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## Earliest Known Material of *Amia*, Bowfin, From The Sentinel Butte Formation (Paleocene), Medora, North Dakota

Abby Grace Moore

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COLUMBUS STATE UNIVERSITY

EARLIEST KNOWN MATERIAL OF *AMIA*, BOWFIN, FROM THE SENTINEL BUTTE  
FORMATION (PALEOCENE), MEDORA, NORTH DAKOTA

A THESIS SUBMITTED TO THE  
HONORS COLLEGE  
IN PARTIAL FULFILLMENT OF THE  
REQUIREMENTS FOR HONORS IN THE DEGREE OF

BACHELOR OF SCIENCE  
DEPARTMENT OF BIOLOGY  
COLLEGE OF LETTERS AND SCIENCES

BY  
ABBY GRACE MOORE

COLUMBUS, GEORGIA

2020

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Earliest known material of *Amia*, bowfin, from the Sentinel Butte Formation (Paleocene),

Medora, North Dakota

By

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Bair

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## ABSTRACT

*Amia calva* is an icon in the field of comparative osteology, yet we have a poor understanding of the evolution of the genus because many fossil amiid bones have gone unidentified. Here we identify new material of the genus, *Amia*, with evidence of two unidentified species. Previously, the oldest known material identifiable as *Amia* cf. *A. pattersoni*, was a specimen from the Paleocene epoch of Alberta, Canada approximately 58 million years in age. Fossils of the two unidentified species of *Amia* were found in the Sentinel Butte Formation, a geologic formation of Paleocene age (~ 60 million years ago) near the town of Medora, North Dakota. The specimens are classified as *Amia* because the coronoid tooth plates exhibit conical teeth and the parasphenoid exhibits a long tooth patch that extends anteriorly past the ascending rami of the bone. This new *Amia* material is distinguished from other species based on three criteria. First, the parasphenoid tooth patch is extremely wide posteriorly, reaching the lateral margins of the bone, but very long and narrow anteriorly. Second, the gular plate is uniquely shaped, not being truncated posteriorly but rather tapering both anteriorly and posteriorly. Third, the teeth of coronoid tooth plates are robust, unlike those of other species of *Amia* which are thinner and more elongated. The frontals of each specimen are very different in shape and proportions suggesting two different taxa. Width and length ratios of bones from the *Amia* specimens were analyzed to further determine fossil characteristics. One of these taxa could attain a large size with a total length well in excess of 1 m. Together, these taxa highlight the necessity to document the evolutionary history of this long and important lineage of *Amia*.

## ACKNOWLEDGMENTS

Many thanks to Becky Barns for preparation of NDGS specimens. This research was funded in part by the Student Research and Creative Endeavors Fund at Columbus State University.

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## INTRODUCTION

A monotypic genus, *Amia calva* is an icon in the field of comparative osteology. We have a poor understanding of the evolutionary history of the genus and its family Amiidae. The lack of an adequate understanding is due to an incomplete fossil record often represented by unidentified or misidentified amiid bones that confound our understanding of the evolutionary history (Grande and Bemis 1998). My goal is to describe new material of the genus, *Amia*, using two new specimens. Previously, the oldest known material identifiable as *Amia* cf., *A. pattersoni* is a fragment of a skull from the Paleocene epoch of Alberta, Canada approximately 58 million years in age. The new material in this study predates *Amia* cf. *A. pattersoni* by two million years. The species *Amia pattersoni* was originally described from complete specimens of the 50 million year old, Green River Formation of Wyoming.

### Extant Species

The bowfin, also known as "dogfish" and "mudfish," is a predatory fish typically found in shallow, weedy lakes, swamps, and backwater areas (Etnier and Starnes 1993; Fig. 1). *Amia calva* is usually found on the coastal plain of Atlantic drainages from Chesapeake Bay region to Colorado River, Texas (Becker 1983). The species is also known from the Great Lakes drainage, Mississippi Basin north to Minnesota, and adjacent areas of Hudson Bay drainage of northwestern Minnesota (Etnier and Starnes 1993). In Canada, they are found in Quebec and Ontario in the upper St. Lawrence River, Lake Champlain, Ottawa River, and all the Great Lakes (Scott and Crossman 1973). A sexually dimorphic species, *A. calva* exhibits sexual maturity at lengths of around 46 cm in males and 70 cm in females at approximately 2-4 years of age (Etnier and Starnes 1993, Koch et al. 2009). The life span in captivity is recorded at a maximum of 30



