dier. Specimens verzameld in Florida.



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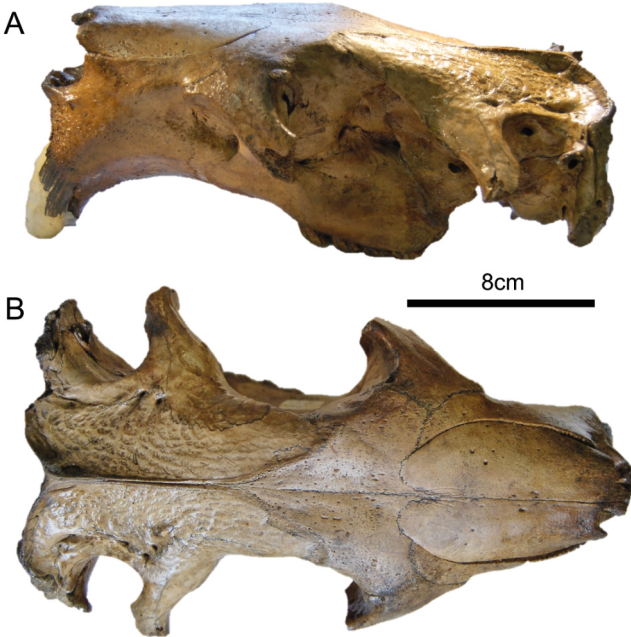
Figure 9. Giant beaver (*Castoroides ohioensis*) "Bone Clones" cranium cast based on an incomplete fossil specimen. The proportions of the maxilla and zygomatic arches may differ from more complete fossil specimens.

Afgietsel door Bone Clones van het cranium van een reuzenbever (*Castoroides ohioensis*), gebaseerd op een incompleet fossiel. De verhoudingen van de bovenkaak en jukbogen kunnen verschillen van die van meer complete fossielen.



Figure 10. Giant beaver (*Castoroides ohioensis*) cranium (A: left side, B: dorsal view). Specimen collected in Ohio. Fragmentary enamel is held together by plaster casts of the front incisors.

Cranium van een reuzenbever (*Castoroides ohioensis*) (A: linkerkant, B: bovenaanzicht). Specimen verzameld in Ohio. Fragmentarisch email wordt bij elkaar gehouden door cementafgietsels van de voorste snijtanden.



OHIO HISTORY CONNECTION