



Carolina Redhorse—a new species of *Moxostoma* (Cypriniformes: Catostomidae) from North Carolina and South Carolina, USA

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Abstract

Recognized as an undescribed species since the mid-1990s, the Carolina Redhorse is herein described as *Moxostoma carolina* **sp. nov.** The Carolina Redhorse is distinguished from all other species described in the genus *Moxostoma* by the number of caudal peduncle scales, the texture and angle of the lower lip, and by pigmentation and tuberculation patterns. It is morphologically similar to *M. erythrurum*, although the two species are allopatric and phylogenetic analysis of the COI mitochondrial gene supports the Carolina Redhorse as a distinct evolutionary lineage. The Carolina Redhorse is rare, localized, and endemic to lower Piedmont streams and run-of-river reservoirs in North Carolina and South Carolina. Characteristics of five of the species with which the Carolina Redhorse is sympatric and *M. erythrurum* are discussed, and a dichotomous key is provided.

Key words: Fishes, Suckers, North America, Atlantic slope, Yadkin-Pee Dee, Cape Fear

Introduction

North Carolina stands out along the Atlantic slope of the United States as a true biodiversity hotspot for suckers in the genus *Moxostoma* Rafinesque 1820. Its waterways host 10 distinct species, more than any other state in the region. By comparison, the next richest states, South Carolina and Virginia, each support only seven species. In 1961, the first known vouchered specimen of a Carolina Redhorse was collected by staff of the North Carolina Wildlife Resources Commission from Mill Creek in the Yadkin-Pee Dee River basin, 2.4 kilometers S center of Cairo in Anson County, North Carolina (NCSM 37251). Additional specimens were collected in 1962 in the Cape Fear River basin from Indian Creek, a tributary of the Deep River, at SR 2306, ca. 15.4 kilometers WNW center of Sanford in Chatham County, North Carolina (NCSM 37255). Up until the early 1990s, Dr. Robert E. Jenkins considered these specimens and several morphologically similar specimens to be hybrids between *M. collapsum* (Cope 1870) and *M. macrolepidotum* (Lesueur 1817) due to their comb-like pharyngeal teeth. In 1995, as Dr. Jenkins encountered and examined additional specimens, he realized that they were not hybrids but an undescribed, rarely collected species. He believed this undescribed species was a sister species to *M. erythrurum*, based upon the nuptial tuberculation pattern, coloration, and other diagnostic characters of the *M. erythrurum* group (Jenkins 2011, pers. obs.).

This form has been referred to as *Moxostoma* sp. or *Moxostoma* sp. “Carolina” Redhorse (Rohde *et al.* 2009; Tracy *et al.* 2020, 2024). In museum collections, it has been misidentified and labeled as *Moxostoma* sp. Brassy Jumprock, *M. sp. cf. erythrurum*, *M. collapsum*, and/or *M. macrolepidotum* (Jenkins 2011). An informal common

name, Carolina Redhorse, was coined in the 1990s by Drs. Jenkins and Wayne C. Starnes (Jenkins 2011) and has appeared as such in published and gray literature and in electronic databases.

Currently, 24 described and at least three undescribed or putative species (*M. sp. cf. austrinum*, *M. sp. cf. lachneri*, and *M. sp. cf. macrolepidotum*) exist in the genus *Moxostoma* (Akin *et al.* 2025; Bagley *et al.* 2018; Clements *et al.* 2012; Fricke *et al.* 2025; Froese & Pauly 2025; Harris *et al.* 2002; Jenkins *et al.* 2025; Tracy *et al.* 2024). However, phylogenetic relationships among *Moxostoma* species are poorly known except for studies based on a few mitochondrial or nuclear markers (Bagley *et al.* 2018; Clements *et al.* 2012; Harris *et al.* 2002). Resolution remains challenging due to family-wide tetraploidy. The only study to include the Carolina Redhorse used a single specimen from the Cape Fear River basin and was based on the mitochondrial cytochrome b gene and nuclear GH1 sequences (Clements *et al.* 2012). Cytochrome b suggested a sister relationship between the Carolina Redhorse and *M. ariommmum* Robins & Raney 1956, and part of a larger clade containing *M. anisurum* (Rafinesque 1820) and *M. collapsum* (Cope 1870). GH1 sequences resolved it as sister to *M. anisurum*. Both results had very low (below 70%) bootstrap support for the respective sister relationships.

With the recent descriptions of *Moxostoma ugidatli* Jenkins, Favrot, Freeman, Albanese, & Armbruster 2025 (Jenkins *et al.* 2025) and *M. antelunare* Akin, Jenkins, & Armbruster 2025 (Akin *et al.* 2025), the Carolina Redhorse, reaching a maximum size of approximately 585 mm TL (Starnes 2004), is now one of the largest newly described vertebrates (i.e., not split from another species) in North America. This species is endemic to the lower Yadkin-Pee Dee River basin in North Carolina and South Carolina and the Cape Fear River basin in North Carolina (Jenkins 2011; Rohde *et al.* 2009; Starnes 2004; Starnes *et al.* 2005; Tracy *et al.* 2020, 2024).

In this study we examined the systematics of seven species in the genus *Moxostoma* occurring along the Atlantic slope through analyses of meristics, morphometrics, and mitochondrial DNA. The seven species were: the Carolina Redhorse, the still-undescribed *M. sp.* Brassy Jumprock, *M. collapsum*, *M. pappillosum* (Cope 1870), and *M. robustum* (Cope 1870), and the Atlantic slope populations of *M. erythrurum* (Rafinesque 1818), and *M. macrolepidotum* (Lesueur 1817). Except for *M. erythrurum*, these species are all sympatric with the Carolina Redhorse and can often be collected together. *Moxostoma erythrurum* is allopatric with the Carolina Redhorse but was chosen for comparison in this study because of its morphological similarity to the Carolina Redhorse, which led Dr. Jenkins to believe that they were closely related. We exclusively examined specimens of both *M. erythrurum* and *M. macrolepidotum* only from the Atlantic slope as both species are widely distributed across the eastern and central United States and there may be hidden species diversity within these two species that has yet to be discovered. Three species of *Moxostoma*, also distributed only along the Atlantic slope, are not discussed herein: *Moxostoma ariommmum*, *M. cervinum* (Cope 1868), and *M. rupiscartes* (Jordan and Jenkins 1889, in Jordan 1889). All three species differ from the Carolina Redhorse in having modally 16 (range 14–16) circumpeduncle scales and do not co-occur with this species (Jenkins & Burkhead 1994; Tracy *et al.* 2020, 2024).

Here we provide a formal description of the Carolina Redhorse as a new species based on morphological characters and phylogenetic analysis of the COI mitochondrial gene. We also include a detailed summary of how to distinguish this species from the five species of *Moxostoma* with which it is sympatric and *M. erythrurum*, as well as a dichotomous key.

Materials And Methods

Meristic, Morphometric, and Descriptive Methods. Data were obtained from Jenkins (1970) and data more recently compiled by Dr. Jenkins through 2006. Specimens examined were from the following collections: ANSP, ASU (ASULAS), CU, CUSC, DE, DPC, DU, GMNH, NCSM, NYSM, RC, TU, UAIC, UF, UMMZ, UNCC, USNM, UT, VIMS, VISR, and VPI (institutional codes follow Sabaj 2020). Dr. Jenkins' original electronic data files (see Supplemental Files S1A–S1G) and paper data sheets for the Carolina Redhorse were obtained from Dr. Jonathan W. Armbruster, Auburn University Museum of Natural History. The paper data sheets for the Carolina Redhorse are now archived in the Brimley Memorial Library of the North Carolina Museum of Natural Sciences, Raleigh, NC.

Errors were encountered throughout Dr. Jenkins' electronic files, which appeared to have modified the original data. Without having access to his original paper data sheets, except for those for the Carolina Redhorse, assumptions as to what the data in these columns should be were not made. Thus, those data were excluded from our analysis.

