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Morphological Diversity of Bowfins (*Amia* spp., Amiidae) Among the Laurentian Great Lakes and South Carolina

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Abstract

The Bowfin genus *Amia* has been considered monotypic since 1896, when 12 nominal species were synonymized with *Amia calva* without scientific analysis or rationale. Since then, only three studies have explored morphological or genetic variation within the genus, all of which found some degree of separation among populations. To further test the 1896 monotypy hypothesis, we analyzed morphological variation of newly collected Bowfins between South Carolina (SC, type localities of *A. calva*, *A. lintiginosa*, and *A. cinerea*), Lake Huron (type localities of *A. ocellicauda* and *A. occidentalis*), and Lake Erie (type localities of *A. canina* and, perhaps, also *A. piquotii*). Results showed significant differences for 15 morphometric and five meristic characters between SC (five sites combined) and lakes Erie and Huron (with data for those two lakes combined). Within the Great Lakes, 13 morphological and two meristic characters were significantly different between Lake Erie and Lake Huron. Finally, within SC, five samples from lower coastal plain sites differed significantly from a sample from an upper coastal plain site for at least 10 morphometric and five meristic characters. Consequently, I reject the 120-year-old monotypy hypothesis. *Amia ocellicauda* was the second nominal species described (from Lake Huron), and therefore among nominal taxa (other than *A. calva*), it has priority and should be resurrected as a valid species. Morphological variation between lakes Erie and Huron, though not as clear, suggests that there likely exists further complexity within the genus. Likewise, in South Carolina there are indications that two species could be present, and that also begs further analyses. The discovery of multiple species of Bowfins raises concerns for conservation and management; a growing market for Bowfin caviar could have detrimental effects on population sizes and genetic variation.

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I also thank Kean Clifford for initiating this new wave of research on Bowfin taxonomy and establishing a solid foundation from which to work, and I thank Madeline Clark for her research on bowfin genetics, which complemented my study.

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Introduction

The Bowfin (*Amia calva* Linneaus) is a species of primitive, ray-finned fish described in 1766. Although three extinct species within the genus have been described from fossils (Grande and Bemis, 1998), *A. calva* is presently recognized as the only extant species within the family Amiidae. Bowfins are found exclusively in North America where their distribution spans from Florida to Lake Champlain and southern Canada, with the Mississippi River and close surrounding tributary waters serving as the westernmost limit. Within their range, Bowfins are relatively common in large, low-elevation lakes and rivers (Warren and Burr, 2014).

Although the current consensus is that the Bowfin exists as one species, 13 nominal species were originally described between1766 and 1870 (Fig. 1), and all three of the fossil species were named after 1870 (Grande and Bemis, 1998). The first proposal to consolidate *Amia* into one species was by Günther (1870), who argued that ten of the 11 nominal species described at the time were synonyms of *A. calva*. In that same year, Duméril (1870) recognized ten previously named taxa and described two additional species, illustrating the lack of consensus at the time (or limited communication between London and Paris). It wasn't until after Jordan and Evermann's (1896) publication, however, that the consolidation of *Amia* into one species became widely accepted. Both Günther (1870) and Jordan and Evermann (1896) made scientific claims, but their synonymies apparently were based on opinion, rather than any scientific analysis or rationale.

Amia calva was the first species to be described (from vicinity of Charleston Harbor, SC), and thus, that taxon took precedence when the later-described species were synonymized. After *A. calva* was described, no new species names were published until 1837, when *Amia ocellicauda* was described from Georgian Bay in Lake Huron (Todd, in Richardson, 1837; Fig.

1). A third species, *Amia occidentalis*, was described by DeKay (1842) based on a specimen from the St. Mary's River (which flows into northern L. Huron and is not far from Georgian Bay). Subsequently, Valenciennes (in Cuvier and Valenciennes, 1847) described eight additional species from several localities. These included *A. marmorata, A. viridis,* and *A. subcoerulea* (all from the Mississippi River basin near New Orleans, LA); *A. ornata* (from an unknown location on the Mississippi River); *A. canina* (from Lake Erie); *A. lintiginosa* and *A. cinerea* (from 'freshwaters of the Carolinas' and Charleston, SC, respectively); and *A. reticulata* (from Wabash River, IL). Duméril (1870) described the final two species: *A. thompsonii* (from Lake Champlain, VT) and *A. piquotii* (based on two syntype specimens presumably from both the upper Mississippi River and Lake Erie, but which specimen came from which locality is not known).

Looking beyond the prevailing consensus that living Bowfins exist as one species, there is reason to suspect that Bowfins could comprise multiple species. There are many similarities between Bowfins and Gars. Both are primitive fishes that together make up the monophyletic group Holostei (Grande, 2010), which could indicate that they are approximately of similar geologic age, having evolved from a common ancestor. Additionally, both occupy similar ecological roles, thrive in similar lowland habitats and are found across similar ranges. Although Gars have a more expansive range than Bowfins, where their ranges overlap there are five different species of Gars within two genera. Given the similarities between the two groups, it begs the question: Why haven't Bowfins followed a similar speciation pattern?

Since the consolidation of Bowfins into one species by Jordan and Evermann (1896), there has been almost no inquiry into the species-level taxonomy of living Bowfins, which is interesting considering that their synonymy had no scientific rationale. Of the three studies on

Bowfin diversity that do exist, all found evidence for some degree of divergence among Bowfins. The first study (Bermingham and Avise, 1986) focused on differences in mitochondrial DNA of Bowfin populations in the southeastern US. They found that populations in the Apalachicola River basin and farther eastward were in fact genetically distinct from populations west of the Apalachicola basin along the Gulf coast, implying that gene flow was constrained across that boundary. That result alone did not demonstrate that multiple species of Bowfins exist, but it did reveal genetic differentiation requiring further study. It is surprising that there have been so few follow up studies.

In 2014, a second study of Bowfin diversity was conducted (Clifford, 2014) with the express purpose of evaluating the possibility that multiple species exist. In that study, Clifford analyzed morphological differences between Bowfins from the Savannah River basin (at the SC-Georgia border, and two nearby rivers in SC) and Central New York. Based on significant regional differences in various morphometric and meristic characters, Clifford (2014) inferred that Bowfins from CNY and SC represented two distinct species. More recently, Clark (2015) explored the genetic diversity of Bowfin populations in the Carolinas and Laurentian Great Lakes using the 'barcode' gene, Cytochrome Oxidase I. Paralleling Clifford's findings, that study also rejected the null hypothesis that the genus *Amia* is monotypic.

The purpose of this study is to expand upon these previous findings. While Clifford analyzed differences between northern and southern Bowfin populations, he did not have population samples available from the type localities of various nominal species (i.e., topotypes). I focus on the morphology of Bowfins specifically collected from the type localities of key nominal species in SC, Lake Erie, and Lake Huron. The over-arching goal is to test the (null) monotypy hypothesis for the genus *Amia* by examining morphological variation among topotypical specimens. This approach can lead to resolution of taxonomic uncertainties.

Materials and Methods

Field Collections

A total of seven distinct Bowfin populations were sampled by state or provincial fisheries resource agencies from South Carolina, Ohio and Ontario (Fig. 2). Samples were collected by boat and backpack electroshocking or in trap nets, depending on the habitat type and water levels, and maintained on ice for up to about 6 h until they could be frozen or preserved. Each fish was given a unique identification number and photographed to record live or fresh color and pigmentation patters. A tissue sample was taken from the right pelvic fin of each fish and preserved in 95% ethanol for later genetic analyses. To prevent internal deterioration and preserve shape of each fish, major muscles were injected with 37% formalin and the specimen laid out in a straight, natural position for at least 40 min. They were then submerged in 10% formalin solution for 4-5 days, to finalize preservation. Next, they were soaked in water for 4-5 days, changing the water every 24 h to remove the formalin. For final, long-term storage they were kept in tanks with 75% ethanol.

Lake Huron was sampled by the Ontario Ministry of Natural Resources (OMNR); *A. ocellicauda* was described from Georgian Bay and *A. occidentalis* was described from the St. Mary's River, a northern tributary to the lake. The primary sampling area was located in southern Georgian Bay near Severn Sound (Fig. 2) and not far from Penetanguishene, ON (type locality of *A. ocellicauda*; Richardson, 1937). OMNR was only able to obtain one specimen from the St. Mary's River, so that site is omitted from our analyses of populations, but the specimen is mentioned briefly as appropriate. Lake Huron specimens were all deposited and processed at the Royal Ontario Museum. Lake Erie was sampled by the Ohio Department of Natural Resources; *A. canina* and one of two syntype specimens of *A. piquotii* originated from that area. Sampling was focused in the southwestern portion of the lake in two general areas, near Monroe, MI, and Sandusky, OH (Fig. 2); the frozen specimens were transported to SUNY-ESF for processing in the laboratory.