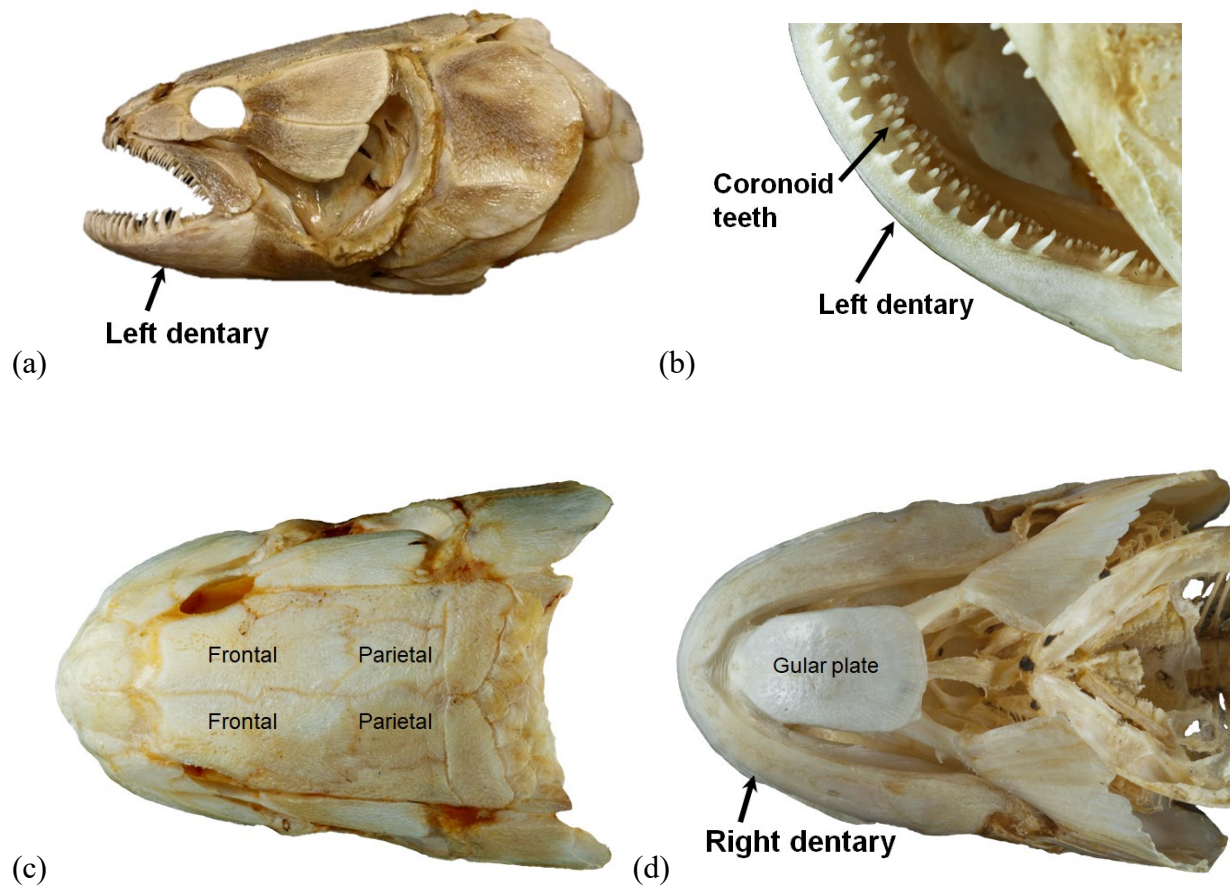
years, with normal populations reaching only about 10 years. Bowfin are used as food in some areas, with good taste, yet of a soft and gelatinous texture (Etnier and Starnes 1993). *Amia calva* provides many avenues of human importance from an occasional food source to a model in comparative osteology (Becker 1983; Fig. 2).



**Figure 1.** *Amia calva*; image modified and taken from <http://gallery.nanfa.org>. Scale bar: 20 mm.

As the only extant species from the order Amiiformes, *A. calva* retains the modified heterocercal caudal fin structure with more advanced, cycloid-like scales with parallel bony ridges. The gular plate, a bone located on the floor of the mouth between the rami of the lower jaws, is unique to other freshwater fishes who have maintained some primitive features, though it appears in some marine fishes (Etnier and Starnes 1993). *Amia calva* possess a long dorsal fin base with approximately 48 rays, and 10-13 branchiostegal rays (Nelson et al. 2016). The anteriormost bones of the skull roof are frontals, followed by parietals, with the posteriormost bones being the extrascapular. On a typical skull roof, there are three paired narrow troughs containing pit-lines (Grande and Bemis 1998). Located on the dentary, coronoid teeth of *Amia* are conically shaped, being smaller and somewhat blunter than dentary teeth. Compared to its extinct sister taxon, *Cyclurus*, the coronoid teeth of *Amia* exhibit a sharper point than the flattened, broadly rounded

tips of *Cyclurus* and can vary between two to six pairs (Grande and Bemis 1998). The ventral surface of the parasphenoid, running from the anterior of the frontals to the posterior of the occipital condyle, contains a small, narrow tooth patch with sharp conical teeth. The gular plate of *A. calva* tapers anteriorly and truncates posteriorly (Grande and Bemis 1998). The bone structure of *A. calva* allows for a useful comparative analysis between the unidentified specimens, other *Amia* species, and their sister taxon, *Cyclurus*.



**Figure 2.** Extant *Amia calva* skull in (a) lateral, (b) occlusal, (c) dorsal, and (d) ventral view. Image (a) modified from <https://www.pbase.com>.

The objectives of this project are to describe and distinguish two specimens as *Amia* from fossils discovered in North Dakota and identify their age and growth. I will use width to length ratios of the frontals, parietals, gular plate, operculum, parietal length to frontal length ratios, and other aspects of their osteology to describe them. With the assumption that ratios remain constant throughout life, I predict that each unidentified specimen will have significantly different ratios for each bone due to the size differences of each, notably the vertebral centra and frontals which give a good comparison on the massive size of the larger specimen. Also, as I compile the ratios into graphical form, I expect each previously described species of *Amia* to be distinct from one another. As the larger specimen possesses a larger vertebral centra compared to the smaller specimen, I predict that it will have a greater radial distance for each year of age and therefore a steeper slope than that of the smaller specimen on the age and growth graph.