Hogue and Tracy verified Dr. Jenkins' methods on all seven species of *Moxostoma* utilizing a subset of NCSM specimens. Supplemental data were recorded from certain NCSM specimens to fill data gaps found within Dr. Jenkins' data.

Twenty-one meristic, 22 morphometric, and 18 descriptive character datasets (see Supplemental file S2 for definitions of characters) were evaluated following the methods described in Hubbs & Lagler (1958), Jenkins (1970), Jenkins (n.d.), Jenkins & Burkhead (1994), and Tracy *et al.* (2024). All counts, measurements, and characters were based upon specimens ≥ 100 mm standard length (SL). Specimens utilized included: 84 Carolina Redhorse, 105–468 mm SL; 252 *M. collapsum*, 100–469 mm SL; 115 *M. erythrurum*, 104–402 mm SL; 232 *M. macrolepidotum*, 100–400 mm SL; 132 *M. pappillosum*, 100–363 mm SL; 142 *M. robustum*, 100–652 mm SL; and 139 *Moxostoma* sp. Brassy Jumprock, 100–385 mm SL (see Supplemental File S3). Interpretations of these three datasets were aided by the following published and unpublished data on these seven species: Cope (1870), Jenkins (1970), Jenkins (1995), Jenkins (2011), Jenkins, pers. comm., Jenkins (n.d.), Jenkins & Burkhead (1994), Jenkins & Freeman (1997), Page & Burr (2011), Robins & Raney (1956), Rohde *et al.* (2009), Smith (1907), Starnes (2004), and Tracy *et al.* (2024). Published and unpublished data are summarized in Supplemental file S4.

Measurements < 130 mm were taken by Dr. Jenkins with needlepoint dial calipers and read to the nearest 0.05 mm, except caudal lobe lengths, which were often taken by dividers and read to the nearest 0.5 mm from a metal ruler (Jenkins 1970). Measurements > 130 mm were taken with a needlepoint beam compass and read to the nearest 0.5 or 1.0 mm from a metal ruler (Jenkins 1970; Jenkins n.d.). Measurements recorded by Hogue and Tracy were recorded to the nearest 0.1 mm using Fisher® electronic digital calipers, traceable, Model 14-648-17, 11783217. Tuberculation patterns recorded by Hogue and Tracy followed Jenkins & Burkhead (1994, Figure 32, page 262).

Slightly gaped mouths were closed, and lips were held in mouth-closed position for measuring dimensions and angles involving the snout tip or lips; these data were not taken on specimens with moderately and very gaped mouths. Counts and measurements were made on the left side of specimens when possible. Cephalic lateralis pores and gill rakers were counted on the right and usually the right pharyngeal arch was studied (Jenkins 1970, n.d.).

The lower lip angle was measured at the posterior margin of the lower lip (Jenkins 1970, n.d.). The origin or pivot point of a clear plastic protractor was placed at the junction of the two halves of the lower lip; a clear straightedge was placed on the lower margin of the left half of the lower lip; this edge and the pivot point intersected at the apex of the medial lip angle. The degree (to the nearest 1°) was read at the intersection of the straightedge with the curved edge of the protractor (Figure 1). If midposterior fleshy extensions were present on the lip (e.g. in *M. robustum*; see Figure 3F), the angle measured was that which would have been present had the extensions been absent. The upper and lower lip morphological terminology was described in Jenkins (1970) and Jenkins & Burkhead (1994).

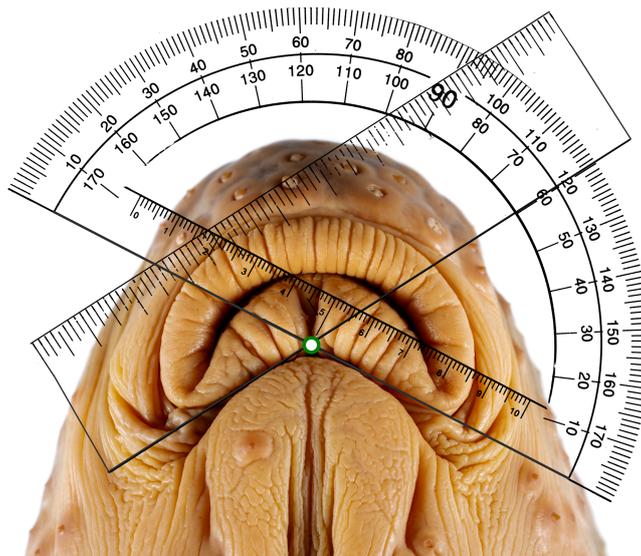


FIGURE 1. Example of measurement of lip angle (ca. 120°) in *Moxostoma carolina* sp. nov., holotype (NCSM 41138). Photograph by J.L. Bissette and S.A. Smith.

Distributional Maps. Distributional maps of all seven species along the Atlantic slope were constructed from vouchered material (whole body specimens, digestive and reproductive system organs, skeletal remains, and fish tissue) obtained from specimens at the North Carolina Museum of Natural Sciences and the Fishnet2 portal (Supplemental file S5). Fish specimen data acquired from the Fishnet 2 portal (<http://www.fishnet2.net>, 14 April 2025) were obtained from the following institutions: ANSP, AUM, CAS, CUMV, INHS, KU, MCZ, MMNS, MSB, OSUM, TCWC, TU, UA, UF, USNM, UT, and YPM (institutional acronyms follow Sabaj 2020). The distributional maps were created using Arc GIS Pro (<https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview>). The maps incorporated a custom vector basemap derived from the World Topographic Map and customized using the ESRI Vector Tile Style Editor. Additional layers from the ESRI Living Atlas included Rivers (https://services7.arcgis.com/oF9CDB4IUYF7Um9q/arcgis/rest/services/North_America_Lakes_and_Rivers/FeatureServer), Watersheds Level II (https://services7.arcgis.com/oF9CDB4IUYF7Um9q/arcgis/rest/services/NA_Watersheds/FeatureServer), State Boundaries (https://services.arcgis.com/P3ePLMYs2RVChkIx/arcgis/rest/services/USA_Census_States/FeatureServer), and Canadian Provinces (https://services.arcgis.com/wjcPoefzjzCgffS/arcgis/rest/services/Provinces_and_Territories_of_Canada/FeatureServer).

Genetic Methods. Tissue samples from 48 *Moxostoma* individuals were obtained from the NCSM collection, including 10 Carolina Redhorse and representative samples of all Atlantic-slope *Moxostoma* species (Table 1). DNA was extracted from these samples using a DNeasy Blood & Tissue Kit (Qiagen Inc., Valencia CA, USA) following manufacturer's instructions and quantified on a NanoDrop spectrometer. We amplified approximately 600 base pairs of the mitochondrial COI gene using universal fish primers designed by Ivanova *et al.* (2007) and the following PCR conditions: 1) initial hold at 94°C for 2 minutes; 2) 35 cycles of: 30 seconds at 94°C; 30 seconds at 54°C; 1 minute at 72°C; 3) final extension at 72°C for 10 minutes. Amplification of PCR products was confirmed from visualization on a 1.5% agarose gel using SYBR Safe DNA stain (Invitrogen). PCR products were cleaned using ExoSAP-IT PCR Product Cleanup Reagent (Applied Biosystems) following manufacturer's instructions. Sequencing of forward and reverse reads was performed by the North Carolina State University Genomic Sciences Laboratory on an Applied Biosystems 3730xl capillary sequencer. Forward and reverse reads were trimmed and assembled with the SangerAnalyseR R package (Chao *et al.* 2021).

TABLE 1. Tissues sampled and GenBank accession numbers for COI sequences generated in this study.