Five sites across the lower coastal plains (i.e., all ≤18 m altitude) of South Carolina were sampled; *A. calva*, *A. lintiginosa*, and *A. cinerea* were all described from South Carolina (Figs. 1 and 2). Those sites from north to south included: 1) Little Pee Dee River, 2) Wee Tee and Ferry Lakes, 3) Little Salkehatchie River, 4) Schultz Lake (which drains into Charleston Harbor, so specimens can be considered topotypes), and 5) Bluff Lake and Savannah River. At all five sites, fishes were collected by the South Carolina Department of Natural Resources, and the frozen specimens were transported to SUNY-ESF for processing in the laboratory. A sixth set of Bowfin samples, mostly from middle reaches of the Savannah River basin (i.e., upper coastal plains, ~60-80 m altitude), was studied by Clifford (2014; precise locality data and museum catalogue numbers are presented in that thesis, pp. 8-9), and subsets of those data were used for comparisons to topotypical *A. calva* collected near Charleston, SC.

Measurements and Meristic Counts

Mostly following the methods of Clifford (2014), 36 morphometric characters (Appendix 2) were measured and eight meristic characters were counted for each specimen. In addition to the characters studied by Clifford (2014), I measured posterior nostril diameter and counted the total number of branchiostegal rays (Clifford counted number of branchiostegal rays on one side only). Morphometric measurements 10 cm or greater were measured to the nearest mm, while those under 10 cm were measured to the nearest tenth mm. A 60 cm digital caliper was used for measurements 30 cm or greater, and a 30 cm digital caliper was used for measurements under 30 cm. Morphometric measurements were converted to ratios relative to standard length (SL, value/SL) to reduce effects of allometry. Parametric statistical analyses were performed on those ratio data, including analyses of covariance (ANCOVA) and principal components analyses (PCA). Meristic values did not vary with fish SL. For all fin ray counts, total numbers of branched and unbranched rays were used.

Data Analyses

Comparative analyses were performed between South Carolina and the Laurentian Great Lakes (lakes Erie and Huron combined) as well as between lakes Erie and Huron. An additional preliminary analysis was conducted to compare five lowland samples from SC with a relatively more upland sample studied by Clifford (2014). For individual morphometric characters, ANCOVA with SL as covariate (e.g., Fig. 3) was used to determine whether statistically significant differences existed between populations. Pair-wise comparisons of population meristic data were done with non-parametric Mann-Whitney U-tests. For all statistical tests, a p-value of 0.05 or less was considered a significant difference. Additionally, PCA (using correlation matrices) were performed incorporating only those morphometric and meristic characters that were found to significantly differ in individual character analyses. The statistical package PAST (Ver. 3.06; Hammer et al., 2001) was used for ANCOVA, Mann-Whitney U-tests, and PCA.

Results

South Carolina versus Great Lakes

Between our five lower coastal plain sites in South Carolina and the Great Lakes, 15 morphometric characters were found to differ significantly (Fig. 3, Table 1). Bowfins from South Carolina were found to have a greater dorsal fin base length, caudal peduncle length, head length, width between posterior nostrils, and orbit diameter. Bowfins from the Great Lakes, in contrast, were found to have a greater pelvic fin length, pre-pectoral fin distance, pectoral fin length, head depth, interorbital width, post-orbital distance, length of gular plate, posterior nostril diameter, longest dorsal fin ray, and longest anal fin ray.

Between lowland sites in South Carolina and the Great Lakes, five meristic characters were found to differ significantly (Table 1). Bowfins from South Carolina were found to have, on average, a greater number of dorsal fin rays, lateral line scales, total branchiostegal rays, and scales between the pelvic fin origin and lateral line. Bowfins from the Great Lakes were found to have a greater number of pelvic fin rays on average, but that was entirely due to higher counts in L. Huron, but not in L. Erie.

Principal components analysis of the 15 morphometric and five meristic characters that differed showed minimal overlap between 95% confidence ellipses (Fig. 4). Component 1 explained 30.44 % of the variance in our data, with 18.91 % explained by component 2, 7.84 % by component 3, and 7.01 % by component 4. The percent variance explained by the first four components totaled 64.20 %.

Lake Erie versus Lake Huron

Between lakes Erie and Huron, 13 morphometric characters were found to differ significantly (Fig. 5, Table 2). Bowfins from Lake Erie were found to have a greater length to caudal origin, pelvic fin length, pelvic fin origin to pectoral fin origin, head width, interorbital width, width between posterior nostrils, snout length, fourth infraorbital length, length of upper jaw, and length of lower jaw. Bowfins from Lake Huron, in contrast, were found to have a greater caudal peduncle depth, caudal peduncle length, and pre-pectoral fin distance.

Between lakes Erie and Huron, two meristic characters were found to differ significantly (Table 2). Bowfins from Lake Erie were found to have, on average, a greater number of lateral line scales, while Bowfins from Lake Huron had a greater average number of pelvic fin rays.

Principal components analysis of the 13 morphometric and two meristic characters that differed showed moderate overlap between 95% confidence ellipses (Fig. 6). Component 1 explained 42.60 % of the variance in the data, with 13.22 % explained by component 2, 11.34 % by component 3, and 6.28 % by component 4. The total percent variance explained by the first four components totaled 73.44 %.

South Carolina Lower versus Upper Coastal Plains

Between Bowfins from the lower (<18 m altitude) and upper coastal plain (approx. 60-80 m altitude) regions of South Carolina, at least 10 morphometric characters were found to differ significantly (Fig. 7, Table 3). Bowfins from the lower coastal plain were found to have a greater orbit diameter, longest anal fin ray, pelvic fin length, dorsal fin base length, snout length, and pectoral fin length. Bowfins from the upper coastal plains, in contrast, were found to have a greater interorbital width, pre-pectoral fin distance, width of premaxillary tooth row, and width between anterior nostrils.

Between those lowland and slightly more upland regions of South Carolina, five meristic characters were found to differ significantly (Table 3). Bowfins from the lowland region were found to have, on average, a greater number of dorsal fin rays, anal fin rays, and pectoral fin rays; Bowfins from the upland region were found to have on a greater average number of scales above the lateral line and scales between the pelvic fin origin and lateral line.

Principal components analysis of the 10 morphometric and five meristic characters that differed showed moderate overlap (comparable to that found between lakes Erie and Huron) between 95% confidence ellipses (Fig. 8). Component 1 explained 25.13 % of the variance in the data, with 18.65 % explained by component 2, 9.32 % by component 3, and 8.90 % by component. The total percent variance explained by the first four components totaled 62.00 %.

Discussion and Conclusions

Based on the findings of multiple, significant morphological differences and little overlap in the principal components analysis between lowlands of South Carolina and the Great Lakes, I reject the monotypy hypothesis for the genus *Amia*. Rejection of the monotypy hypothesis further supports the arguments put forth in the 1800's by Cuvier and Valenciennes (1847) and Duméril (1870), and supported more recently by Bermingham and Avise (1986), Clifford (2014), and Clark (2015), that multiple species of Bowfins exist.

The Bowfins sampled from the five lowland locations within South Carolina did not show morphological variation beyond what would be expected at the population level, and all overlapped broadly with topotypical specimens from Schultz Lake (Fig. 8). Close proximity and drainage connection of Schultz Lake to the type locality of *A. calva* leads me to infer that all of the South Carolina lowland samples most likely consisted of *A. calva*.

The second described species of Bowfin is *A. ocellicauda*, which has its type locality in close proximity to the OMNR sampling area in Georgian Bay, ON. The holotype for that nominal taxon was lost in transit, so I propose to designate a neotype from among the freshly collected topotypes to stabilize the taxonomy. *Amia occidentalis* was the third described species (from the St. Mary's River, a northern tributary to Lake Huron); there are no physical barriers to migration between those two type localities, which are just over 300 km apart. Morphological characteristics of the single topotypical specimen of *A. occidentalis* that I was able to study indicated close similarity to topotypical specimens of *A. ocellicauda*, so it seems likely that these two nominal taxa will be synonyms. The holotype of *A. occidentalis* also has been lost, so likewise, it will be necessary to designate a neotype to clearly establish identity of these two nominal forms. Freshly collected specimens that could serve as neotypes for these two nominal taxa are now deposited in the Royal Ontario Museum. Still, it would be desirable to have a larger population sample from the St. Mary's River before drawing final taxonomic conclusions.