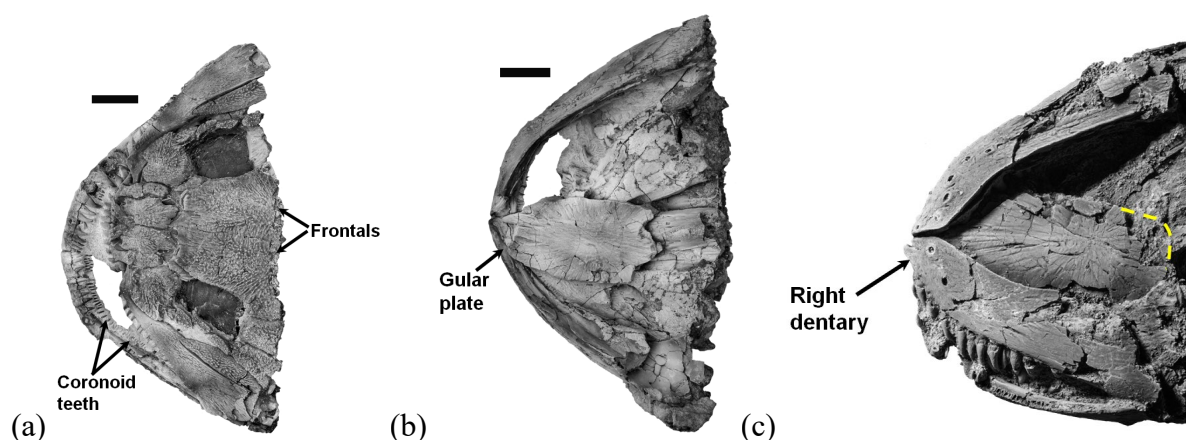
## MATERIALS AND METHODS

### Study Site

Fossil material was found in the Sentinel Butte Formation of Medora, North Dakota with two important localities known as “Poker Jim,” site of the smaller specimen, and “Medora,” site of the larger specimen. The new *Amia* material of the “Poker Jim” locality consists of a partial skeleton including the frontals, parietals, left extrascapular, right postinfraorbital, right dentary with a second coronoid tooth plate, left operculum, right cleithrum, several precaudal vertebrae, and many scales. “Medora” locality material consists of disarticulated material including 42 isolated fossils that articulate to assemble a large head of *Amia*.

## Osteological Comparison

I described new material of the two unidentified species of *Amia* collected from the Sentinel Butte Formation, Paleocene in age (~60 million years ago), near the town of Medora, North Dakota. I compared the new *Amia* fossils to bones of *A. calva*, *Amia hesperia*, *Cyclurus*, and the previously described *Amia* cf. *A. pattersoni* (Fig. 2; Fig. 3). Ammonium chloride dusting was used to coat the individual bones for photography and comparison.



**Figure 3.** Comparative specimens of *Amia* and *Cyclurus*; (a) *Amia* cf. *A. pattersoni* in dorsal view (ULAVP 37150) and (b) ventral view; (c) *Cyclurus fragosus* in ventral view (ULAVP 5505) with hashed line indicating outline missing margin from impression. Scale bars: (a), (b)=20 mm; (c)=10 mm.

After measurements of unidentified bones were collected, graphs of *Amia* and *Cyclurus* width to length ratios of the frontals, parietals, gular plate, and operculum in addition to a parietal to frontal length ratio were created for comparison (Figs. 4-5). I included 47 specimens from five taxa of amiids for comparative length/width ratios including *A. calva* (n=13), *A. pattersoni* (n=7), *Cyclurus kehreri* (n=14), *Cyclurus gurleyi* (n=6), and *Cyclurus efremovi* (n=7) for data analysis

(Grande and Bemis 1998). I ran one-sample t-tests to compare means between each unidentified specimens and both *A. calva* and *A. pattersoni*, then ran independent t-tests to compare the means between *A. calva* and *A. pattersoni*. Square root transformation of the ratios were used to run the statistical tests to account for normality of the data.

### **Age and Growth**

Previous studies have described the age and growth of bowfin bones using multiple methods with varying results. Analyzing the extant *A. calva*, studies have used methods such as mean back-calculated lengths, gular plates, centra, and sectioned pectoral fin rays to determine growth of the species (Cooper and Schafer 1954, Cartier and Magnin 1967, Becker 1983, Koch et al. 2009, Eberle et al. 2010; Brinkman et al. 2014). When compared to a previous study, the growth estimates for *A. calva* using a mean back-calculated length method showed similar trends of increasing size of approximately 150-600 mm from ages one to six, but inconsistencies were found after age seven with one study ranging from around 600-750 mm, considerably smaller than the other (Koch et al. 2009). With other age and growth measurements, there are contradictions among studies using the same methodology of pectoral fins and gular plates (Koch et al. 2009). Inconsistencies in age and growth estimates can be attributed to small sample sizes for varying ages, spatial variations in growth, or different methods for describing growth estimates.