Species	Tissue No.	Waterway	Latitude	Longitude	GenBank No.
<i>Moxostoma anisurum</i>	NCSM 74333.1	Hiawassee River, Mississippi basin	35.09372	-84.04031	PX837106
<i>M. ariommmum</i>	NCSM 50166.1	Smith River, Albemarle Sound basin	36.50660	-79.75580	PX837099
<i>M. breviceps</i>	NCSM 48272.1	French Broad River, Mississippi basin	35.79360	-82.71070	PX837096
<i>M. breviceps</i>	NCSM 74334.1	Hiawassee River, Mississippi basin	35.09372	-84.04031	PX837107
<i>M. carinatum</i>	NCSM 74331.1	Hiawassee River, Mississippi basin	35.09372	-84.04031	PX837105
<i>M. carolina sp. nov.</i>	NCSM 34052.1	Lake Tillery, Yadkin-Pee Dee basin	35.39228	-80.06840	PX837072
<i>M. carolina sp. nov.</i>	NCSM 35946.1	Little River, Yadkin-Pee Dee basin	35.27450	-79.90800	PX837075
<i>M. carolina sp. nov.</i>	NCSM 37980.1	Deep River, Cape Fear basin	35.48820	-79.38470	PX837081
<i>M. carolina sp. nov.</i>	NCSM 39587.1	Deep River, Cape Fear basin	35.47790	-79.52510	PX837084
<i>M. carolina sp. nov.</i>	NCSM 41682.1	Pee Dee River, Yadkin-Pee Dee basin	34.97843	-79.86590	PX837085
<i>M. carolina sp. nov.</i>	NCSM 41864.1	Deep River, Cape Fear basin	35.48970	-79.38680	PX837086
<i>M. carolina sp. nov.</i>	NCSM 44081.1	Mountain Creek, Pee Dee River, Yadkin-Pee Dee basin	35.05450	-79.87580	PX837088
<i>M. carolina sp. nov.</i>	NCSM 44091.1	Little River, Yadkin-Pee Dee basin	35.31890	-79.86780	PX837089
<i>M. carolina sp. nov.</i>	NCSM 44237.1	Pee Dee River, Yadkin-Pee Dee basin	35.05190	-79.87880	PX837090
<i>M. carolina sp. nov.</i>	NCSM 62610.1	Cape Fear River, Cape Fear basin	35.53923	-78.99036	PX837102
<i>M. carolina sp. nov.</i>	NCSM 63446.1	Cape Fear River, Cape Fear basin	35.53711	-78.98866	PX837103
<i>M. carolina sp. nov.</i>	NCSM 74351.1	Pee Dee River, Yadkin-Pee Dee basin	34.93850	-79.86600	PX837109
<i>M. carolina sp. nov.</i>	NCSM 91970.1	Pee Dee River, Yadkin-Pee Dee basin	34.97568	-79.86269	PX837113

.....continued on the next page

TABLE 1. (Continued)

Species	Tissue No.	Waterway	Latitude	Longitude	GenBank No.
<i>M. cervinum</i>	NCSM 37918.1	Archies Creek, Dan River, Albemarle Sound basin	36.55019	-80.43263	PX837078
<i>M. cervinum</i>	NCSM 43600.1	Warren Creek, Eno River, Pamlico Sound basin	36.06805	-78.91695	PX837087
<i>M. cervinum</i>	NCSM 46803.1	Smith River, Albemarle Sound basin	36.50650	-79.75570	PX837092
<i>M. collapsum</i>	NCSM 29879.1	Pee Dee River, Yadkin-Pee Dee basin	34.93430	-79.86120	PX837069
<i>M. collapsum</i>	NCSM 32355.1	Broad River, Santee basin	34.82590	-81.47230	PX837071
<i>M. collapsum</i>	NCSM 37979.1	Deep River, Cape Fear basin	35.48820	-79.38470	PX837080
<i>M. collapsum</i>	NCSM 38031.1	Little River, Yadkin-Pee Dee basin	35.29090	-79.88800	PX837082
<i>M. collapsum</i>	NCSM 48266.1	Yadkin River, Yadkin-Pee Dee basin	36.24590	-80.45920	PX837093
<i>M. collapsum</i>	NCSM 59149.1	Big Alamance Creek, Cape Fear basin	35.98397	-79.65710	PX837100
<i>M. duquesnei</i>	NCSM 35922.1	Little Tennessee River, Mississippi basin	35.22077	-83.37222	PX837074
<i>M. duquesnei</i>	NCSM 48275.1	French Broad River, Mississippi basin	35.79360	-82.71070	PX837097
<i>M. erythrurum</i>	NCSM 35921.1	Little Tennessee River, Mississippi basin	35.22077	-83.37222	PX837073
<i>M. erythrurum</i>	NCSM 36684.1	Back Creek, Roanoke River, Albemarle Sound basin	37.17580	-79.98870	PX837076
<i>M. erythrurum</i>	NCSM 37887.1	South Double Creek, Dan River, Albemarle Sound basin	36.43155	-80.29839	PX837077
<i>M. erythrurum</i>	NCSM 48271.1	French Broad River, Mississippi basin	35.79360	-82.71070	PX837095
<i>M. erythrurum</i>	NCSM 74335.1	Hiwassee River, Mississippi basin	35.09372	-84.04031	PX837108
<i>M. macrolepidotum</i>	NCSM 29876.1	Pee Dee River, Yadkin-Pee Dee basin Pee Dee basin	34.91670	-79.85240	PX837067
<i>M. macrolepidotum</i>	NCSM 60766.1	Cape Fear River, Cape Fear basin	34.40370	-78.29250	PX837101
<i>M. pappillosum</i>	NCSM 29778.1	Deep River, Cape Fear basin	35.47760	-79.51960	PX837066
<i>M. pappillosum</i>	NCSM 38045.1	Roanoke River, Albemarle Sound basin	37.25110	-79.86250	PX837083
<i>M. pappillosum</i>	NCSM 48267.1	Yadkin River, Yadkin-Pee Dee basin	36.24590	-80.45920	PX837094
<i>M. robustum</i>	NCSM 46018.1	Savannah River, Savannah basin	33.30340	-81.88170	PX837091
<i>M. robustum</i>	NCSM 88446.1	Pee Dee River, Yadkin-Pee Dee basin	34.91413	-79.85226	PX837112
<i>M. rupiscartes</i>	NCSM 37934.1	Catheys Creek, Second Broad River, Santee basin	35.45889	-81.97889	PX837079
<i>M. rupiscartes</i>	NCSM 50160.1	Mill Creek, Catawba River, Santee basin	35.63630	-82.21870	PX837098
<i>M. rupiscartes</i>	NCSM 65072.1	Green River, Santee basin	35.24691	-82.38903	PX837104
<i>M. rupiscartes</i>	NCSM 86939.1	Bushy Creek, First Broad River, Santee basin	35.32790	-81.59386	PX837111
<i>M. sp. Brassy Jumprock</i>	NCSM 29878.1	Pee Dee River, Yadkin-Pee Dee basin	35.14350	-80.07640	PX837068
<i>M. sp. Brassy Jumprock</i>	NCSM 30415.1	Haw River, Cape Fear basin	35.71670	-79.09610	PX837070
<i>M. sp. Brassy Jumprock</i>	NCSM 75520.1	Horne Creek, Yadkin River, Yadkin-Pee Dee basin	36.26755	-80.49132	PX837110

Assembled DNA sequences were aligned in Mafft v7.490 (Katoh & Standley 2013) with the addition of a *Hypentelium nigricans* outgroup sequence obtained from GenBank (MT455538). The alignment was visualized and trimmed at the edges where there was low sequence representation in AliView (Larsson 2014). We inferred a Maximum Likelihood (ML) gene tree in IQ-Tree v2.2.2.7 (Minh *et al.* 2020), partitioning the alignment into three codon positions and selecting the best substitution model with ModelFinder (Kalyaanamoorthy *et al.* 2017). Branch support was evaluated with 1000 ultrafast bootstrap replicates (Minh *et al.* 2013).

Statistical Methods. Simple, descriptive statistics (i.e., range, mean, mode, and standard deviation) were calculated for the meristic and morphometric data using Microsoft® Excel for Mac Version 16.80. Morphometric data were standardized to the percentage of Standard Length.