The identity of the population sampled from Lake Erie remains uncertain. Fewer individual characters differed between fishes from lakes Erie and Huron than between South Carolina and the Great Lakes, and there was more overlap in the 95% confidence ellipses from the PCA. The percent variance explained by the first four components, however, was greater for Erie versus Huron than for lower coastal plains of South Carolina versus Great Lakes. Ultimately, it is not clear whether the Lake Erie and Lake Huron populations are distinct enough to be considered separate species. Morphological patterns, for example, could potentially represent a N-S cline influenced by a temperature gradient, in which case, the name *A. occellicauda* could apply to Bowfins from L. Erie and also perhaps the Mississippi basin.

If the Lake Erie population is in fact a separate species from *A. calva* and *A. ocellicauda* (+*occidentalis*), it is still unclear which nominal species it might be. Both *A. canina* (holotype lost) and one of two syntypes of *A. piquotii* were described from Lake Erie (Fig. 1), which increases our uncertainty. To further complicate matters, the fourth described nominal Bowfin is *A. marmorata* from the lower Mississippi basin near New Orleans, and the fifth and sixth nominal taxa are also from the Mississippi drainage (Fig. 1). It is possible (or even plausible) that a taxon from the Mississippi drainage also is distributed northward into L. Erie, but not farther north or east of there. Following glacial retreat approximately 10,000–11,000 years ago, Bowfins and many other fishes recolonized the Great Lakes from the Mississippi River basin (Bailey and Smith, 1981). The Spotted Gar (*Lepisosteus oculatus*) is distributed along the Gulf Coast and Mississippi River, and its natural range extends northward only into southern L. Michigan and L. Erie within the Great Lakes (Warren and Burr, 2014). For Spotted Gar, there is evidence for variation in growth patterns influenced by the N-S gradient in temperature (David et al., 2015). Thus, broad comparisons between Bowfins from the Mississippi and L. Erie basins will be necessary to resolve taxonomic identity of Lake Erie Bowfins with reasonable certainty.

It also should be noted that although a set of five samples were spread widely over some 250 km of lower coastal plain habitats of South Carolina (Fig. 2), and all of those fishes might be considered *A. calva*, there is evidence for a possible second species of Bowfin in South Carolina (e.g., Figs. 7 and 8). If further analyses of existing and future collected specimens give added support for a second species, then the task is to determine which (if any) of the available nominal taxa most closely matches that population. As with L. Erie, first considerations need to go to the earliest described nominal taxa, including those from the Mississippi basin. In that context, Bermingham and Avise (1986) found that Bowfins from the Gulf Coast and lower Mississippi were genetically distinct from southeast coast fishes, which is perhaps a first clue that Bowfin names proposed for Mississippi (and Great Lakes?) fishes might not apply to South Carolina. Both *A. lintiginosa* and *A. cinerea* were described from South Carolina (the eighth and tenth nominal taxa, respectively), and it is possible that one or both of those nominal species could have been collected from the upper coastal plain. Such habitats are just over 100 km inland from Charleston Harbor.

Genetic Evidence for Bowfin Diversity

The limited studies on Bowfin genetics reveal some interesting patterns that require further study. In addition to an east-west genetic discontinuity at the Apalachicola River basin (mentioned above), Bermingham and Avise (1986) found that Bowfins from Florida showed small but consistent genetic differences from those in Georgia and South Carolina, and also were different from the Gulf Coast populations. The SC localities that they sampled appear to be from upper coastal plain habitats, so it is possible that they never studied topotypical *A. calva* from the lower coastal plains. Clark (2015), in contrast, compared samples from the lowlands to others from North Carolina and the Great Lakes. She found the SC and Great Lakes samples were most strongly differentiated, and thus, similar to my morphometric results, and NC modestly so versus SC (I did not analyze NC fishes). Clark (2015) did not have any genetic samples from upland habitats of SC. She noted, however, that the mitochondrial gene COI showed a relatively low level of divergence, compared to what one often finds, for example, with species of advanced teleosts. In future studies, genetic markers showing greater variation at the species level will be useful for distinguishing among closely related taxa.

Implications for Conservation, Management, and Future Directions

While this study has moved our understanding of the diversity in the genus *Amia* forward by rejecting the monotypy hypothesis from 1896, much research remains to be done to resolve the taxonomy of Bowfins. As previously mentioned, the statuses of Bowfins from L. Erie, the Mississippi River basin (particularly areas surrounding New Orleans, LA), the Gulf Coast, Florida, upland South Carolina, and North Carolina are still unclear. Similarly, Bowfins from Lake Champlain need further study as *A. thompsonii* was described from there, and there are various examples of fish species with range boundaries at Niagara Falls or in western to central New York (e.g., Smith, 1985).

It is of utmost importance that we reach an accurate understanding of the true nature of Bowfin diversity, whether it be distinguishing multiple species or uniquely adapted localized populations (e.g., evolutionarily significant units, ESU's; Moritz, 1994). As members of Holostei, Bowfins are among the most closely related fishes to the Teleostei (Grande, 2010), which includes about 96% of extant fish species (Nelson, 2006). Bowfins are thus often used as a standard out- or sister-group when constructing phylogenies to improve our understanding of evolutionary relationships among teleosts, and in that regard, it is imperative that we fully understand the taxonomy of Bowfins. A broader perspective on intra- and inter-population variation in morphology of living Bowfins also can contribute to resolving the taxonomy of fossil amiiform fishes, which can be found throughout the world (Grande and Bemis, 1998)

Recognizing the diversity of Bowfins is also a time-sensitive issue due to the relatively recent development and growth of a market for Bowfin caviar (e.g., Clifford, 2014). As with any fishery, there is potential for over-exploitation, but when harvesting fishes for caviar threats are compounded by targeting a vulnerable life-stage – gravid females. Additionally, this market is increasingly using aquaculture to raise and harvest Bowfins as the demand for their caviar grows; an increase in aquaculture will surely lead to an increase in translocations (Koch et. al., 2009). With this, the need to recognize the diversity of Bowfins becomes urgent from a management perspective. We need to formulate effective policies regarding wild harvests as well as translocations, because cultured fishes often escape and then mix with local wild populations. This can ultimately result in the loss of genetic diversity through introgressive hybridization, mortality from transfer of diseases, and other detrimental effects on wild populations. If there are species (or ESU's) with geographically restricted ranges, overharvest of spawning females could even lead to extinction. Until recently, Bowfins have not been of commercial interest, so most populations remain in relatively undisturbed condition – notwithstanding destruction of wetland habitats and introductions of possible exotic competitors like snakeheads (*Channa* spp.) – but time to act is running short.

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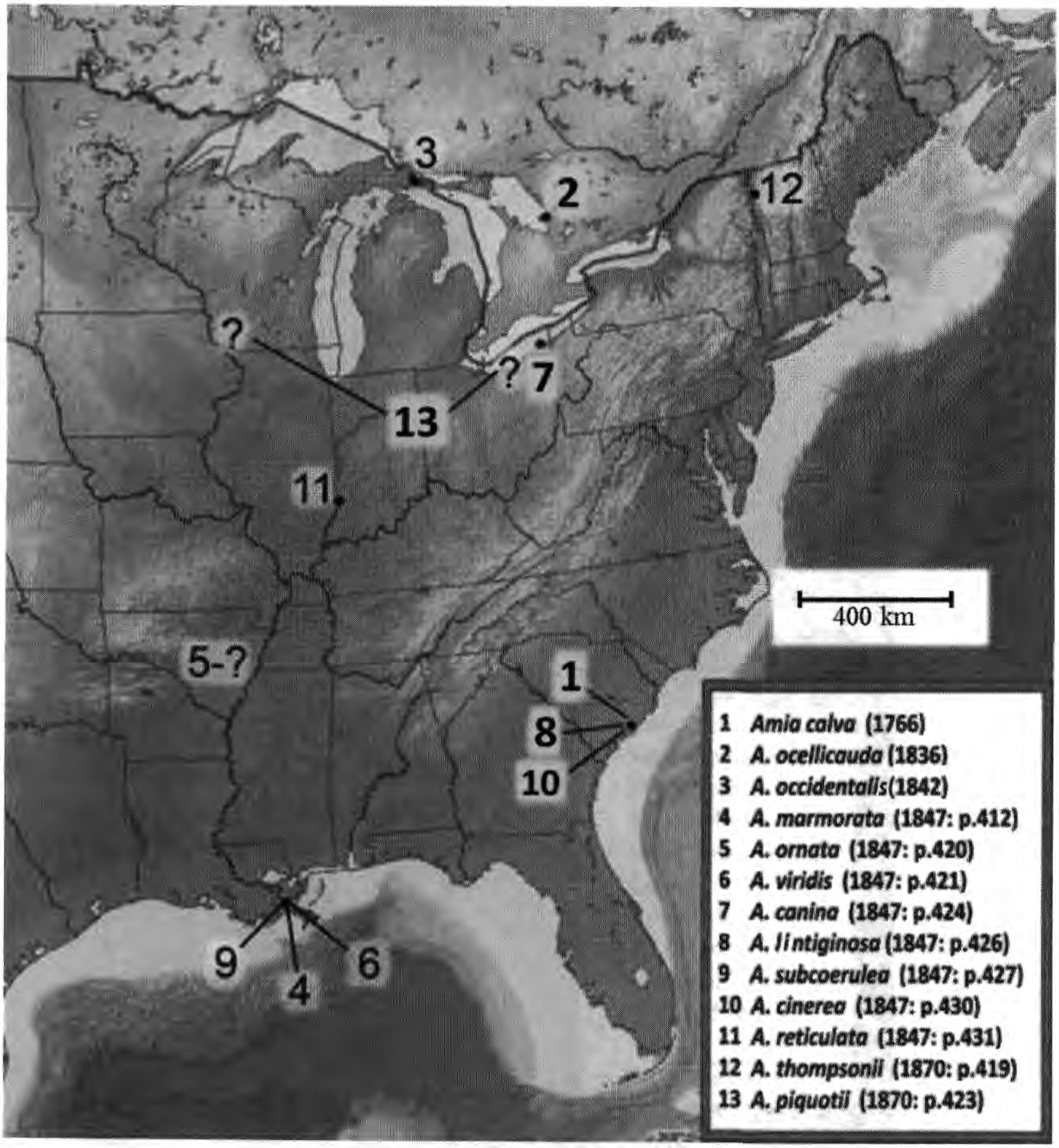

