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Evidence for a Greater Pleistocene Distribution for the Copper Redhorse in North America (Catostomidae: *Moxostoma hubbsi*)

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Abstract: A pharyngeal jaw and loose pharyngeal teeth from Prairie Creek, Indiana, and loose pharyngeal teeth and two basioccipital pharyngeal processes from Bell Cave, Alabama, appear to be those of *Moxostoma hubbsi* (Copper Redhorse). Among suckers, only *M. carinatum*, *M. hubbsi*, *M. robustum*, and *M. ugidatli* have molariform teeth on their pharyngeal jaws, with *M. hubbsi* having the teeth of the largest relative size. Measurements of most of the teeth from Prairie Creek overlap with those of *M. hubbsi*, and the largest tooth from Bell Cave is the largest pharyngeal tooth measured. The more complete pharyngeal process of the basioccipital possesses a small condyle and stout processes along it that are indicative of *M. hubbsi* as well as a smaller centrum for articulation with the Weberian complex. *Moxostoma hubbsi* currently occupies an area around Montreal, Canada, that was glaciated at the time the fossils were laid down, and the area was later occupied by the Champlain Sea and Lampsilis Lake before becoming riverine about 6000–5000 years ago, meaning that *M. hubbsi* had to have arrived at its current distribution relatively recently and been extirpated from elsewhere.

Keywords: pharyngeal jaw; basioccipital; fossil; Canada; molariform; glaciation; biogeography

Key Contribution: The endangered Copper Redhorse is only known from the St. Lawrence River around Montreal, Canada, an area that was covered in ice during the last glacial cycle. However, based on fossil evidence, the distribution of the species once included Indiana and Alabama in the Mississippi River basin.

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1. Introduction

Fishes of the family Catostomidae (suckers) are found mostly in North America, but one species, *Myxocyprinus asiaticus*, is found only in Asia and one species (*Catostomus catostomus*) has populations that recolonized Asia from North America [1]. Castostomids, as members of the order Cypriniformes, lack oral teeth but do have well developed pharyngeal teeth. Cypriniformes have a thickened, muscularized palatal organ supported by the pharyngobranchials, epibranchials, and the basioccipital pharyngeal process (a bony extension of the basioccipital that extends below and posterior to the occipital condyle). The palatal organ functions to separate food from inorganic materials. In cyprinids and catostomids, there is also the presence of a chewing pad, which is a keratinized portion of the palatal organ (catostomids) or the basioccipital (cyprinids) [2,3].

In eastern North America, the most speciose genus of suckers is *Moxostoma* or Redhorses and Jumprocks. Most *Moxostoma* have narrow pharyngeal teeth arranged in a comb-like fashion (Figure 1A), but four species of Redhorse have molariform teeth that

occlude against the chewing pad for crushing mollusk shells [2–4]: *M. ugidatli* Jenkins, Favrot, Freeman, Albanese, and Armbruster (Sicklefin Redhorse, Figure 1B), *M. carinatum* (Cope) (River Redhorse, Figure 1C), *M. robustum* (Cope) (Robust Redhorse, Figure 1D), and *M. hubbsi* Legendre (Copper Redhorse, Figure 1E). Based on the most complete phylogeny to date for catostomids [5], it is likely that molariform pharyngeal teeth evolved three times with the Sicklefin and River Redhorse as sister species. Today, *M. carinatum* is found throughout the Great Lakes, Mississippi River, Gulf of Mexico coastal drainages from the Escambia River to the Pearl River, and is sympatric with *M. hubbsi* in the St. Lawrence River; *M. robustum* occurs along the south Atlantic slope from North Carolina to Georgia; *M. ugidatli* is in the Little Tennessee and Hiwassee of North Carolina and Georgia; and the distribution of *M. hubbsi* is only in the Saint Lawrence River basin around Montreal, Canada in Quebec and Ottawa ([6]; Figure 2). No other freshwater fish species has a distribution even remotely like that of *M. hubbsi* [7], and the St. Lawrence was covered by glaciers that did not begin to recede until about 14,500 years ago and was later occupied by the Champlain Sea [8,9]. Among the molariform *Moxostoma*, *M. hubbsi* represents an extreme of tooth development (Figure 1D), and because of this, it is likely possible to identify the species from its pharyngeal teeth.