Results

Genetics. Our final sequence alignment contained 561 base pairs of the COI mitochondrial gene. ModelFinder proposed TNe+I+R2 as the best model for the first codon position, F81+F+I for the second, and TN+F+G4 for the third. Our ML gene tree recovers all *Moxostoma carolina* sp. nov. sequences as monophyletic with a long subtending branch, sister to a clade containing *M. anisurum* and *M. collapsum* (Figure 2). All species-level groups were monophyletic, and most had 100% ultrafast bootstrap support, including *M. carolina* sp. nov. Support values were low at deeper nodes in the gene tree. Most *M. carolina* sp. nov. sequences are identical, and there do not appear to be any differences associated with specimens from the Cape Fear River versus the Yadkin-Pee Dee River basins. *Moxostoma erythrurum* does not appear to be closely related and is sister to *M. pappillosum* in our gene tree, with very low support. While genetic data clearly distinguish *M. carolina* sp. nov. from other *Moxostoma*, significantly more data are needed to address relationships in this genus. Sequences are available under GenBank accession numbers PX837066-PX837113 (Table 1).

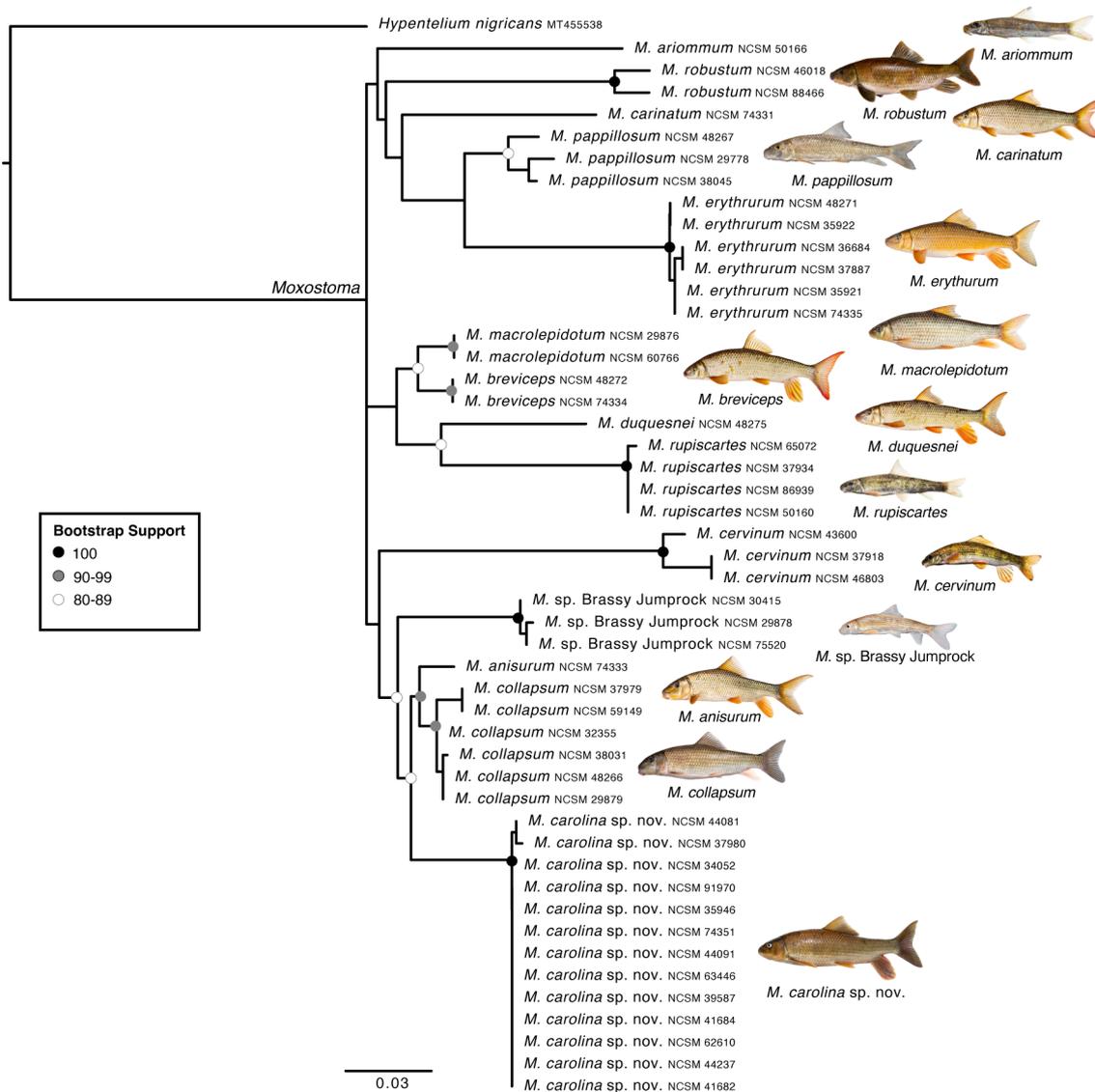


FIGURE 2. Maximum likelihood gene tree of COI sequences across *Moxostoma*, including all Atlantic slope species. Photographs used with permission from NCFishes.com.

Comparison of Seven Species of *Moxostoma* Along the Atlantic Slope—Meristics and morphometrics—

Comparisons of 21 meristic and 22 morphometric characters for seven species of *Moxostoma* along the Atlantic slope can be found in Table 2. Meristically, there were no differences in modal values between *Moxostoma carolina* sp. nov. and the other six species in the number of vertebrae, anal-fin and caudal-fin rays, predorsal scales, and lower lip plicae. Differences in the other 16 characters observed were either greater or less than the modal values of *M. carolina* sp. nov. The distributions and variabilities of meristic characters that were modally different between *M. carolina* sp. nov. and at least five other species included the number of circumferential scales, circumferential scales above the lateral line, dorsal-fin rays, lateral-line scales (Table 3), infraorbital pores, and preopercular-mandibular pores (Table 2). The number of circumpeduncle scales differed between *M. sp. Brassy Jumprock* and the other six species. With regards to morphometric characters, no visual differences in mean were detected in distributional plots between *M. carolina* sp. nov. and the other six species in caudal peduncle length, body width, orbit length, dorsal fin height at longest ray, caudal-fin lower lobe length, pelvic fin length, and anal fin length. There were only four characters that differed between *M. carolina* sp. nov. and three or more of the other species: snout length, head length, lip length, and pectoral fin length. Caudal peduncle depth, head depth at occiput, head width, and lip width differed between *M. carolina* sp. nov. and only one other species.

TABLE 2. Meristic and morphometric character dataset for seven species of *Moxostoma* along the Atlantic slope. * = not measured; SD = standard deviation.