Figure 1. Locations of nominal species of *Amia* (in chronological order by year of publication, and within year, by page in the publication); those emphasized in this study are highlighted in yellow (modified from Clifford, 2014).

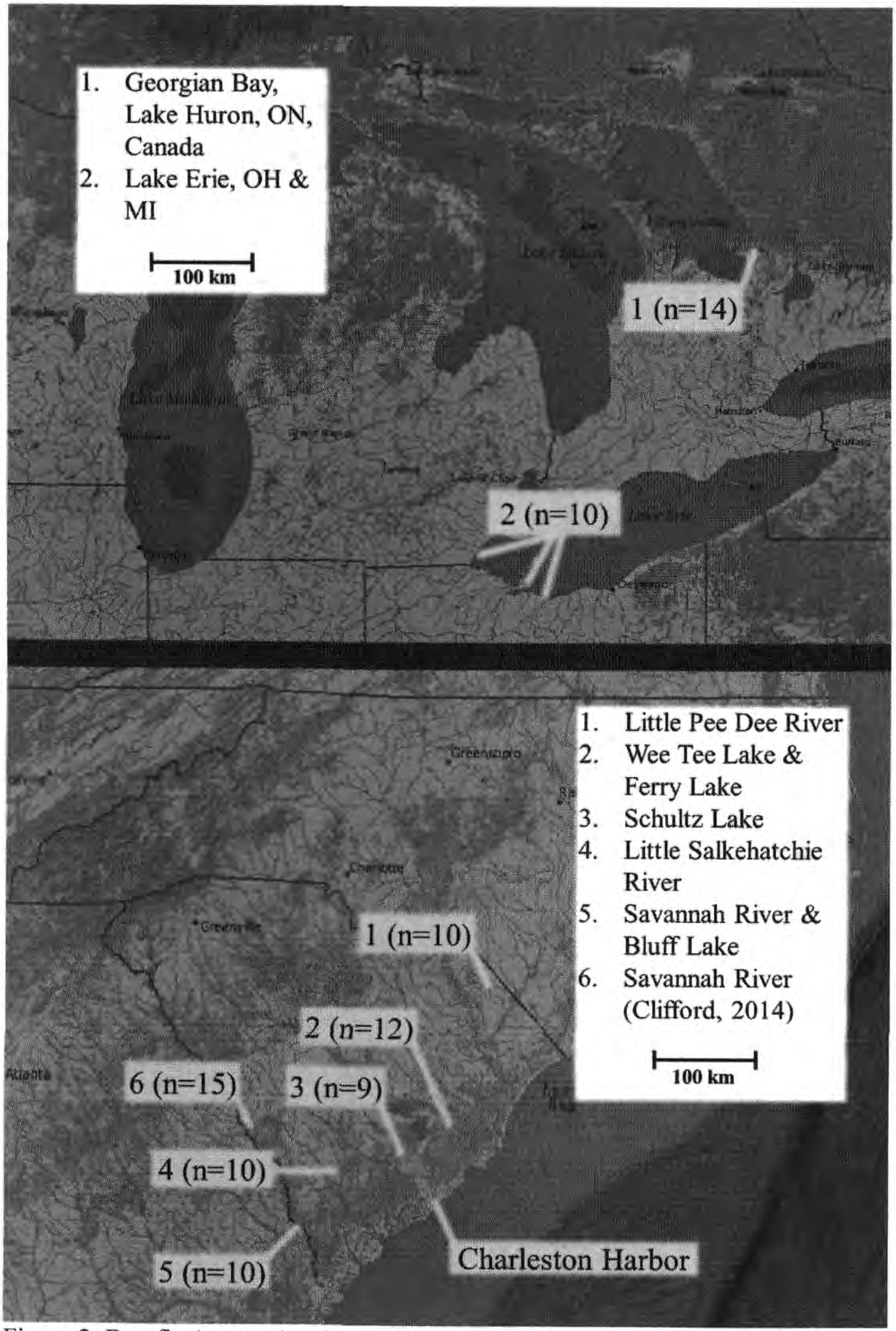

Figure 2. Bowfin (genus *Amia*) sampling locations from Lake Huron, Lake Erie, and various sites within South Carolina, with associated sample sizes in parentheses.