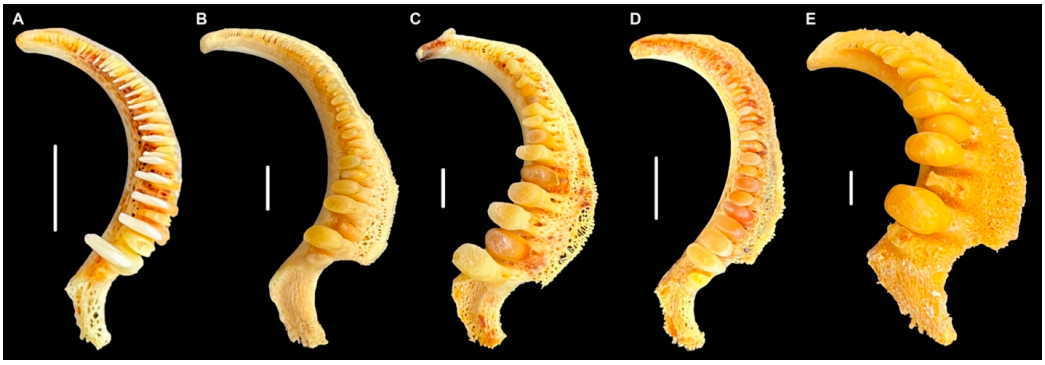


Figure 1. Left pharyngeal jaws, occlusal view, of (**A**) *Moxostoma breviceps* Cope, AUM uncataloged isolated jaw from Swain Co., NC; (**B**) *Moxostoma ugidatli*, AUM 86400; (**C**) *M. carinatum*, AUM 86333; (**D**) *M. robustum*, AUM 86420, and (**E**) *M. hubbsi*, CU 52912. Scale = 1 cm. Photos by J.W. Armbruster.

Two main collections suggest that *M. hubbsi* may have had a broader distribution in the Pleistocene. The first is a collection from Prairie Creek, Indiana, in Zone D. The discovery of mastodon bones in 1972 brought researchers to study the Prairie Creek Area of Daviess Co., Washington, IN, USA [10]. Zone D of Prairie Creek was believed to have been a lake in the Late Pleistocene that preserved some aquatic life as it drained ~14,000 years ago [10–12]. Among the fossils found were some fish microfossils [10] including a relatively large pharyngeal jaw of a sucker, a smaller pharyngeal jaw, and some loose teeth. The large pharyngeal jaw (left side) is a fragment from the second tooth from the ventral end to about the sixth tooth, and it bears two full, molariform teeth (teeth 2 and 3) and the eroded bases of teeth 4–6 (Figure 3A). One of us (REJ) had borrowed the specimens believing that the large jaw and teeth could be of the Copper Redhorse (*Moxostoma hubbsi*).

The second collection is from Bell Cave, Alabama, and was collected in 1987 (note that the cave is now closed and illegal to enter). The herpetofauna of Bell Cave has been described [13] and fish specimens were mentioned as having been found. Fish specimens were eventually described including specimens purportedly of *M. carinatum*, *M. macrolepidotum* (Lesueur) (Shorthead Redhorse), and the extinct *M. lacerum* (Jordan and Brayton) (Harelip Sucker) as well as other sucker genera [14]. A pharyngeal tooth examined from Bell Cave was thought to be that of *M. carinatum*. Unavailable for the Jacquemin et al. [14] study was a set of *Moxostoma* pharyngeal teeth collected from Zone 1/2, 3 in

Bell Cave. Amongst the teeth is the largest pharyngeal tooth we have observed (Figure 4). Zone 1/2 was dated as 11,820 +480/−500 BP, so roughly the same time as the Indiana specimens with both near the end of the Pleistocene (end at 11,700 BP). Some fossil teeth at Bell Cave were also found in Zone 4, which is 26,500 +870/−990 BP [14]. Also found was an isolated basioccipital pharyngeal process from Zone 3 (which is not dated; Figure 5C) that can be identified to species and a fragment of a basioccipital pharyngeal process from Zone 1/2. Our objective was to determine the species identity of these pharyngeal teeth and basioccipitals to have a better picture of catostomid biodiversity in what is now the Mississippi River basin.