	<i>M. carolina</i> sp. nov.	<i>M.</i> <i>collapsum</i>	<i>M.</i> <i>pappillosum</i>	<i>M.</i> <i>erythrurum</i>	<i>M.</i> <i>macrolepidotum</i>	<i>M.</i> <i>robustum</i>	<i>M. sp. Brassy</i> <i>Jumprock</i>
Meristic Characters (No.)—(Range) Mode							
Post-Weberian Vertebrae	(38–39) 39	(37–39) 37	(37–39) 38	(37–39) 38	(38–40) 39	(36–39) 37	(39–40) 40
Dorsal-Fin Rays	(13–17) 14	(12–17) 14	(11–15) 13	(12–15) 13	(11–14) 13	(12–14) 13	(11–13) 12
Pectoral-Fin Rays	(16–19) 17	(16–20) 18	(15–20) 18	(15–18) 17	(14–18) 17	(14–18) 16	(16–18) 17
Pelvic-Fin Rays	(9–10) 10	(7–11) 9	(8–10) 9	(8–10) 9	(8–10) 9	(9–11) 10	(8–9) 9
Anal-Fin Rays	(7) 7	(7–9) 7	(7–8) 7	7	7	(6–7) 7	(7–8) 7
Caudal-Fin Rays	18	(17–18) 18	(16–18) 18	(16–19) 18	(18–19) 18	(17–18) 18	18
Lateral-Line Scales	(43–47) 45	(38–45) 41	(39–46) 43	(39–45) 42	(40–48) 43	(40–46) 42	(42–48) 46
Circumferential Scales	(32–36) 34	(28–37) 32	(29–35) 32	(29–36) 32	(28–37) 32	(28–32) 30	(32–39) 36
Circumferential Scales above Lateral Line	(13–15) 15	(11–16) 13	(12–14) 13	(12–15) 13	(11–17) 13	(11–14) 13	(13–17) 15
Circumferential Scales below Lateral Line	(16–19) 17	(10–20) 17	(15–19) 17	(15–19) 17	(15–19) 17	(14–17) 15	(16–21) 19
Circumpeduncle Scales	(11–13) 12	(12–14) 12	(11–12) 12	(12–14) 12	(12–16) 12	(11–12) 12	(15–17) 16
Predorsal Scales	(13–18) 15	(12–18) 14	(14–18) 15	(13–19) 16	(14–19) 16	(13–17) 15	(14–19) 16
Gill Rakers	(22–27) 24	(24–32) 28	(26–32) 29	(25–33) 29	(22–29) 25	(21–27) 25	(27–37) 30
Lower Lip Angle (°)	(98–140) 117	(103–129) 114	(72–109) 105	(100–152) 110	(123–180) 180	(134–177) 164	(120–186) 180
Upper Lip Plicae	(19–38) 33	N/A	N/A	(33–43) 39	(21–32) 27	(26–33) 30	(24–34) 30
Lower Lip Plicae	(14–24) 18	N/A	N/A	(18–28) 22	(10–21) 18	(14–23) 18	(16–23) 19
Supratemporal Pores	(4–29) 16	(9–22) 18	(14–21) 16	(13–21) 17	(15–26) 17	(12–33) 19	(7–25) 17
Postorbital Pores	(5–11) 7	(4–10) 6	(3–13) 13	(3–9) 6	(4–12) 6	(3–12) 6	(3–10) 6
Supraorbital Pores	(13–27) 20	(14–32) 24	(17–34) 18	(18–27) 20/23	(17–36) 25	(16–36) 19/20	(6–26) 18
Infraorbital Pores	(21–43) 29	(20–45) 31	(23–44) 34/36	(21–34) 26	(13–26) 21/23	(20–41) 24	(15–36) 23
Preopercular-Mandibular Pores	(14–28) 17	(12–28) 26	(14–31) 24	(14–24) 17	(13–29) 21	(10–29) 14	(5–22) 13/14

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TABLE 2. (Continued)

	<i>M. carolina</i> sp. nov.	<i>M.</i> <i>collapsum</i>	<i>M.</i> <i>pappillosum</i>	<i>M.</i> <i>erythrurum</i>	<i>M.</i> <i>macrolepidotum</i>	<i>M.</i> <i>robustum</i>	<i>M. sp.</i> Brassy Jumprock
Morphometric Characters (standardized to % SL)—Mean ± SD							
Snout Length	10.0 ± 0.5	12.2 ± 0.7	12.1 ± 0.7	11.0 ± 0.5	9.7 ± 0.8	10.4 ± 1.2	10.2 ± 0.7
Postorbital Length	9.8 ± 0.5	9.5 ± 0.5	9.0 ± 0.5	9.6 ± 0.5	7.9 ± 0.6	9.0 ± 0.9	8.4 ± 0.7
Head Length	23.6 ± 0.6	26.0 ± 1.0	25.4 ± 1.0	24.0 ± 0.9	21.6 ± 1.3	23.1 ± 1.6	22.2 ± 1.2
Caudal Peduncle Length	13.0 ± 0.6	13.5 ± 1.3	14.0 ± 1.1	12.9 ± 0.7	14.2 ± 0.8	13.5 ± 1.5	15.2 ± 1.8
Caudal Peduncle Depth	10.8 ± 0.7	10.9 ± 1.0	9.5 ± 0.5	9.9 ± 0.5	10.6 ± 0.6	10.7 ± 0.6	10.3 ± 0.5
Body Depth at Dorsal-Fin Origin	27.5 ± 1.2	26.7 ± 1.4	23.9 ± 1.6	25.0 ± 1.4	27.2 ± 1.7	28.2 ± 2.1	23.7 ± 1.3
Head Depth at Occiput	18.1 ± 0.5	19.9 ± 0.8	17.8 ± 1.0	17.9 ± 0.7	17.8 ± 1.1	19.0 ± 1.9	17.1 ± 1.0
Body Width	18.1 ± 1.1	17.3 ± 1.1	16.6 ± 0.8	17.5 ± 1.3	17.6 ± 1.5	18.5 ± 2.2	16.7 ± 1.3
Head Width	16.8 ± 0.5	16.6 ± 0.7	16.0 ± 0.9	15.8 ± 0.5	15.3 ± 2.5	16.7 ± 1.4	15.1 ± 0.9
Interorbital Width	9.8 ± 0.4	9.9 ± 0.8	11.1 ± 0.5	9.5 ± 0.3	10.3 ± 0.6	11.2 ± 1.2	8.5 ± 0.7
Orbit Length	4.2 ± 0.5	5.4 ± 0.8	5.4 ± 0.8	4.8 ± 0.6	4.5 ± 0.4	4.1 ± 0.6	4.1 ± 0.5
Lip Width	5.9 ± 0.4	5.9 ± 0.6	6.2 ± 0.7	7.1 ± 0.6	5.9 ± 0.8	6.9 ± 1.2	5.7 ± 0.6
Lip Length	2.7 ± 0.3	*	*	4.0 ± 0.4	3.2 ± 0.5	4.6 ± 1.2	3.9 ± 0.5
Dorsal Fin Height at Longest Ray	20.0 ± 2.3	21.2 ± 1.9	20.0 ± 0.9	21.3 ± 1.2	23.3 ± 1.9	19.1 ± 3.1	19.1 ± 2.1
Caudal-Fin Lower Lobe Length	25.7 ± 2.0	26.9 ± 1.8	24.6 ± 1.1	24.8 ± 1.7	26.3 ± 2.8	25.5 ± 3.1	22.7 ± 2.5
Pectoral Fin Length	21.8 ± 1.2	19.1 ± 1.4	18.1 ± 1.1	18.4 ± 1.3	19.9 ± 1.2	20.8 ± 1.6	18.1 ± 2.2
Pelvic Fin Length	16.7 ± 1.3	15.4 ± 0.8	15.1 ± 1.2	15.3 ± 1.8	16.1 ± 0.0	15.6 ± 1.6	14.5 ± 1.3
Anal Fin Length	23.7 ± 1.5	23.0 ± 4.3	23.4 ± 2.5	21.9 ± 1.5	25.3 ± 2.8	24.0 ± 2.6	20.1 ± 2.5

TABLE 3. Distribution and variability of select meristic characters for seven species of *Moxostoma* along the Atlantic slope. Mode is bolded.