Using vertebral centra as the means to determine age and growth of unidentified specimens follows similar studies conducted on both extant and extinct amiid bones (e.g., Brinkman et al. 2014). Under a binocular dissecting microscope, growth for the centra is made by marking the notochord foramen with an ocular grid and measuring all annuli in radial distance (RD mm)

toward the distal margin (Eberle et al. 2010). Annuli are identified as concentric valleys following a concentric ridge on the amphicoelous face of the centrum. In Brinkman et al. (2014), amiid centra were used to determine age and growth with the oldest recorded specimen age at 11 years with a radial distance of approximately 5.8 mm. As with other age and growth curves of centra, we expect to see a positive slope with linear tendencies.

## RESULTS

### Width to Length Ratios

Grande and Bemis (1998:p.40) published ranges of width to length ratios for *A. calva*; frontal 0.45-0.65 (n=13), parietal 0.6-0.89 (n=13), gular plate 0.55-0.65 (n=13), opercle 0.84-1.0 (n=13), parietal/frontal length 0.4-0.77 (n=13)(Figs. 4-5). The ranges of width to length ratios for *A. pattersoni* are also listed for each osteological element; frontal 0.31-0.36 (n=11), parietal 0.59-0.8 (n=11), gular plate 0.37-0.38 (n=2), opercle 0.81-0.96 (n=9), and parietal/frontal length 0.37-0.44 (n=10)(Grande and Bemis 1998:p.189)(Figs. 4-5).

The width to length ratios for the larger unidentified specimen are compared to the previous species; frontal 0.38 (NDGS 3562), parietal 0.63 (NDGS 3564), gular plate 0.43 (NDGS 3576), opercle 0.83 (NDGS 3568), and parietal/frontal length 0.47 (NDGS 3564/NDGS 3562)(Figs. 4-5). A mostly complete skull roof of the small *Amia* specimen (NDGS 2151) includes the frontals, parietals, and an extrascapular (Fig. 6). Width to length ratios for the smaller unidentified specimen (NDGS 2151) are also recorded for comparison; frontal 0.47, parietal 0.85, opercle 0.88, and parietal/frontal length 0.43 (Figs. 4-5).

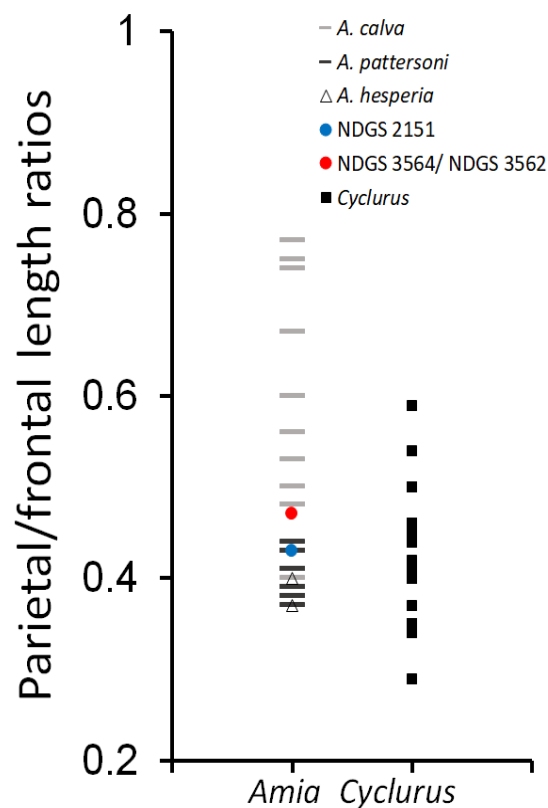


In the frontals of the two species, there is no overlap observed between *A. calva* and *A. pattersoni* with *A. calva* having an overall smaller width/length ratio due to more narrow frontal bones (Fig. 5a). Frontal width/length ratio of the *A. calva* specimens (M=0.7235, SD=0.0353) were significantly different from both the small and large specimens ( $t_{12}=3.874$ ,  $p=0.002$ ;  $t_{12}=10.945$ ,  $p<0.0001$ ). Frontal ratios of the *A. pattersoni* specimens (M=0.5891, SD=0.0139) were also significantly different from both the small and large specimens ( $t_{10}=-22.979$ ,  $p<0.0001$ ;  $t_{10}=-6.492$ ,  $p<0.0001$ ). Frontal and parietals of the smaller specimen (NDGS 2151) have length/width ratios more similar to ancient *Cyclurus* than its most closely related species of *A. pattersoni*, but fall within the range of the extant *A. calva* (Fig. 5a-b; frontal = 0.47, parietal = 0.85, Grande and Bemis 1998). Not only are the unidentified specimens significantly different, but the frontal width to length ratios of the 13 *A. calva* specimens compared to the 11 *A. pattersoni* specimens were also significantly different ( $t_{22}=11.841$ ,  $p<0.0001$ ).