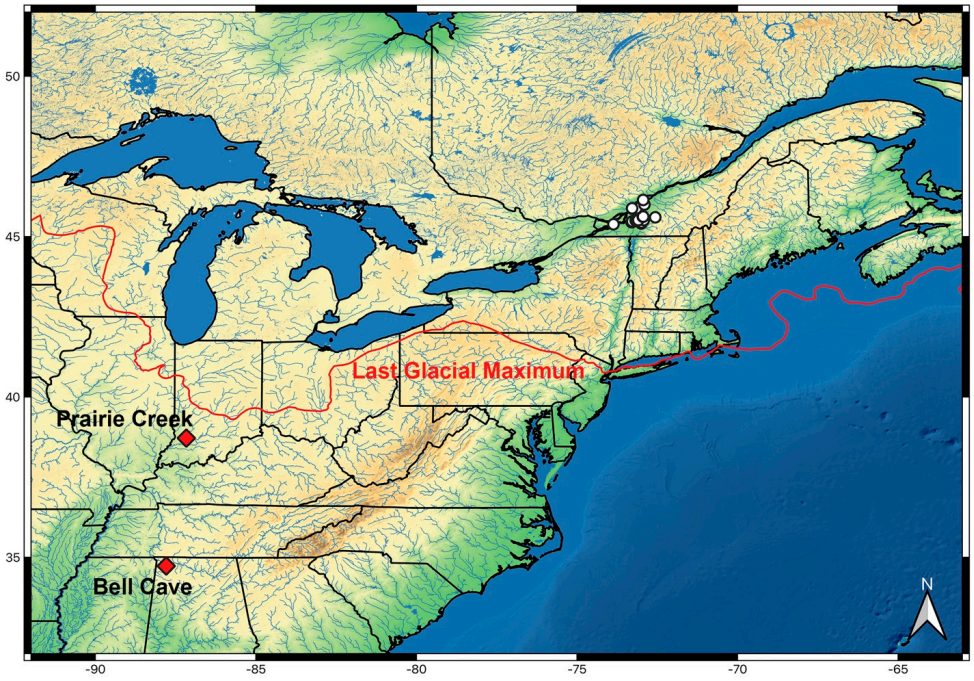


Figure 2. Distribution of *M. hubbsi* (white dots) and fossil localities (red diamonds). Maximum extent of last glacier indicated (~20.7–18.0 Ka). Glacial extent from Dalton et al. [15].



Figure 3. Portions of pharyngeal jaws from Prairie Creek, Indiana. (**A**) Large specimen, INSM L-849; (**B**) small specimen INSM L-1188. Scale = 1 cm. Photos by J.W. Armbruster.



Figure 4. Pharyngeal teeth from Bell Cave, Al, side (bottom) and occlusal (top) views. MSC 51132. Scale = 1 cm. Photos by J.W. Armbruster.

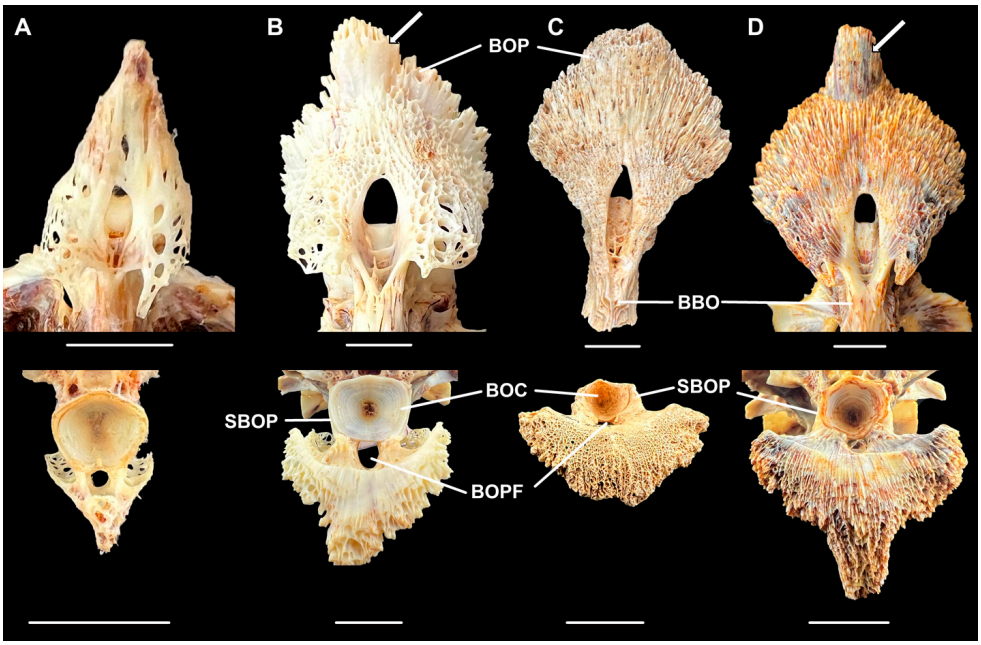


Figure 5. Basioccipital pharyngeal processes in ventral (top) and posterior (bottom) views of (**A**) *Moxostoma breviceps*, AUM 86339; (**B**) *M. carinatum*, AUM 86330; (**C**) *M. hubbsi*, Bell Cave, AL, fossil, MSC 45256; and (**D**) *M. hubbsi*, AUM 86391. BBO: body of basioccipital, BOC: basioccipital centrum, BOP: basioccipital pharyngeal process, BOPF: basioccipital pharyngeal process foramen, and SBOP: strut of basioccipital pharyngeal process. Scale = 1 cm. Photos by J.W. Armbruster.