Circumferential Scales

	28	29	30	31	32	33	34	35	36	37	38	39	n
<i>M. carolina</i> sp. nov.					4	24	24	20	8				80
<i>M. collapsum</i>	2	4	2	13	54	34	20	17	6	2			154
<i>M. pappillosum</i>		5	13	32	43	5	3	1	0				102
<i>M. erythrurum</i>		1	7	19	30	24	8	2	3				94
<i>M. macrolepidotum</i>	2	5	21	26	41	21	19	9	2	1			147
<i>M. robustum</i>	3	17	48	20	4								92
<i>M. sp.</i> Brassy Jumprock					3	7	13	22	45	3	3	2	98

Circumferential Scales above Lateral Line

	11	12	13	14	15	16	17	n
<i>M. carolina</i> sp. nov.			5	35	40			80
<i>M. collapsum</i>	2	9	99	27	11	1		149
<i>M. pappillosum</i>		9	88	5				102
<i>M. erythrurum</i>		1	48	37	6			92
<i>M. macrolepidotum</i>	1	6	69	29	15	1	1	122
<i>M. robustum</i>	1	18	71	1				91
<i>M. sp.</i> Brassy Jumprock			5	21	68	4	1	99

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TABLE 3. (Continued)

Dorsal-Fin Rays

	11	12	13	14	15	16	17	n
<i>M. carolina</i> sp. nov.			5	44	29	3	1	82
<i>M. collapsum</i>		2	23	134	71	1	2	233
<i>M. pappillosum</i>	2	42	72	6	1			123
<i>M. erythrurum</i>		4	66	37	2			109
<i>M. macrolepidotum</i>	2	66	140	11				219
<i>M. robustum</i>		14	63	17				94
<i>M. sp.</i> Brassy Jumprock	8	89	18					115

Lateral-Line Scales

	38	39	40	41	42	43	44	45	46	47	48	n
<i>M. carolina</i> sp. nov.						10	30	32	9	1		82
<i>M. collapsum</i>	4	9	30	58	48	15	4	4				172
<i>M. pappillosum</i>		1		9	33	35	19	3	1			101
<i>M. erythrurum</i>		1	5	17	44	29	7	1				104
<i>M. macrolepidotum</i>			2	11	39	60	34	28	8	1	1	184
<i>M. robustum</i>			2	11	30	29	17	2	1			92
<i>M. sp.</i> Brassy Jumprock					1	1	15	28	34	7	3	89

Pelvic-Fin Rays

	7	8	9	10	11	n
<i>M. carolina</i> sp. nov.			21	59		80
<i>M. collapsum</i>	1	14	180	7	1	203
<i>M. pappillosum</i>		13	95	2		110
<i>M. erythrurum</i>		2	79	24		105
<i>M. macrolepidotum</i>		23	171	16		210
<i>M. robustum</i>			16	98	2	116
<i>M. sp.</i> Brassy Jumprock		3	79			82

Lip Morphology. Lip morphology and lower lip angle are generally diagnostic for differentiating species (Figure 3). Plicate lips are lips that are longitudinally grooved or pleated, appearing folded. Papillose lips have small round papillae or pimple-like structures; the papillae may be slightly elevated, appearing pebbled. In subplicate lips, the plicae of a portion of the lips are deeply, transversely, or obliquely subdivided, and many of them are elongated (Jenkins 1970; Jenkins & Burkhead 1994). *Moxostoma carolina* sp. nov., *M. erythrurum*, and *M. robustum* have plicate lips. Both *M. macrolepidotum* and *M. sp.* Brassy Jumprock have plicate upper lips and subplicate or partly subplicate lower lips. *Moxostoma collapsum* and *M. pappillosum* have papillose upper lips and papillose or semi-papillose lower lips. The modal lip angle for *M. carolina*, *M. collapsum*, *M. erythrurum*, and *M. pappillosum* is ca. < 117°. In contrast, for *M. macrolepidotum*, *M. robustum*, and *M. sp.* Brassy Jumprock the modal lip angle is ca. > 164° (Table 2).

Supratemporal Canal. The supratemporal canal, whether it is not interrupted (i.e., complete) or interrupted (i.e., incomplete with a discernible interruption) (Figure 4) is generally diagnostic for differentiating these seven species. The canal was found to be complete in 100% of the *M. collapsum*, *M. erythrurum*, *M. pappillosum*, and *M. macrolepidotum* and interrupted in 59% of the *M. sp.* Brassy Jumprock, 72% of *M. robustum*, and 98% of *M. carolina* that were examined.

Pharyngeal Teeth and Arches. The pharyngeal teeth and arches were similar in appearance for six of the seven species (Figure 5). Except for the teeth and arches of *Moxostoma robustum*, all other species had thin to

moderately thick arches with comb-like teeth. In *M. robustum*, the pharyngeal arch is very stout with molariform teeth (Armbruster & Jenkins 2025).

Species Distributions. *Moxostoma carolina* **sp. nov.** is endemic to North Carolina in the mainstem of the Pee Dee River downstream from Blewett Falls Dam to the state line; in the mainstem of the Cape Fear River downstream from the mouth of Daniels Creek to just downstream from Buckhorn Dam; in the mainstem of the Deep River; run-of-river reservoirs upstream of dams along the Deep and Little rivers; and in inshore areas of the upper reaches of Blewett Falls and Tillery reservoirs. In South Carolina, the Carolina Redhorse has only been found in the mainstem of the Pee Dee River from the state line downstream to Florence, SC (Figures 6B, 10).

Moxostoma collapsum is found in the Chowan River basin in North Carolina south to the Altamaha River basin in Georgia (Figure 6C); it was recently introduced into the New River basin (Mississippi River drainage) in Virginia (Tracy *et al.* 2020). *Moxostoma erythrurum* occurs along the Atlantic slope from the Potomac River basin in Maryland and Virginia, where it is introduced, south to the Roanoke River basin in North Carolina (Figure 6D). *Moxostoma macrolepidotum* occurs along the Atlantic slope from the Hudson River basin in New York south to the Santee River basin in South Carolina (Figure 6E). *Moxostoma pappillosum* is restricted to the Roanoke and Chowan River basins in Virginia south to the Santee River basin in South Carolina (Figure 6F). *Moxostoma robustum* is found in the Altamaha and Savannah River basins in Georgia, in the Pee Dee, Santee (not shown in Figure 6G), and Savannah River basins in South Carolina, and in the Yadkin-Pee Dee River basin in North Carolina (Figure 6G). *Moxostoma* sp. Brassy Jumprock occurs from the Cape Fear River basin in North Carolina south to the Oconee River basin in Georgia (Jenkins 1980a, 1980b, 1980c, 1980d, 1980e, 2011; Jenkins & Burkhead 1994; Page & Burr 2011; Rohde *et al.* 2009; Starnes 2004; Starnes *et al.* 2005; Tracy *et al.* 2020, 2024; Figure 6H).