Parietal width to length ratio of the *A. calva* specimens (M=0.8335, SD=0.0570) were significantly different from both the small and large specimens ( $t_{12}=-5.597$ ,  $p<0.0001$ ;  $t_{12}=2.516$ ,  $p=0.027$ ). Parietal ratios of the *A. pattersoni* specimens (M=0.8492, SD=0.0417) were also significantly different from the small and large specimens ( $t_{10}=-5.787$ ,  $p<0.0001$ ;  $t_{10}=-4.412$ ,  $p=0.001$ ). There was no significant difference between the parietal ratios of the *A. calva* and *A. pattersoni* specimens ( $t_{22}=-0.758$ ,  $p=0.457$ ).

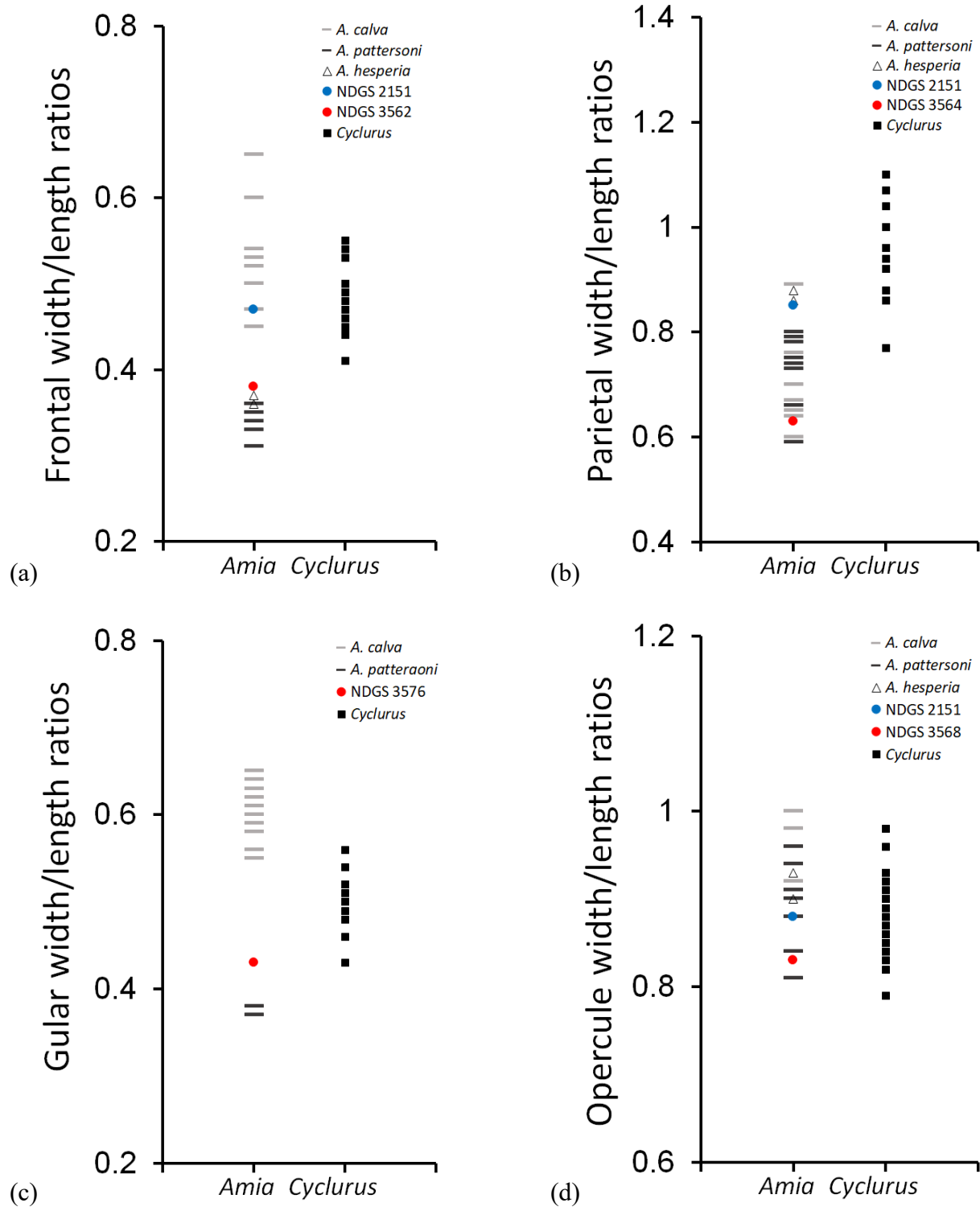
Fossils from the Medora locality of the large specimen resemble the proportionally longer skull of *A. pattersoni*, yet the parietal/frontal length ratio of 0.47 reveals a greater size than previously discovered with elongated left frontal 10.2 cm and left parietal 4.8 cm, showing the immense size of the new species (Fig. 4; Grande and Bemis 1998). With the parietal to frontal length ratio, the *A. calva* specimens (M=0.7686, SD=0.0767) were significantly different from both the small and

large specimens ( $t_{12}=5.304$ ,  $p<0.0001$ ;  $t_{12}=3.899$ ,  $p=0.002$ ), and the *A. pattersoni* specimens ( $M=0.6346$ ,  $SD=0.0193$ ) were significantly different from both the small and large specimens ( $t_9=-3.470$ ,  $p=0.007$ ;  $t_9=-8.377$ ,  $p<0.0001$ ). The parietal to frontal length ratios of the 13 *A. calva* and 10 *A. pattersoni* specimens were significantly different from the other ( $t_{13,9}=6.054$ ,  $p<0.0001$ ).