2. Materials and Methods

The first three pharyngeal teeth (from ventral side) were examined for their length (perpendicular to the long axis of the pharyngeal jaw, L), their greatest width (parallel to the long axis of the pharyngeal jaw, W), and their height (H, measured on the lateral side from the jaw to the maximum height). In addition, the length of the pharyngeal base encompassing teeth 2 and 4 ($L_{2–4}$) was measured as was the greatest width of the pharyngeal jaw (W_P). Measurements were taken with Mitutoyo digital calipers to the nearest 0.1 mm. Ratios were made of W/L, and both W and L to $L_{2–4}$, and W_P. In addition, the greatest cross-sectional area of the tooth (CS) was approximated as an oval (1/2W * 1/2L * pi). Ratios were calculated of CS to $L_{2–4}$ and W_P. In addition, loose pharyngeal teeth were measured for W and L with area calculated as above. Maximum tooth cross-sectional area (CS_{MAX}) was also calculated as the tooth with the greatest CS and compared against $L_{2–4}$ and W_P. Measurements were taken for the jaws that REJ had available for *M. carinatum*, *M. robustum*, and *M. hubbsi* as well as the fossil specimens. Standard lengths (SL) of whole

specimens were taken from the tip of the snout to the end of the vertebral column along the midline. The Sicklefin Redhorse and Robust Redhorse were not further examined here because their teeth are considerably smaller than the other molariform species, and the fossil samples are clearly not Sicklefin or Robust Redhorse. Plots were made by ranking the specimens based on $CS_{MAX}/L_{2–4}$ and CS_{MAX} creating bar graphs with those measurements and SL (Figures 6 and 7). An estimate is provided based on the distribution of CS_{MAX} on which fossils are likely *M. hubbsi* and which are inconclusive, given that it is impossible to standardize measurements on isolated teeth and that it is unclear if the isolated teeth are among the top three widest teeth.

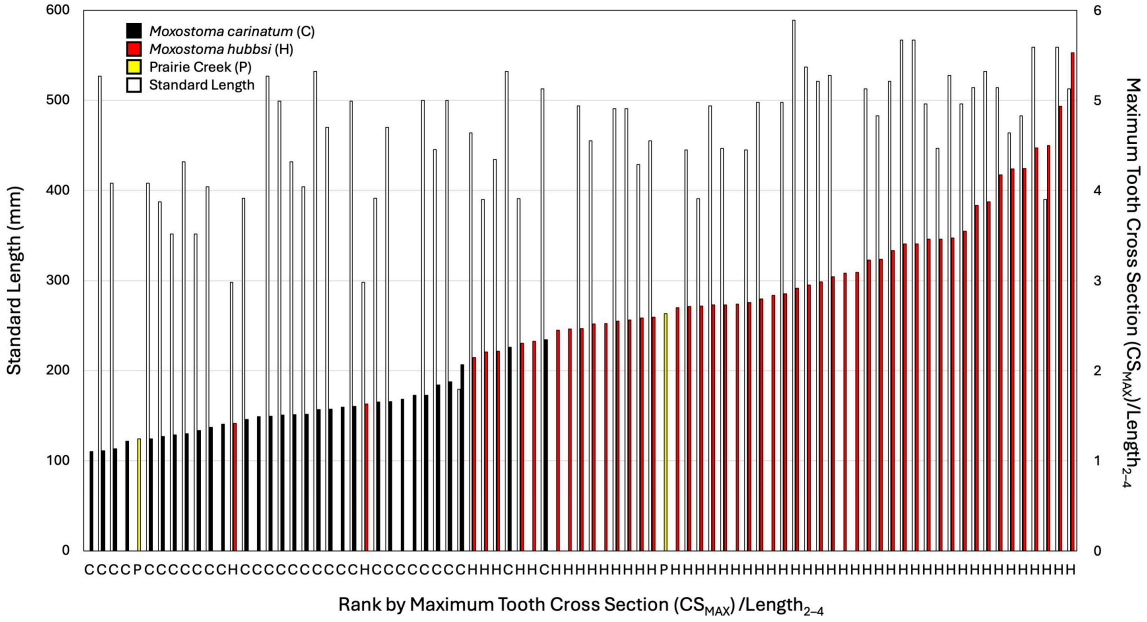


Figure 6. A graphical ranking of maximum tooth area (CS_{MAX}) to length of arch between second and fourth tooth ($L_{2–4}$) ratio. Left bar is standard length (when available, white bars), right bar is maximum tooth cross section to length of the base from tooth 2 to 4 (species or population colored per legend). Species/population also indicated along the x axis per the legend.