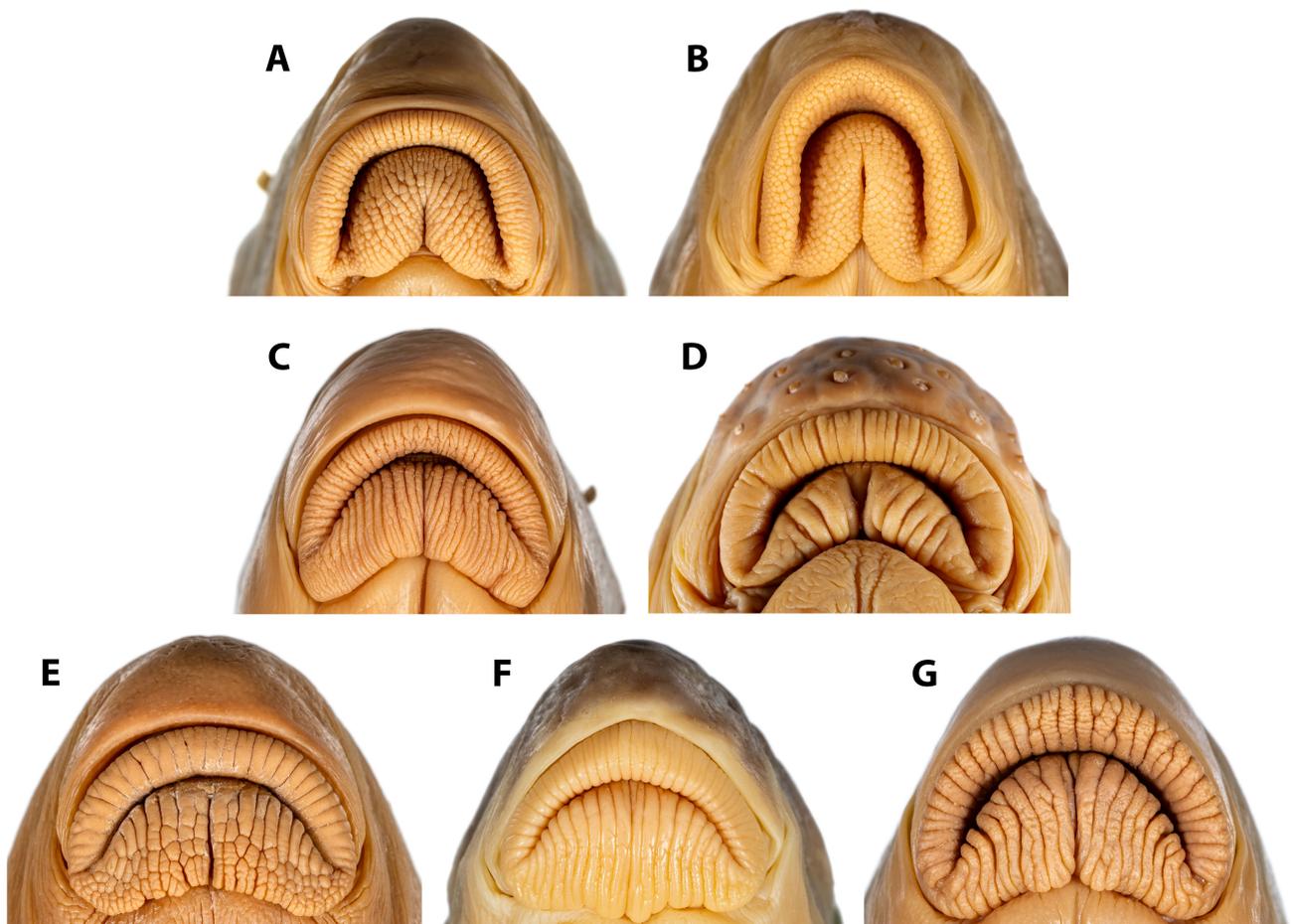


FIGURE 3. Lip morphology in seven species of *Moxostoma* along the Atlantic slope. A—*M. collapsum* (NCSM 38042, Spec. No. 6), B—*M. pappillosum* (NCSM 12943), C—*M. erythrurum* (NCSM 36684, Spec. No. 3), D—*M. carolina* **sp. nov.**, holotype (NCSM 41138), E—*M. macrolepidotum* (NCSM 3748), F—*M. robustum* (NCSM 30516), and G—*M.* sp. Brassy Jumprock (NCSM 26929, Spec. No. 1). Photographs by J.L. Bissette and S.A. Smith.

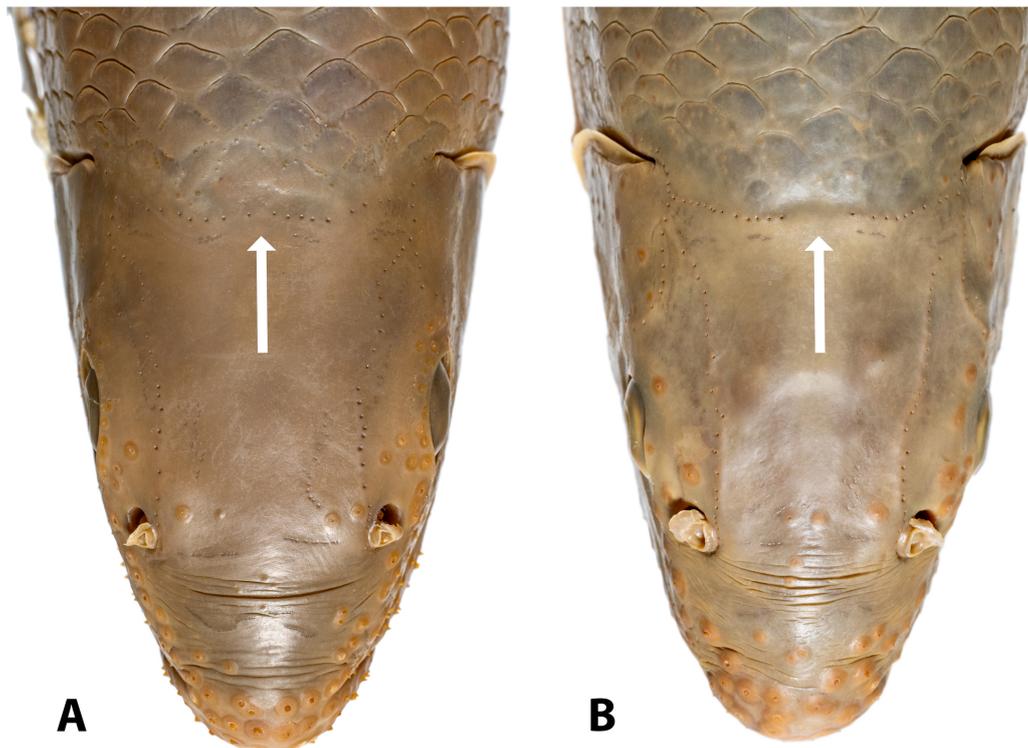


FIGURE 4. Arrows indicating location of supratemporal canal. A—not interrupted (complete) (*Moxostoma erythrurum*, NCSM 38043, Specimen No. 1); B—interrupted (incomplete) (*Moxostoma carolina* sp. nov., holotype, NCSM 41138). Photographs by J.L. Bissette and S.A. Smith.



FIGURE 5. Pharyngeal arches and teeth. A—*Moxostoma carolina* sp. nov. (NCSM 39873), B—*M. robustum* (NCSM 23865). Photographs by J.L. Bissette and S.A. Smith.

Of note is that no species of *Moxostoma* occurs in the adjacent Lumber River basin in North Carolina or South Carolina (Rohde *et al.* 2009; Tracy *et al.* 2020, 2024). The only large-bodied species of catostomid found in this basin is *Minytrema melanops* (Rafinesque 1820). The absence of these species may be the result of low productivity, low pH of the darkly stained (tannic) waters, or the lack of suitable cobble and large gravel spawning shoals.