**Figure 4.** Parietal to frontal length ratios of *Amia* species, *Cyclurus* species, and the two unidentified specimens. The large specimen is represented by the red dot and the small specimen is represented as the blue dot.





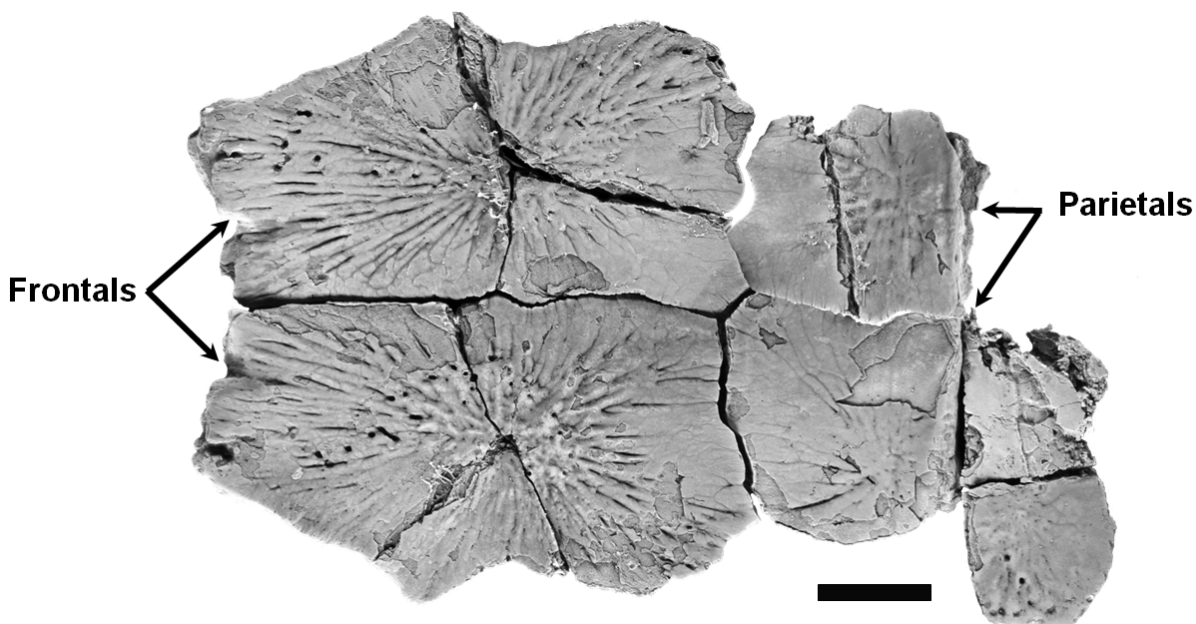
**Figure 5.** Width to length ratios of (a) frontals, (b) parietals, (c) gular plate, and (d) opercule of *Amia* species, *Cyclurus* species, and the two unidentified specimens. The large specimen is represented by the red dot and the small specimen is represented as the blue dot.

Almost no difference is observed in opercule width to length ratios of *Amia* or *Cyclurus* (Fig. 5d). The opercule width to length ratios of the *A. calva* specimens (M=0.9810, SD=0.0277) were significantly different from both the small and large specimens ( $t_{12}=5.582$ ,  $p<0.0001$ ;  $t_{12}=9.107$ ,  $p<0.0001$ ). Opercule ratios of the *A. pattersoni* specimens (M=0.9443, SD=0.0248) were only significantly different from the large specimen ( $t_8=4.029$ ,  $p=0.004$ ). The 13 *A. calva* specimens compared to the nine *A. pattersoni* specimens were significantly different from each other ( $t_{20}=3.186$ ,  $p=0.005$ ).

The parasphenoid tooth patch of the undescribed *Amia* (NDGS 3575) are long and narrow anteriorly, yet wide posteriorly, extending to the lateral margins of the bone compared to a *Cyclurus* specimen (NDGS 3575) found at the same site (Fig. 7). *Cyclurus* exhibits a narrower anterior and wider posterior of the bone (Fig. 7). A long tooth patch is seen in all other *Amia* sp. (Grande and Bemis 1998).

Teeth of the coronoid tooth plates of *Amia* (NDGS 2151) are elongate and conical in contrast to those styliiform teeth of *Cyclurus* (Fig. 8).