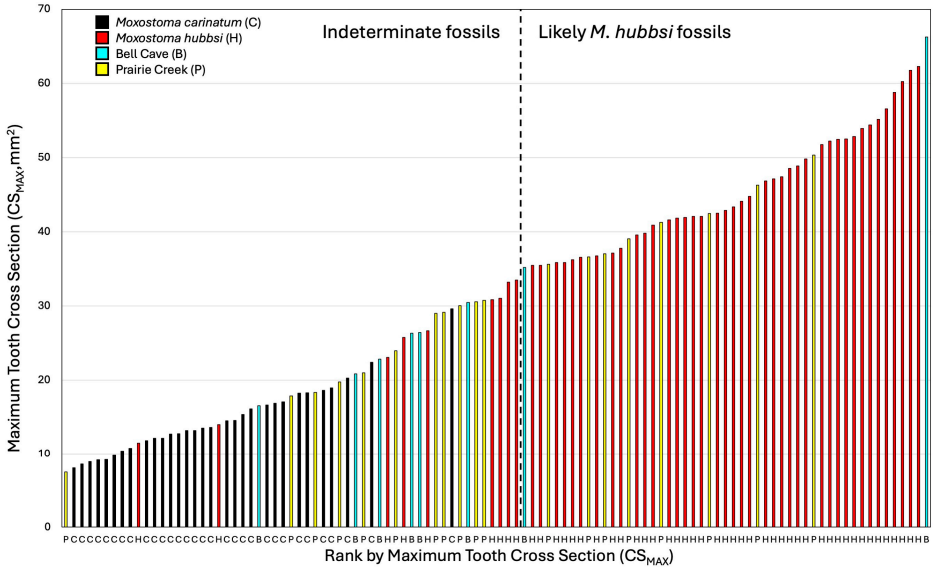


Figure 7. A graphical ranking of maximum tooth area in specimens examined (species or population colored per legend). Species/population also indicated along the x axis per the legend. The dashed line separates fossil specimens to the right that are likely specimens of *M. hubbsi* because they are outside the known distribution of *M. carinatum* from fossils whose identities are uncertain to the left.

The basioccipital pharyngeal process was compared to the large skeletal collection that was assembled by REJ and that is now mostly cataloged at the Auburn University Museum of Natural History (AUM). Gross comparisons were made and the maximum width of the fossil basioccipital was compared against the largest *M. carinatum* and *M. hubbsi* to qualitatively determine differences in basioccipital centrum shape. Measurements taken were basioccipital condyle width and height and basioccipital pharyngeal process maximum width. Ratios were made of condyle height to width and basioccipital pharyngeal process maximum width to condyle width.

Specimens Examined

Institutional acronyms follow Sabaj [16] with the exception that UT is referring to the Zooarchaeological Collection of the McClung Museum at the University of Tennessee and not the fish collection and TU refers to the osteological collection at Tulane University. Numbers of specimens include the number of full skeletal specimens and then the total number of pharyngeal jaws (some collections only had pharyngeal jaws). County is abbreviated as Co. and Regional County Municipality as RCM. *Moxostoma carinatum*: AUM 86330 (1 specimen, 2 pharyngeal jaws), Indiana, Pulaski Co., Tippecanoe River, 6.25 miles SSW of Winamac, 40.9754, −86.65636; AUM 86333 (2, 4), Virginia, Russel Co., Clinch River at Nash Ford, 7.3 miles NNE of junction of 19 and 82 in Lebanon, 36.96758, −82.07946; AUM 86334 (2, 4), North Carolina, Macon Co., Little Tennessee River, 3.4 miles NW of Iotla, 35.26012, −83.44573; AUM 86335 (0, 1), Quebec, unknown locality; AUM 86336 (1, 2), Quebec, Montérégie RCM, Bassin de Chambly, Richelieu River, at Chambly, 43.44985, −73.28924; AUM 86338 (1, 2), Arkansas, Marion Co., Bull Shoals River, in reservoir, ~18 miles W of Mountain Home, 33.44027, −92.6891; AUM 86428 (1, 3), Alabama, Cherokee Co., Coosa River, below Sewell's Ferry, 34.19746, −85.58526; AUM 86465 (0, 1), Kentucky, Franklin Co., Kentucky River, at mouth and lower 500 m of Elkhorn Creek, 38.31913, −84.8569; AUM 86593 (0, 2), North Carolina, Macon Co., Iotla Creek, ~40 m above mouth, at Rt. 28 bridge, at Iotla, 35.23449, −83.39623; AUM Uncataloged (1, 1), GMNH 549 (2, 2), Alabama Cherokee Co., Coosa River, 1 mile downstream from Sewell's Ferry, ~34.2083, ~−85.6185; GMNH 550 (1, 2), Alabama Cherokee Co., Coosa River, at first bend below Alexis' Ferry, ~34.2021, ~−85.5677; TU Osteology 646 (1, 2), Alabama, Wilcox Co., Alabama River at Black Bluff Landing, river mile 123.2, 32.0010, −87.47210; UT Zooarchaeology 140 (1, 1), Missouri, Jefferson and St. Louis Co., Meramec River, Times Beach, 38.50176, −90.59122; UT Zooarchaeology 4087 (1, 2), Illinois, Kankakee Co., Kankakee River.