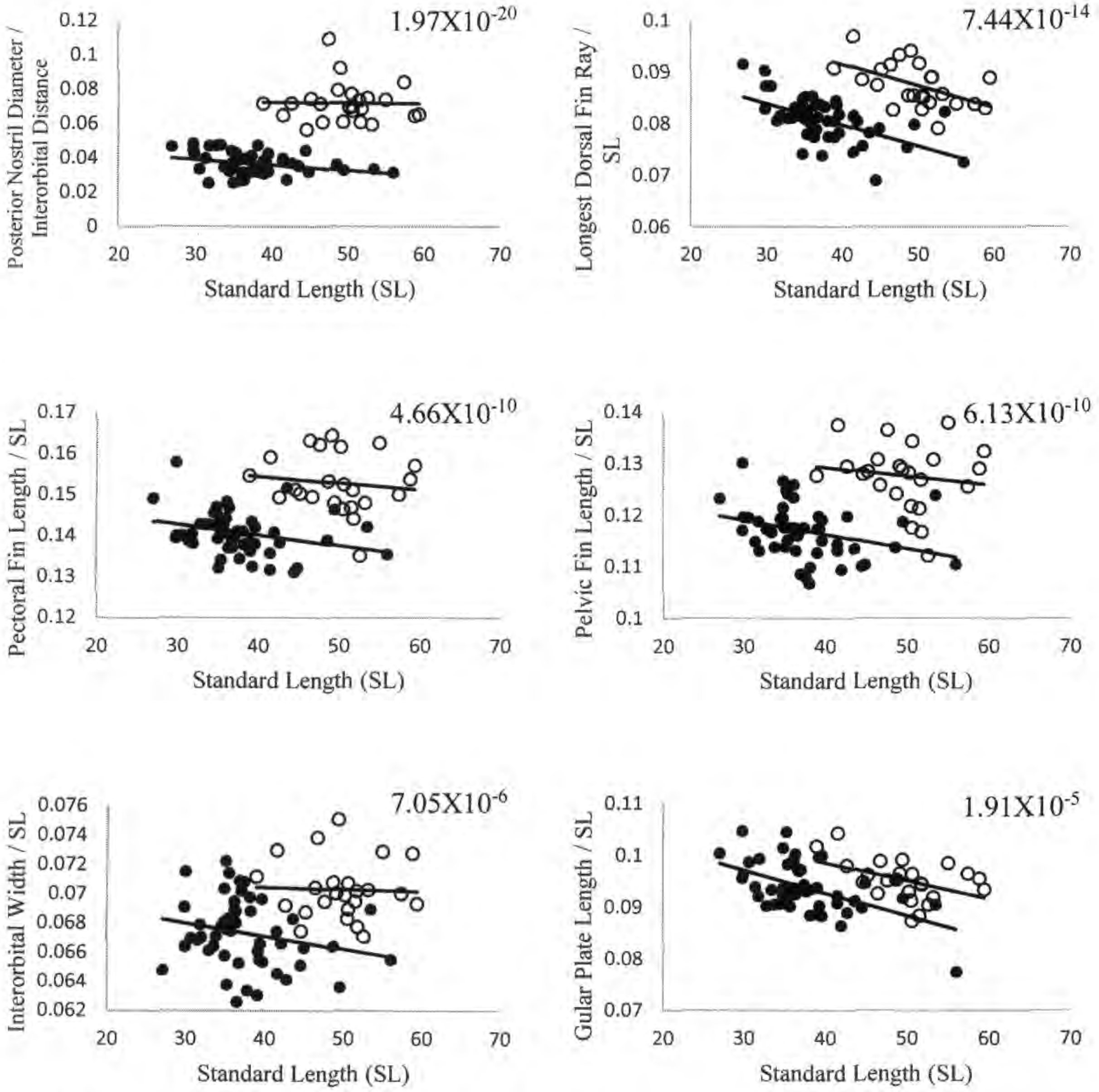

Figure 3. Bivariate plots of six most significantly different morphometric characters between lower coastal plains of South Carolina (solid circles) and the Great Lakes (lakes Huron and Erie combined, open circles) and associated P-values from ANCOVA.

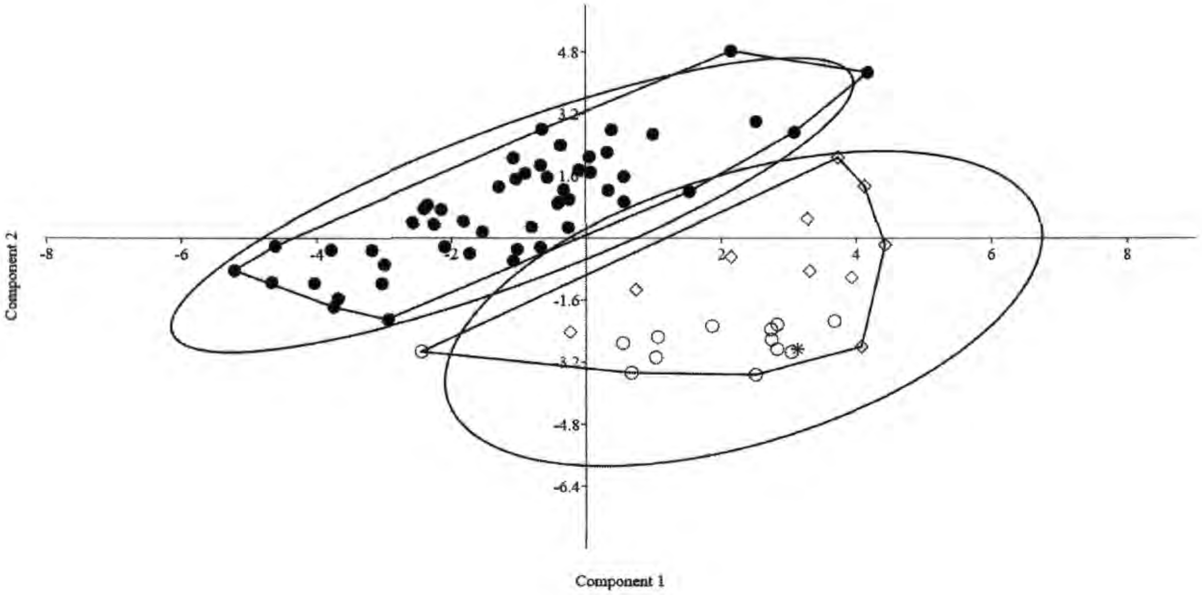

Figure 4. Principal components analysis (using correlation matrix) with 95% confidence ellipses (and convex hull outlines) based on 15 morphometric and five meristic characters that differed significantly between South Carolina (solid circles) and lakes Erie (open diamonds) and Huron (open circles). Possible neotype of *A. ocellicauda* indicated with star.

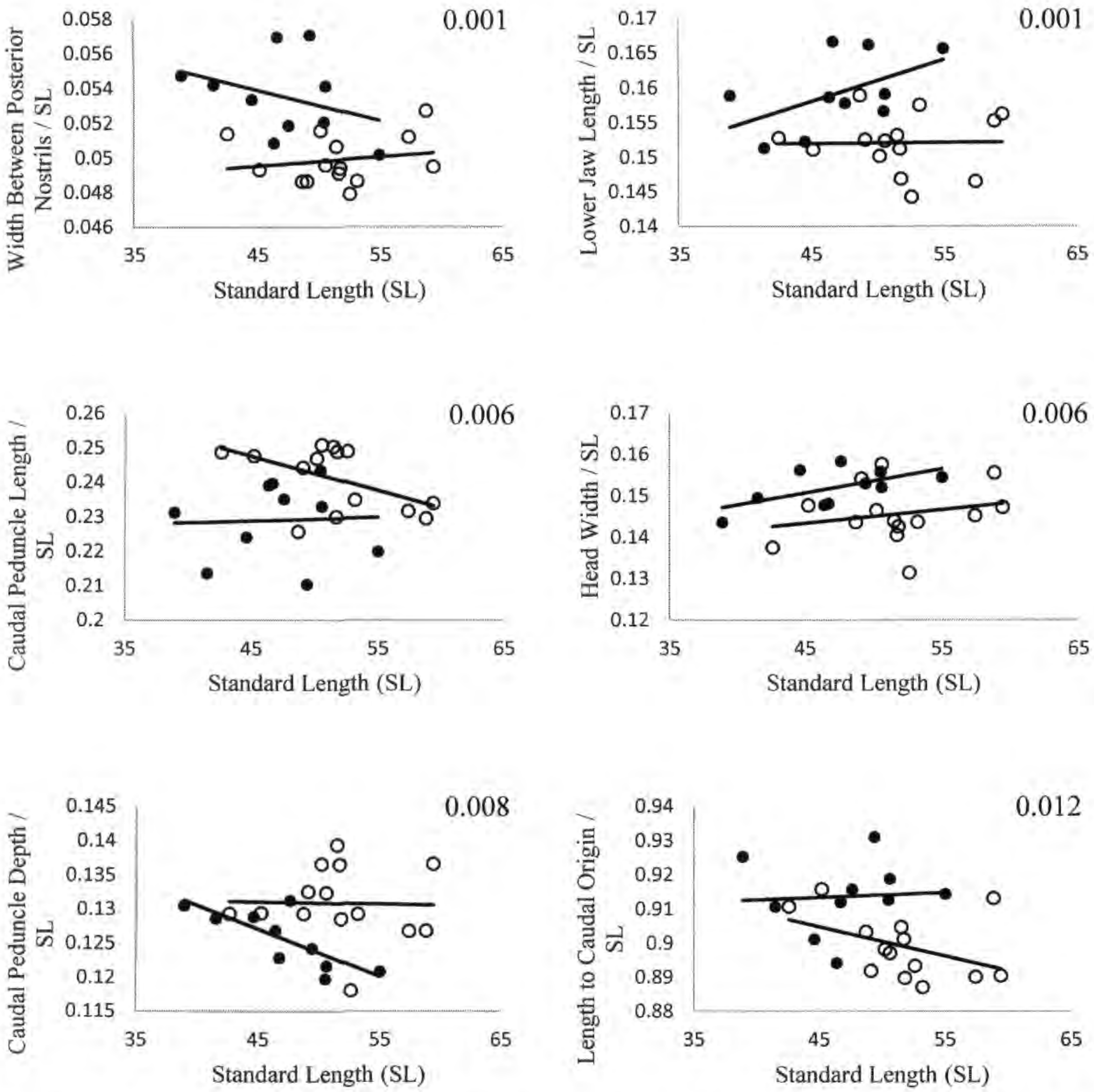

Figure 5. Bivariate plots of significantly differing morphometric characters between lakes Erie (solid circles) and Huron (open circles) and associated P-values from ANCOVA.