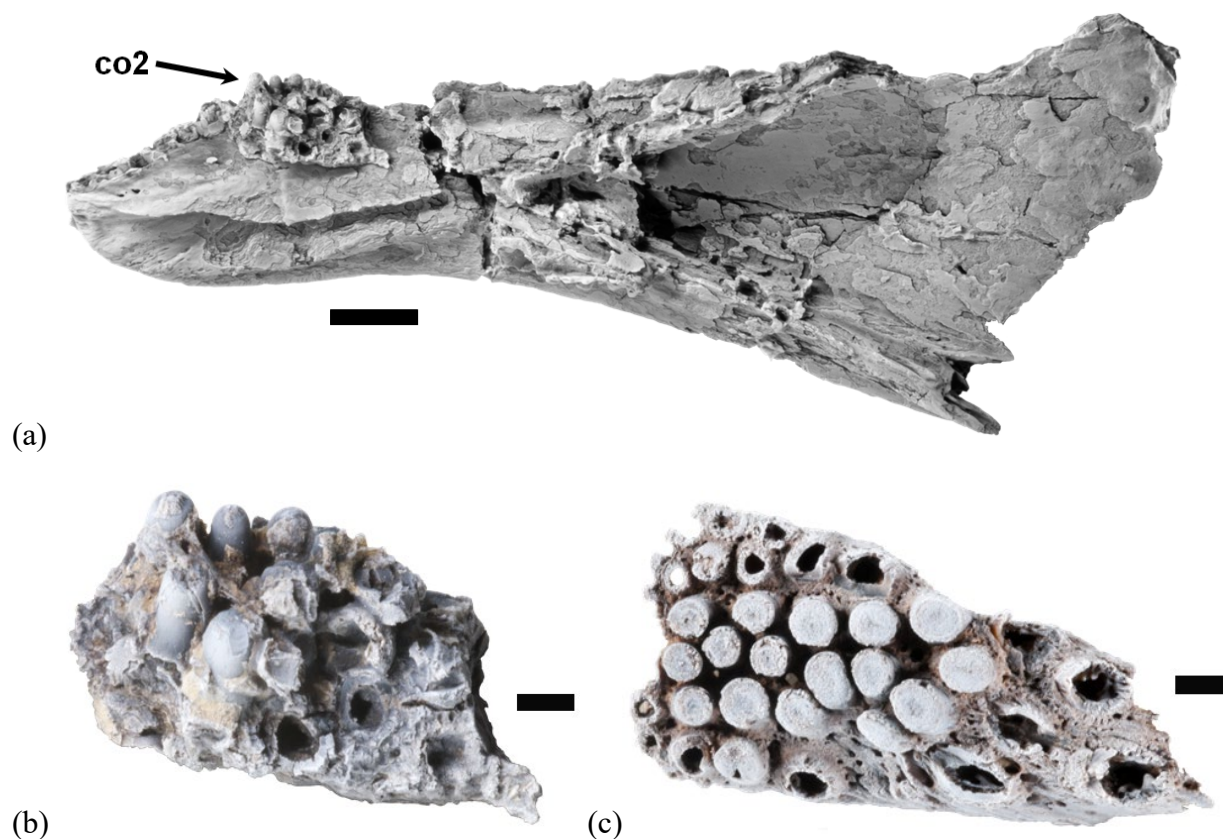
The gular plate ratio of the large specimen (NDGS 3576) is in between ratios of *A. calva* and *A. pattersoni*, though more closely resembles the latter (Fig. 5c). It is long, narrow, and tapers posteriorly as in *A. pattersoni* (Fig. 9). There was no gular plate preserved for the small specimen (NDGS 2151), but there was a significant difference between the gular plate ratios of the *A. calva* specimens (M=0.7738, SD=0.0220) and the large specimen ( $t_{12}=19.336$ ,  $p<0.0001$ ). No significant difference was found between the ratios of the large specimen and *A. pattersoni* (M=0.6124, SD=0.0058), but there was a significant difference between the 13 *A. calva* and two *A. pattersoni* specimens ( $t_{13}=10.017$ ,  $p<0.0001$ ).



**Figure 6.** The skull roof of undescribed *Amia* skeleton (NDGS 2151) from the Sentinel Butte Formation (Paleocene), in dorsal view. Scale bar: 10 mm.



**Figure 7.** Isolated parasphenoids in ventral view from the Sentinel Butte Formation (Paleocene), anterior to left; (a) undescribed *Amia* (NDGS 3575); (b) *Cyclurus* (NDGS 3610). Scale bars: (a)=10 mm, (b)=15 mm.



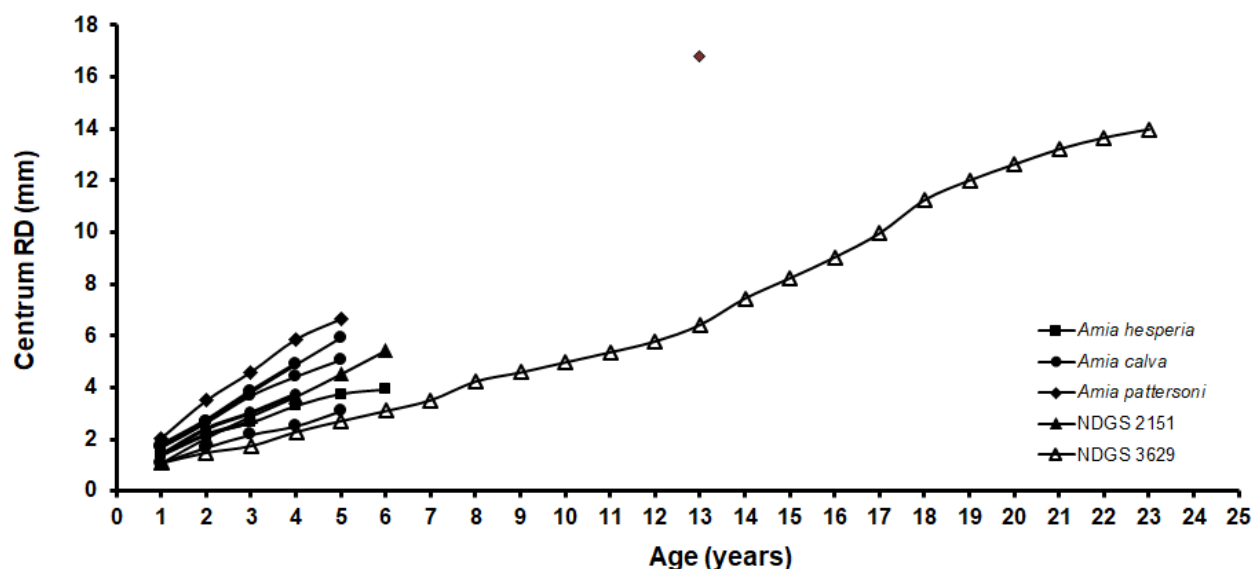
**Figure 8.** Coronoid teeth from the Sentinel Butte Formation (Paleocene); (a) medial view of right dentary from undescribed *Amia* (NDGS 2151) with articulated second coronoid tooth plate (co2, see arrow); (b) co2 of *Amia* (NDGS 2151) in occlusal view exhibiting conically-shaped teeth; (c) right co1 of *Cyclurus* (NDGS 3602) in occlusal view exhibiting flattened, truncated teeth. Scale bars: (a)=5 mm, (b)=1 mm, (c)=2 mm.