Moxostoma hubbsi: All collections Quebec. AUM 86391 (1, 2), D'Autray RCM, St. Lawrence River. At Lavaltrie, N side, 45.89713, −73.26318; AUM 86392 (1, 2), Montérégie RCM, Bassin Chambly, Richelieu River at Chambly, 45.44985, −73.28924; AUM 86393 (1, 2), Pierre-De Saurel RCM, Richelieu River, at Saint-Ours, left side of river about 300 m below the lock, 45.86582, −73.14904; CUMV 25512 (0, 3), Rouville RCM, Yamaska River near St. Césaire, 45.41211, −72.99993; CUMN 47986 (0, 1), Les Maskoutains RCM, Yamaska River above Saint Hyacinthe, Station 53, 45.43652, −72.98712; CUMV 52911 (0, 2), Montérégie RCM, Bassin de Chambly at St. Mathias, at E of channel between lines 17 and 19, 45.47341, −73.27233; CUMV 52912 (0, 1), Rouville RCM, Yamaska River, upstream from mouth of Noire River (Station 75), 45.40747, −72.99971; CUMN 52913 (0, 2), Les Maskoutains RCM, Yamaska River in region (town of) Saint Hyacinthe, 45.62388, −72.93806; CUMV 52915 (0, 2), Les Maskoutains RCM, Noire River, ~0.3 and 1.2 miles downstream from dam at Saint-Pie (Stations 20 and 34), 45.51248, −72.91945. Loose pharyngeal jaws from Canadian institutions may not be cataloged and are in the process of being repatriated. Assumptions on the origins of these specimens and their identification numbers are: FAPAQ 291B127B639E (0, 2), FAPAQ 291B284B8577 (0, 1), FAPAQ 291B306CDF3A (0, 2), FAPAQ

291B31B8E3DA (0, 1), FAPAQ 291B32D4DB8E (0, 2), FAPAQ 291B504E89DD (0, 2), and FAPAQ 291B5F7BABAC (0, 2), Pierre-De Saurel RCM, Richelieu River, Saint-Ours, ~45.8838, ~−73.1536; FAPAQ 291B1C063056 (0, 2), Montérégie RCM, Bassin de Chambly, Richelieu River; QPM 17915 (0, 2), locality unknown; QPM 29336 (0, 2), 29354 (0, 1), and 29564 (0, 2), Montérégie RCM, Bassin de Chambly; QPM Uncataloged 1999 (0, 8), Quebec, St. Lawrence River?, locality unknown; QPM Uncataloged 2005, Quebec, dead at Montreal Biodome, locality unknown.

Fossil material. All collections Pleistocene, Wisconsinan, Bell Cave, Colbert Co., Alabama, Acb-2 (zone 1–2 11,820 +48−/−500 BP, zone 3 unknown, zone 4 26,500 +870/−990 BP) [13]: MSC 4254, zone 1/2, pit 2, museum expedition, July 1984, 2 loose pharyngeal teeth; MSC 4839, zone 4, pit 1, museum expedition, July 1984, 1 loose pharyngeal tooth; MSC 4942, zone 3, pit 3, museum expedition, July 1984, partial basioccipital pharyngeal process; MSC 5179, zone 1/2, pit 4, museum expedition, July 1984, 2 loose pharyngeal teeth; MSC 45256, zone 3, pit 3, museum expedition, July 1984, basioccipital pharyngeal process; MSC 51132, 11 June 1987, 3 loose pharyngeal teeth. Prairie Creek Site, Daviess Co., Washington, IN, USA, ~3 mi. N of Washington, Zone D, Pleistocene, Wisconsinan (14,010 BP) [10]: INSM L-200, 4 loose pharyngeal teeth; INSM L-354, 4 loose pharyngeal teeth; INSM L-849, large pharyngeal jaw fragment (2 teeth measured); INSM L1188 2 loose pharyngeal teeth; INSM L-1188, small pharyngeal jaw fragment (3 teeth measured); INSM L-1632, 4 loose pharyngeal teeth; INSM L-2693, 2 loose pharyngeal teeth; and INSM L-2703, 1 loose pharyngeal tooth.

3. Results

Comparisons

Tooth height was an unreliable measurement as teeth are clearly lost and replaced through life. The reason for including the first three teeth is that the largest tooth is among these three, but it is not always the same tooth. New teeth grow from between the bases of the remaining teeth after being lost, and they will expand to fit the available area, ensuring a relatively continuous edge. Jaws were seen in the process of replacing one or two of these teeth, but it was rare to have all three fully developed. The surfaces of the teeth were clearly worn from abrasion.