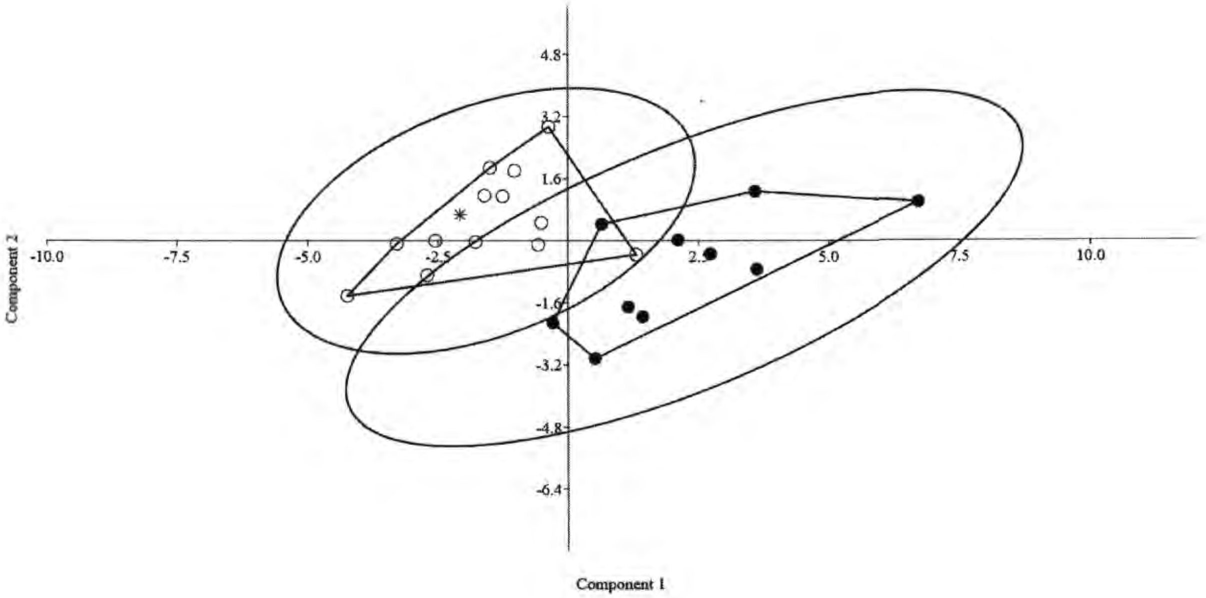

Figure 6. Principal components analysis (using correlation matrix) with 95% confidence ellipses (and convex hull outlines) based on 13 morphometric and two meristic characters that differed significantly between Lake Erie (solid circles) and Lake Huron (open circles). Possible neotype of *A. ocellicauda* indicated with star.

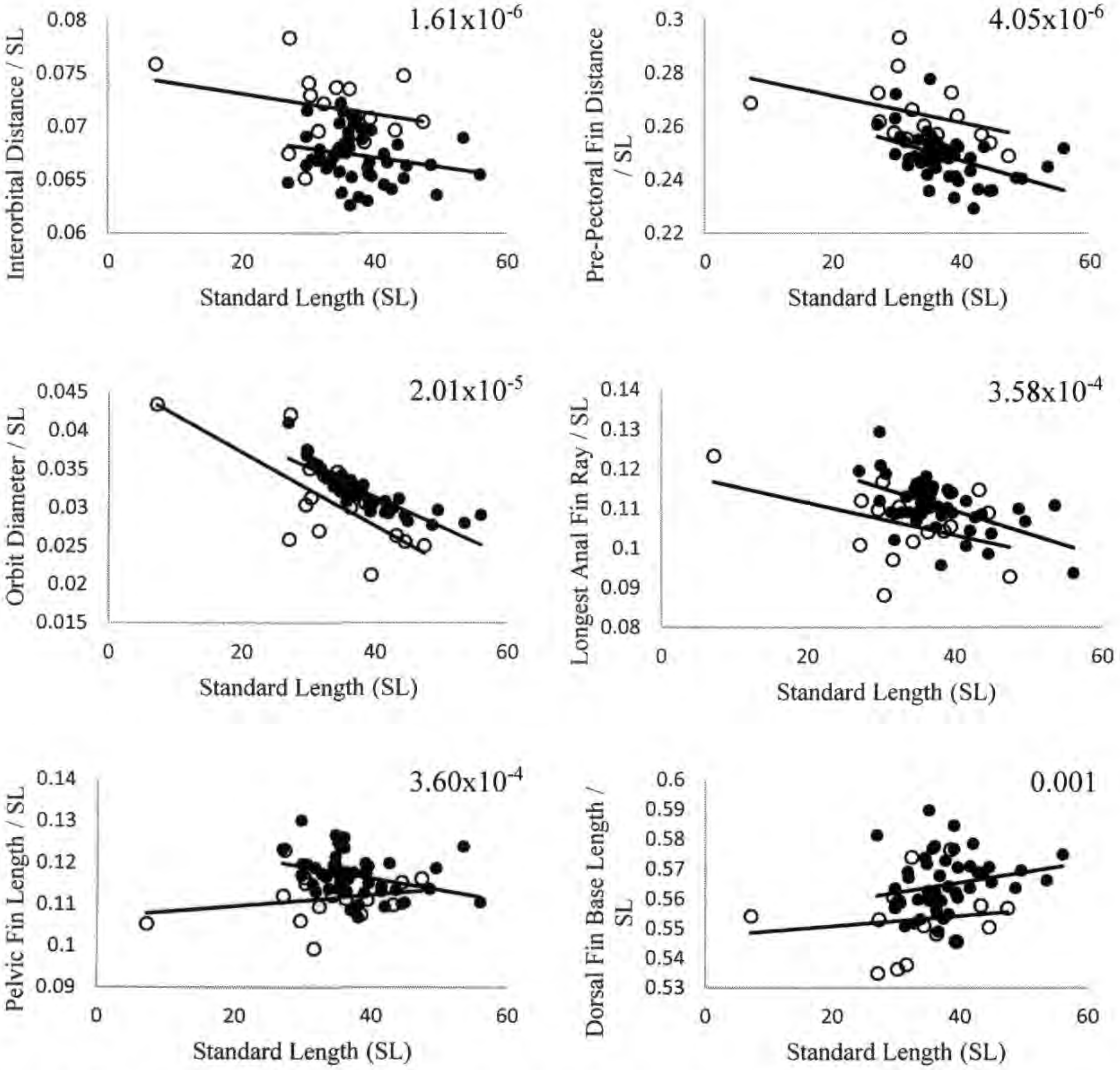

Figure 7. Bivariate plots of six most significantly differing morphometric characters (from preliminary analysis) between lower coastal plain (*A. calva*, solid circles) and upper coastal plain (Clifford, 2014, open circles) habitats in South Carolina and associated P-values from ANCOVA.

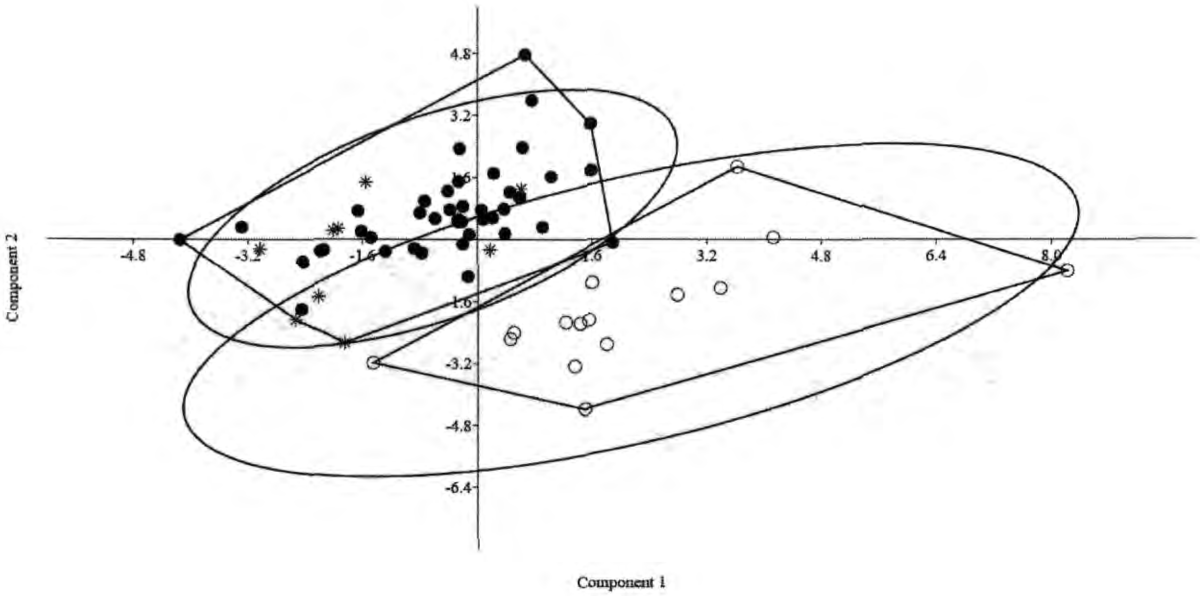

Figure 8. Principal components analysis (using correlation matrix) with 95% confidence ellipses (and convex hull outlines) based on ten morphometric and five meristic characters that differed significantly between lower coastal plain (solid circles/stars) and upper coastal plain (open circles) habitats in South Carolina. Sample of typotypical specimens of *A. calva* from Schultz Lake indicated by stars.