**Figure 9.** Isolated gular plate of *Amia* (NDGS 3576) in ventral view. Scale bar: 10 mm.  $p < 0.0001$ . The gular plates of *Cyclurus* exhibit a straight posterior margin opposed to the tapering *Amia* characteristic (Fig. 2).

## Age and Growth

With the combination of data from previous studies and measurements taken from the unidentified specimens, the age and growth of each species maintains the common trend of a positive slope with linear tendencies. *Amia* species included *A. calva* (n=6), *A. pattersoni* (n=2), and *A. hesperia* (n=1). For the smaller specimen (NDGS 2151), radial distance was recorded at 1.08 mm for age 1 and 5.43 mm for age 6. The larger specimen (NDGS 3629) radial distance was recorded at 1.09 mm at age 1 and 13.98 mm at age 23. Compared to NDGS 2151, the large specimen exhibited a slower growth rate, but both show a steady size increase over time (Fig. 10).



**Figure 10.** A composite of growth profiles for documented and unidentified specimens. Growth was measured in radial distance (RD, mm).



## DISCUSSION

In all ratio aspects except for the gular plate ratios of *A. pattersoni*, the large specimen is significantly different from both *Amia* species and tends to be more similar to those ratios of *A. pattersoni*. Except for no significant difference in parietal width to length ratios, *A. calva* exhibits smaller ratios and *A. pattersoni* exhibits larger ratios and are significantly different (Figs. 4-5).

The small specimen (NDGS 2151) is significantly different from other groups in all ratio aspects except for the opercule of *A. pattersoni* specimens. The teeth of coronoid tooth plates are robust, unlike those of other species of *Amia* which are thinner and more elongated. Though not defining phylogenetic relationships, ratios can be used to differentiate species which supports that the unidentified specimens could be new species. Frontal width/length ratios are important in helping to identify and categorize the unidentified species with data from previously identified *Amia* specimens.

This new *Amia* representing the large specimen is distinguished from other species based on three criteria. First, the frontals of the larger specimen are proportionately longer and narrower than the extant *A. calva* and exceed the range of previously studied *A. pattersoni* specimen with a width to length ratio of 0.38 for both (Fig. 5a; Grande and Bemis 1998). Second, the parasphenoid tooth patch is extremely wide posteriorly, reaching the lateral margins of the bone, but very long and narrow anteriorly. Third, the gular plate is uniquely shaped, not being truncated posteriorly but rather tapering both anteriorly and posteriorly. Together, these taxa highlight the necessity to document the evolutionary history of this long and important lineage of *Amia*.

As with most aspects of comparison, the age and growth of the small specimen follows the slope patterns of the *A. calva* specimens. *Amia pattersoni* is much larger at a younger age than the large specimen of *Amia*. Furthermore, the large specimen of *Amia* has a much smaller size in the earlier years than the small specimen. Variability in growth patterns can be explained by temperature which has a strong influence on growth rate and metabolic rate. Metabolic rates are higher in warmer water and significant climatic changes result in a shift to larger centrum sizes which could explain the longevity and size of the large specimen (Newbrey et al. 2008). *Amia pattersoni* from the Green River Formation occurs in a warmer climate than those from North Dakota (Zachos et al. 2001). The large specimen has the smallest slope among all amiid specimens, yet attains an older age. Due to the tradeoff between longevity and growth rates, the decreased growth rates of the large specimen allow it to survive longer than the smaller specimen, which does not attain a greater size than the large specimen (Newbrey et al. 2008).

My research suggests there are two new species of *Amia* in the Sentinel Butte Formation. These important and rare fossils represent the oldest material known for the species. The results of the osteological comparisons, width/length ratios, and age and growth results showcase the osteological and biological distinctions between the two taxa and highlight the necessity to document the evolutionary history of the long and important lineage of *Amia*.

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