When scaled with $L_{2–4}$, the CS_{MAX} of the large pharyngeal jaw from Prairie Creek (INSM L-849) was greater than all *M. carinatum* with the closest *M. carinatum* being a 512.7 mm SL specimen (AUM 84645; Figure 6). When scaled with W_P, INSM L-849 falls well within the range of the largest *M. hubbsi* examined; however, it is possible that the width of the fossil has been eroded. The smaller Prairie Creek specimen is among the smallest measured, leaving two possibilities: that it is a juvenile *M. hubbsi* or that it is *M. carinatum*.

With just CS_{MAX}, the only specimen of *M. carinatum* to overlap with the larger fossil specimens examined and *M. hubbsi* was one of the largest specimens of *M. carinatum* examined (AUM 84645, 512.7 mm SL; Figure 7). Body size and tooth size are certainly correlated, but the largest specimens examined of the two species did not have the largest teeth. The smallest *M. hubbsi* (CU 52911 #13, 298 mm SL) had teeth from both left and right sides falling out within *M. carinatum*; however, the specimen is considerably smaller than similarly ranked *M. carinatum* (Figures 5 and 6). The large Bell Cave tooth with CS_{MAX} of 66.3 mm^2 was the largest tooth examined with the second largest a tooth from a 512.7 mm SL specimen of *M. hubbsi* (AUM 86392, right jaw, CS_{MAX} = 62.3 mm^2). The largest specimen of *M. hubbsi* (559.2 mm SL) had CS_{MAX} of 61.8 mm^2 (left) and 60.3 mm^2 (right). The smaller pharyngeal jaw from Prairie Creek (ISM L-1188; Figure 3B) had the smallest CS_{MAX} (7.47 mm^2), making its identification inconclusive.

Two sucker basioccipital pharyngeal processes were found, one of which is near complete (MSC 45256, Figure 5C). The near complete process appears to lack a posterior extension of the basioccipital present in *M carinatum* and *M. hubbsi* (extension indicated by arrows in Figure 5B,D) and some of the anterior and lateral portions. In comparison with other suckers, the basioccipital pharyngeal process of *M. carinatum* and particularly *M. hubbsi* are hypertrophied (Figure 5B,D), with the trabeculae fusing to form a more solid bone (vs. trabeculae forming a lattice, Figure 5A). *Moxostoma hubbsi* has very few holes piercing all the way through the basioccipital pharyngeal process while *M. carinatum* has several large holes anterolaterally and has a weaker, more crenulate posterior margin. MSC 45256 has the basioccipital pharyngeal process with few complete holes and a less crenulate posterior margin, as in *M. hubbsi.* In comparing skull size and the basioccipital centrum (the connection point of the skull to the vertebral column), the basioccipital centrum is comparatively smaller, given the width of the basioccipital pharyngeal process. The maximum width of the basioccipital pharyngeal process to centrum width ratio is 253.6–273.0% (N = 3) in *M. hubbsi* and 169.6–222.8% (N = 14) in *M. carinatum* while the Bell Cave basioccipital is within the range of *M. hubbsi* at 265.5%, and it appears to be eroded slightly. Only one specimen of *M. carinatum* has a wider basioccipital pharyngeal process than the Bell Cave fossil (37.6 vs. 37.5 mm), but the centrum width is much larger (19.7 vs. 14.1 mm). The basioccipital pharyngeal process envelops the basioccipital centrum with stout struts in *M. hubbsi* and the Bell Cave fossil that are clearly visible in posterior view through their entire height (about three fourths height of basioccipital centrum; Figure 5C,D) while the processes are thin and only their bases are visible in *M. carinatum* (Figure 3B). In addition, there is an opening below the basioccipital centrum for the dorsal aorta, and this opening is more parallel with the basioccipital pharyngeal process in the fossil and *M. hubbsi* than in *M. carinatum* (Figure 5B vs. Figure 5C,D). Given these characteristics, the Bell Cave fossil basioccipital is more similar to that of *M. hubbsi* than to *M. carinatum.* The second basioccipital (MSC 4942) is not complete but it is strongly ossified (no trabeculae) and consistent with *M. hubbsi* as well.