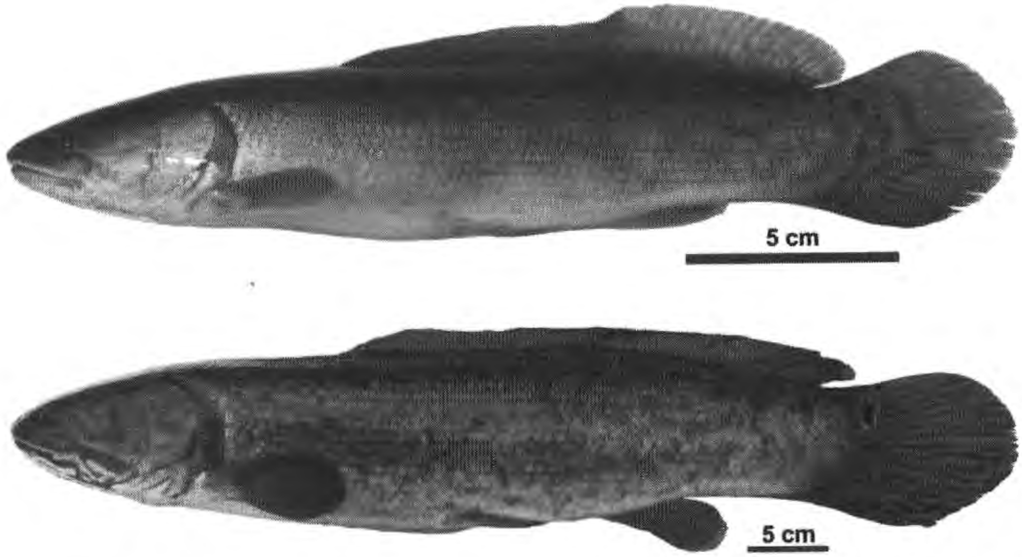

Figure 9. Lateral views of *Amia calva* (top, with caudal fin deep red from top to bottom, and whitish belly; total length = 39.0 cm), and *Amia ocellicauda* (bottom, with dark green paired fins, caudal fin and belly typical of a breeding male; total length = 60.9 cm).

Figure 10. Caudal fin of a large adult *Amia calva* (total length = 75 cm); from Little Pee Dee Rive, SC.

Figure 11. Bald Cypress swamp surrounding Bluff Lake, SC; typical of lower coastal plains habitats for Bowfins.

Table 1. Statistically different individual morphometric (top) and meristic (bottom) characters and associated P-values from ANCOVA's (standard length as covariate) and Mann-Whitney U-Tests from comparisons between lowlands of South Carolina (n=51) versus lakes Erie and Huron combined (n=24).

Morphometric Character	**P-Value**
Posterior Nostril Diameter/Interorbital Width	1.97E-20
Longest Dorsal Fin Ray	7.44E-14
Pectoral Fin Length	4.66E-10
Pelvic Fin Length	6.13E-10
Interorbital Width	7.05E-06
Gular Plate Length	1.91E-05
Pre-Pectoral Fin Distance	1.92E-05
Orbit Diameter	3.40E-05
Longest Anal Fin Ray	9.25E-05
Head Length	0.001
Caudal Peduncle Length	0.005
Dorsal Fin Base Length	0.005
Head Depth	0.006
Post-Orbital Distance	0.008
Width Between Posterior Nostrils	0.009

Meristic Character	**P-Value**
Lateral Line Scales	5.39E-08
Dorsal Fin Rays	6.01E-07
Pelvic Fin Rays	1.59E-06
Scales Between Pelvic Origin and Lateral Line	0.001
Total Branchiostegal Rays	0.009

Table 2. Statistically different individual morphometric (top) and meristic (bottom) characters and associated P-values from ANCOVA's (standard length as covariate) and Mann-Whitney U-Tests from comparisons between Lake Erie (n=10) and Lake Huron (n=14).

Morphometric Character	**P-Value**
Width Between Posterior Nostrils	0.001
Lower Jaw Length	0.001
Caudal Peduncle Length	0.006
Head Width	0.006
Caudal Peduncle Depth	0.008
Length to Caudal Origin	0.012
Pelvic Origin to Pectoral Origin	0.016
Upper Jaw Length	0.018
4th Infraorbital Length	0.033
Pelvic Fin Length	0.034
Interorbital Width	0.037
Snout Length	0.043
Pre-Pectoral Fin Distance	0.048

Meristic Character	**P-Value**
Pelvic Fin Rays	6.04E-05
Lateral Line Scales	0.010

Table 3. Statistically different individual morphometric (top) and meristic (bottom) characters and associated P-values from ANCOVA's (standard length as covariate) and Mann-Whitney U-Tests from comparisons between lower (n=51) and upper (n=15) coastal plain habitats in South Carolina.

Morphometric Character	**P-Value**
Interorbital Width	1.61E-06
Pre-Pectoral Fin Distance	4.05E-06
Orbit Diameter	2.01E-05
Longest Anal Fin Ray	3.58E-04
Pelvic Fin Length	3.60E-04
Dorsal Fin Base Length	0.001
Snout Length	0.002
Width of Premaxillary Tooth Row	0.002
Pectoral Fin Length	0.003
Width Between Anterior Nostrils	0.003

Meristic Character	**P-Value**
Scales Between Pelvic Origin and Lateral Line	1.80E-04
Anal Fin Rays	0.001
Scales Above Lateral Line	0.003
Dorsal Fin Rays	0.013
Pectoral Fin Rays	0.029

Table 4. Frequency distributions of counts for meristic characters for Bowfins from lower coastal plains sites in South Carolina, Lake Erie, and Lake Huron, with modal values in bold. Values for *A. calva* holotype indicated with asterisks (*) where comparable data are available.

Dorsal Fin Rays	48	49	50	51	52
South Carolina		7	20	**21**	3
Lake Erie	**4**	**4**	1	1	
Lake Huron	**7**	3	2	2	

Anal Fin Rays	9	10	11	12	13
South Carolina	1	**29**	17*	3	1
Lake Erie		4	**6**		
Lake Huron		4	**8**	2	

Pelvic Fin Rays	6	7	8
South Carolina	1	**50**	
Lake Erie	1	**9**	
Lake Huron		2	**12**

Lateral Line Scales	63	64	65	66	67	68	69	70	71	72
South Carolina				2	7	13	**18**	9	2	*
Lake Erie				2	**4**	3	1			
Lake Huron	1	2	3	3	**4**	1				

Scale Above Lateral Line	8	9	10
South Carolina	17	**32**	2*
Lake Erie	**8**	2	
Lake Huron	**8**	3	3

Total Branchiostegal Rays	20	21	22	23	24	25	26
South Carolina		3	6	**20**	13	7	2
Lake Erie	1	1	**4**	**4**			
Lake Huron		1	**4**	**4**	**4**	1	

Pectoral Fin Rays	16	17	18	19	20
South Carolina	8*	**32**	10		1
Lake Erie	3	**4**	2	1	
Lake Huron	2	**6**	5	1	

Scales Between Lateral Line and Pelvic Origin	10	11	12	13	14	15
South Carolina	1	5	**31**	14		*
Lake Erie		2	**8**			
Lake Huron		**8**	5	1		

Appendix 1: Sampling Locations

South Carolina

Little Pee Dee River, South Carolina; 33.83161, -79.24972; boarder of Horry and Marion Counties; 11.5 miles west of Conway, SC; 3.7 meters above sea level; 11 August 2014.

Wee Tee Lake, South Carolina; 33.38581, -79.77649; Williamsburg County; Wee Tee State Forest; 8.5 miles east of St. Stephen, SC; 2.6 meters above sea level; 30 July 2014.

Ferry Lake, South Carolina; 33.32583, -79.68765; Williamsburg County, Wee Tee State Forest; 2.75 miles north of Jamestown, SC; 1.2 meters above sea level; 1 August 2014.

Schultz Lake, South Carolina; 32.97239, -80.27346; Dorchester County; 3.5 miles southwest of Knightsville, SC; 13.0 meters above sea level; 10 July 2014 & 15 August 2014.

Little Salkehatchie River, South Carolina; 32.989623, -80.870158; Colleton County; 13 miles northwest of Walterboro, SC; 18.0 meters above sea level; 14 August 2014.