4. Discussion

Although an argument could be made that the Prairie Creek teeth could be from very large specimens of *M. carinatum*, the fact that there is only one specimen of *M. carinatum* that overlaps *M. hubbsi* in CS_{MAX} makes it much more likely that several of these teeth represent something more like *M. hubbsi*. The large Bell Cave tooth is the largest tooth measured and would imply a ~560 mm SL+ specimen of *M. hubbsi* (largest *M. hubbsi* specimen examined is 559.2 mm SL) and something much larger than the measured maximum size of *M. carinatum* from the second author's records of over 1100 specimens of *M. carinatum* examined. Although tooth area does correlate with size, this comparison is not perfect. The greatest CS_{MAX} for *M. carinatum* (29.6 mm^2, 512.7 mm SL) is only 44% the area of the Bell Cave specimen. The largest specimen of *M. carinatum* examined (uncataloged specimen form the Tippecanoe River, Indiana, 532 mm SL) is among the largest specimens in REJ's records for morphometry of *M. carinatum* and it has CS_{MAX} of 22.4 mm^2 (right) and 19.0 mm^2 (left). This leaves only *M. hubbsi* as an extant species as a possibility for the largest Bell Cave tooth at a minimum. For the teeth to be that of *M. carinatum*, the size of *M. carinatum* during the Pleistocene would have had to have been much greater than it is today. Some of the teeth were not measured from Bell Cave because they did not appear to be teeth within the first three from the ventral side, but smaller, dorsal teeth.

The fossil basioccipital (MSC 45256) also was more similar to that of *M. hubbsi* than to that of *M. carinatum* in the greater fusion of the trabeculae, stouter struts of the basioccipital pharyngeal process along the basioccipital centrum, as well as in overall shape. For their

size, *M. hubbsi* have shorter skulls with smaller basioccipital condyles than *M. carinatum*, and this is seen in the fossil as well (Figure 5C). There may be some differences, though. The fossil has a longer body to the basioccipital when compared to *M. hubbsi* and the struts along the basioccipital condyle are much thicker.

It is possible that the fossils instead represent an extinct species, but it is unlikely that fragmentary evidence like this is sufficient to decide if a new species is warranted. Given that the current distribution of *M. hubbsi* is so unusual, it is certain that the current distribution does not match with its Late Pleistocene distribution. The maximum extent of the Wisconsin Glaciation event would have covered the current distribution of *M. hubbsi* until about 12,000 years ago (Figure 2), and the Prairie Creek locality is located just to the southwest of the maximum southern extent of the glacier. *Moxostoma hubbsi*'s current distribution was inundated after the glaciers began to melt by the Champlain Sea until about 10,000 years ago and then by Lampsilis Lake, which did have some marine incursions. The St. Lawrence probably did not become riverine until about 6000–5000 years ago, meaning that *M. hubbsi* would have had to have entered into their current distribution in the Holocene [8,9].

As the ice sheet began to melt, flow from the Great Lakes region was mostly to the southwest and into the Mississippi basin. As the glacier retreated northwards, flow in the lower Great Lakes began to shift to the east, and this period would have given access to *M. hubbsi* into the lower Great Lakes region. Six species in the Ottawa River (a tributary of the St. Lawrence) were thought to have entered the river through the Mississippi basin while only the Copper Redhorse was considered to have entered via the St. Lawrence [8]. It would seem more logical to suggest that *M. hubbsi* also gained entrance into the region through the Mississippi basin. Sympatric with the Copper Redhorse in the St. Lawrence is an apparently disjunct population of *M. carinatum*). River and Copper Redhorse may have become isolated in the St. Lawrence through similar geological processes except that Copper Redhorse became extirpated from the remainder of its distribution.

Bell Cave includes fossils of the Muskellunge (*Esox masquinongy* Mitchill) [13], which although relatively recently was found down the Appalachians, was not found as far down the Tennessee River as Bell Cave [16]. This suggests that the area of Bell Cave had cool waters suitable for *M. hubbsi*. With the unusual and clearly relictual distribution of *M. hubbsi* and the similarity of both the Indiana and Alabama teeth and the Alabama basioccipitals to *M. hubbsi,* we suggest that the distribution of *M. hubbsi* once included the current Mississippi River basin. Given the difficulty in identifying species of Redhorse, we would encourage curators to re-examine old specimens of *M. carinatum* to assure their species status. Bones of *M. lacerum* (Harelip Sucker) were also found in Bell Cave [14], and *M. lacerum* went from being discovered to its last specimen being collected in just about 30 years in the 1800s [1]. Perhaps *M. hubbsi* was missed from early collections in the Mississippi River basin.

The discovery of fossils of *M. hubbsi* is particularly important because the Copper Redhorse is considered endangered due to its small distribution and low population size [17,18]. Although there is no evidence for inbreeding [19], the species is in decline [20,21]. Perhaps learning the conditions *M. hubbsi* once inhabited and why it is no longer in that part of its range will aid fisheries managers who seek to propagate the species and increase population numbers.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/fishes10030101/s1, Table S1: morphometric data and analyses.

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