Bluff Lake, South Carolina; 32.57386, -81.31239; Hampton County; James W. Webb Wildlife Center and Management Area; 4.5 miles southwest of Garnett, SC; 8.4 meters above sea level; 12 August 2014.

Savannah River and backwaters, South Carolina; 32.55777, -81.28524; Hampton County; 4.15 miles south-southwest of Garnett, SC; 7.7 meters above sea level; 12 August 2014.

Lake Erie

East Harbor, Lake Erie, Ohio; 41.54464, -82.801345; Erie County; East Harbor State Park; 7.5 miles east northeast of Port Clinton, OH.; 27 October 2014.

Brest Bay, Lake Erie, Michigan; 41.921333, -83.335907; Monroe County; Sterling State Park; Located on edge of Lake Erie directly east of Monroe, MI.; 10 September 2014.

Sheldon Marsh, Lake Erie, Ohio; 41.42409, -82.61838; Erie County; Sheldon Marsh State Nature Preserve; 5 miles east-southeast of Sandusky, OH; 26 June 2014.

Lake Huron

Severn sound, Georgian Bay, Ontario; 44.7878, -79.7396; 1.2 miles south of Port Severn, ON, Canada; 27 May 2014.

Severn Sound, Georgian Bay, Ontario; 44.7896, -79.7586; 1.6 miles southwest of Port Severn, ON, Canada; 27 May 2014.

Severn Sound, Georgian Bay, Ontario; 44.8645, -79.8616; 2.2 miles west of Honey Harbour, ON, Canada; 28 May 2014.

Severn Sound, Georgian Bay, Ontario; 44.8691, -79.8455; 1.4 miles west of Honey Harbour, ON, Canada; 28–29 May 2014.

St. Mary's River, Ontario; 46.325535, -84.071964; near Pine Island 2.4 miles southeast of Neebish, ON, Canada; August 2014.

Appendix 2: Morphometric Measurements

Standard Length	Anterior tip of snout to posterior tip of lateral line on caudal fin base
Length to Caudal Origin	Anterior tip of snout to anterior origin of caudal fin on the ventral midline
Pre-Anal Fin Distance	Anterior tip of snout to anterior origin of anal fin base
Pre-Dorsal Fin Distance	Anterior tip of snout to anterior origin of dorsal fin base
Dorsal Fin Base Length	Anterior origin of dorsal fin base to posterior end of dorsal fin base
Longest Dorsal Fin Ray	Dorsal fin ray from its base to distal tip of ray
Anal Fin Base Length	Anterior origin of anal fin base to posterior end of anal fin base
Longest Anal Fin Ray	Anal Fin ray from its base to distal tip of ray
Anal Base to Caudal Flex	Posterior end of anal fin base to anterior origin of caudal fin on ventral midline
Caudal Peduncle Depth	Posterior end of dorsal fin base vertically to ventral margin of peduncle, including posteriorly reflexed procurrent caudal fin rays.
Caudal Peduncle Length	Posterior end of anal fin base to posterior end of lateral line on caudal fin base
Pre-Pelvic Fin Distance	Anterior tip of snout to anterior origin of pelvic fin base
Pelvic Fin Length	Anterior origin of pelvic fin base to distal tip of pelvic fin
Pelvic Fin Interspace	Width between anterior origins of left and right pelvic fin bases
Pelvic Origin to Center Anus	Anterior origin of pelvic fin base to center of anus
Body Depth at Pelvic Origin	Center point on belly between pelvic fin origins to dorsal fin base (measured vertically perpendicular to anterior-posterior axis of fish)
Pelvic Fin Origin to Dorsal Fin Origin	Anterior origin of pelvic fin base to anterior origin of dorsal fin base
Pelvic Fin Origin to Pectoral Fin Origin	Anterior origin of pelvic fin base to anterior origin of pectoral fin base
Pre-Pectoral Fin Distance	Anterior tip of snout to anterior origin of pectoral fin base
Pectoral Fin Length	Anterior origin of pectoral fin base to distal tip of pectoral fin
Head Length	Anterior tip of snout to posterior fleshy margin of opercular flap
Head Depth	Top of head at occiput to ventral margin of head (measured vertically perpendicular to anterior-posterior axis)
Head Width	Maximum distance across opercula
Interorbital Width	Minimum distance between bony dorsal margins of left and right orbits
Width Between Anterior Nostrils	Width between left and right anterior nostrils (measured at centers of tube bases)
Width Between Posterior Nostrils	Width between left and right posterior nostrils (measured at centers of nostrils)
Orbit Diameter	Maximum distance between bony rims of orbit (along anterior-posterior axis)
Snout Length	Anterior tip of snout to anterior rim of orbit
Post-Orbital Distance	Posterior orbital rim to posterior fleshy margin of opercular flap
Fourth Infraorbital Length	Anterior [at orbital rim] to posterior margin of 4th infraorbital (maximum distance)
Width of Mouth	Width between lateral margins of dentaries (where maxilla overlaps dentary)
Length of Upper Jaw	Anterior tip of upper jaw [midline of pre-maxillary] to distal tip of maxilla
Length of Lower Jaw	Anterior tip to posterior tip of lower jaw
Width of Pre-Maxillary Tooth Row	Distance between lateral margins of left- and right-most teeth on premaxilla
Length of Gular Plate	Anterior to posterior tip of gular plate, measured along mid-line
Width of Gular Plate	Maximum distance across gular plate (measured perpendicular to anterior-posterior axis of gular plate)
Posterior Nostril Diameter	Maximum distance between interior fleshy margins of posterior nostril (usually occurring along anterior-posterior axis)

Appendix 3: Data Sheet

BOWFIN PROJECT	LOCALITY					
Photos						
Station Number						
Specimen Number						
CHARACTER						
DATA COLLECTION DATE						
SEX						
WEIGHT (Pounds)						
TOTAL LENGTH						
STANDARD LENGTH						
LENGTH TO CAUDAL ORIGIN						
PRE-ANAL FIN DISTANCE						
PRE-DORSAL FIN DISTANCE						
DORSAL FIN BASE LENGTH						
LONGEST DORSAL FIN RAY						
ANAL FIN BASE LENGTH						
LONGEST ANAL FIN RAY						
DORSAL BASE TO CAUDAL FLEX						
ANAL BASE TO CAUDAL FLEX						
CAUDAL PEDUNCLE DEPTH						
CAUDAL PEDUNCLE LENGTH						
PRE-PELVIC FIN DISTANCE						
PELVIC FIN LENGTH						
PELVIC FIN INTER-SPACE						
PELVIC ORIGIN TO CENTER ANUS						
BODY DEPTH AT PELVIC ORIGIN						
PELVIC FIN ORIGIN TO DORSAL FIN ORIG.						
PELVIC ORIGIN TO PECTORAL ORIG.						
PRE-PECTORAL FIN DISTANCE						
PECTORAL FIN LENGTH						
HEAD LENGTH (to tip opercular flap)						
SKULL LENGTH						
HEAD DEPTH AT OCCIPUT						
HEAD WIDTH (greatest, across operculi)						
INTERORBITAL WIDTH						
WIDTH BETWEEN ANTERIOR NOSTRILS						
WIDTH BETWEEN POSTERIOR NOSTRILS						
ORBIT DIAMETER						
SNOUT LENGTH						
PRE-ORBITAL DISTANCE						
POST-ORBITAL DISTANCE						
4TH INFRAORBITAL LENGTH						
WIDTH OF MOUTH (to rictus)						
LENGTH OF THE UPPER JAW						
LENGTH OF THE LOWER JAW						
WIDTH OF PRE-MAXILLARY TOOTH ROW						
Length of gular plate						
Width of gular plate						
Width between mandibles post end gular						

BOWFIN PROJECT						
Photos						
Station Number						
Specimen Number						
CHARACTER						
CAUDAL FIN RAYS[unbr+bru+brl+unbr]						
DORSAL FIN RAYS						
ANAL FIN RAYS						
PECTORAL FIN RAYS						
PELVIC FIN RAYS						
LATERAL LINE SCALES						
BRANCHIOSTEGAL RAYS						
Scale Rows Abv lat line						
Scales Rows lat line to pelvic origin						
Pelvic Fin/Anus (Before, Ontop, Beyond)						
Scales between pectoral bases						
Scales between pelvic bases						
Gill rakers (raised)						
Comments:						

Note: Morphometric characters dorsal base to caudal flex, skull length, and pre-orbital distance and meristic characters caudal fin rays, scales between pectoral bases, and scales between pelvic bases were not included in analyses.