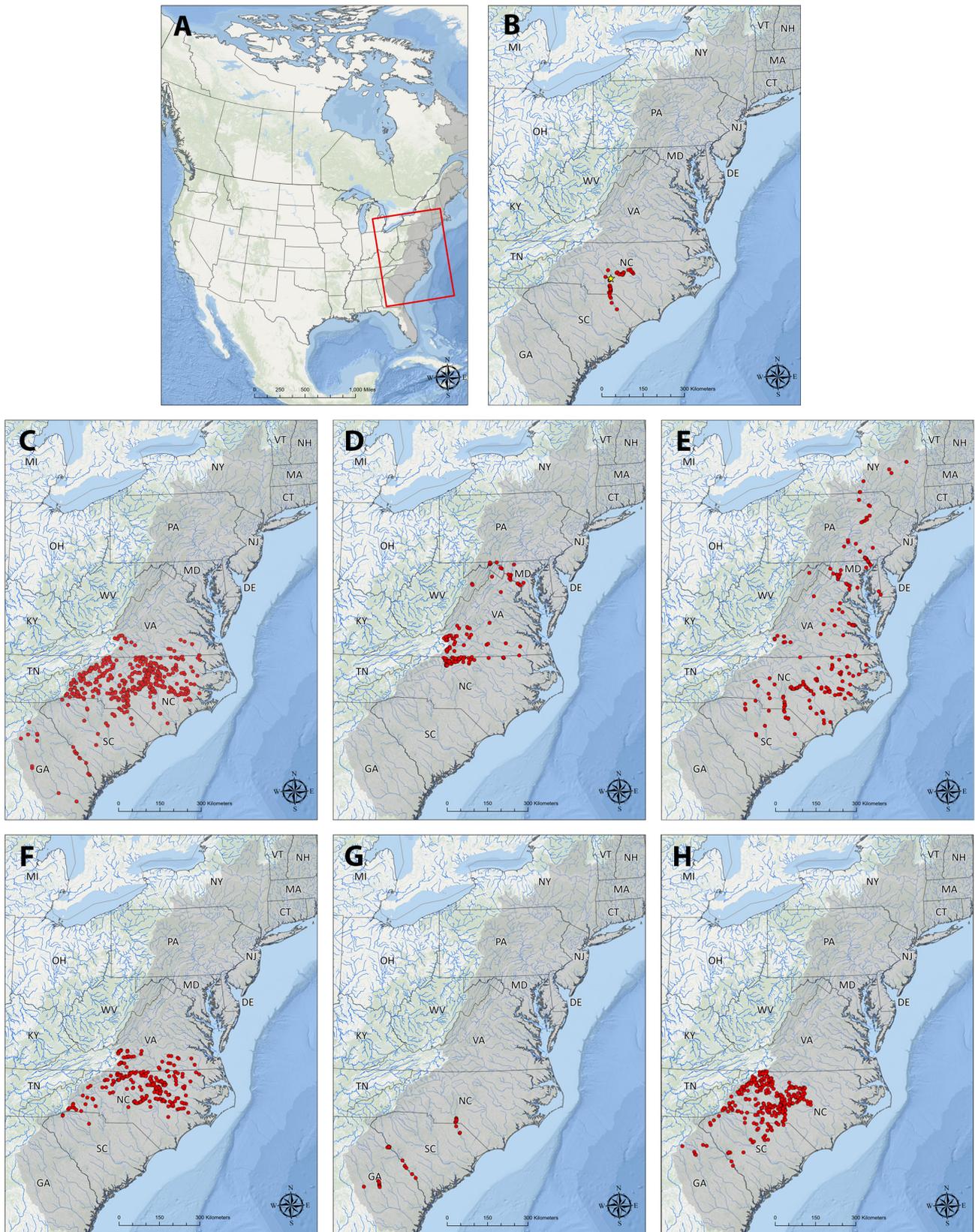


FIGURE 6. Distributions of seven species of *Moxostoma* along the Atlantic slope (gray shading), USA. Red dots indicate localities based upon vouchered specimens (Data in Supplemental Files). A—Atlantic slope region of interest; B—*Moxostoma carolina* sp. nov., yellow star indicates type locality; C—*M. collapsum*, recent introduction into New River, VA not shown; D—*M. erythrurum*, Atlantic slope distribution only; E—*M. macrolepidotum*, Atlantic slope distribution only; F—*M. pappilosum*; G—*M. robustum*; and H—*M. sp.* Brassy Jumprock.

Summary of the Characters Separating *Moxostoma carolina* sp. nov. from Six Other Atlantic Slope Species of *Moxostoma*. *Moxostoma carolina* sp. nov. can be separated from the following six species occurring along the Atlantic slope by the following meristic, morphometric (Tables 2, 3), and descriptive characters (see Supplemental files S3, S4).

Moxostoma collapsum—by having fewer pectoral-fin rays (modally 17 vs. 18), gill rakers (modally 24 vs. 28), supratemporal pores (modally 16 vs. 18), supraorbital pores (modally 20 vs. 24), infraorbital pores (modally 29 vs. 31), and preopercular-mandibular pores (modally 17 vs. 26); more pelvic-fin rays (modally 10 vs. 9), lateral-line scales (modally 45 vs. 41), circumferential scales (34 vs. 32), and circumferential scales above the lateral line (modally 15 vs. 13); shorter snout length (10.0 vs. 12.2% SL), head length (23.6 vs. 26.0% SL), and head depth at occiput (18.1 vs. 19.9% SL); longer pectoral fin length (21.8 vs. 19.1% SL); lower lip surface entirely deeply plicate and relatively smooth-surfaced versus semipapillose (Figures 3D vs. 3A); upper lip surface entirely plicate, plicae thin and numerous, relatively smooth-surfaced versus semipapillose (Figures 3D vs. 3A); snout round or nearly blunt versus moderately prominent; supratemporal canal interrupted versus not interrupted (Figures 4B vs. 4A).

Moxostoma pappillosum—by having fewer pectoral-fin rays (modally 17 vs. 18), gill rakers (modally 24 vs. 29), postorbital pores (modally 7 vs. 13), infraorbital pores (modally 29 vs. 34 & 36), and preopercular-mandibular pores (modally 17 vs. 24); more dorsal-fin rays (modally 14 vs. 13), pelvic-fin rays (modally 10 vs. 9), lateral-line scales (modally 45 vs. 43), circumferential scales (modally 34 vs. 32), circumferential scales above the lateral line (15 vs. 13), and supraorbital pores (modally 20 vs. 18); shorter snout length (10.0 vs. 12.1% SL), head length (23.6 vs. 25.4% SL), and interorbital width (9.8 vs. 11.1% SL); and longer caudal peduncle depth (10.8 vs. 9.5% SL), body depth at dorsal-fin origin (27.5 vs. 23.9% SL), and pectoral fin length (21.8 vs. 18.1% SL); lateral scale bases lacking pigmented crescents (Figure 8) versus having pigmented crescents; dorsal-fin margin slightly to moderately concave, S-shaped or straight (Figures 7, 9) versus slightly falcate; lower lip corner abruptly thinning to junction with upper lip occurring along anterolateral area of lower lip versus not thinning (Figures 3D vs. 3B); lower lip surface entirely deeply plicate and relatively smooth-surfaced versus papillose (Figures 3D vs. 3B); upper lip surface entirely plicate, plicae thin and numerous, relatively smooth-surfaced versus papillose (Figures 3D vs. 3B); snout round or nearly blunt (Figures 7–9) versus moderately prominent or truncate; supratemporal canal interrupted versus not interrupted (Figures 4B vs. 4A); body shape moderately elongate to very robust and stout (Figures 7, 9) versus shallow or slender.

Moxostoma erythrurum—by having fewer gill rakers (modally 24 vs. 29); more dorsal-fin rays (modally 14 vs. 13), lateral-line scales (modally 44 vs. 42), circumferential scales (34 vs. 32), circumferential scales above the lateral line (modally 15 vs. 13), and infraorbital pores (modally 29 vs. 26); fewer upper lip plicae (modally 33 vs. 39) and lower lip plicae (modally 18 vs. 22); shorter snout (10.0 vs. 11.0% SL) and lip length (2.7 vs. 4.0% SL); narrower lip width (5.9 vs. 7.1% SL); and longer pectoral-fin length (21.8 vs. 18.4% SL); breast scales embedded versus exposed; lower lip corner abruptly thinning to junction with upper lip occurring along anterolateral area of lower lip versus not thinning (Figures 3D vs. 3C); supratemporal canal interrupted versus not interrupted (Figures 4B vs. 4A); and geographical distribution confined to the Yadkin-Pee Dee and Cape Fear River basins in North Carolina and South Carolina versus Roanoke River basin northward along the Atlantic slope (Figures 6, 10).

Moxostoma macrolepidotum—by having narrower lower lip angle (modally 117° vs. 180°); fewer suborbital pores (modally 20 vs. 25) and preopercular-mandibular pores (modally 17 vs. 21); more dorsal-fin rays (modally 14 vs. 13), lateral-line scales (modally 45 vs. 43), circumferential scales (modally 34 vs. 32), circumferential scales above the lateral line (15 vs. 13), upper lip plicae (modally 33 vs. 27), and infraorbital pores (modally 29 vs. 21 & 23); longer postorbital length (9.8 vs. 7.9% SL) and head length (23.6 vs. 21.6% SL); breast scales that are embedded versus exposed; lateral scale bases lacking pigmented crescents (Figure 8) versus having pigmented crescents; dorsal-fin margin slightly to moderately concave, S-shaped or straight (Figures 7, 9) versus distinctly concave or slightly falcate; rear edge of lower lip moderately angled and indented in an inverted U-shape versus nearly straight (Figures 3D vs. 3E); lower lip corner abruptly thinning to junction with upper lip versus not thinning (Figures 3D vs. 3E); lower lip surface that is entirely deeply plicate and relatively smooth-surfaced versus subplicate (Figures 3D vs. 3E); snout round or nearly blunt (Figures 7–9) versus conical not projecting far beyond the small mouth; supratemporal canal interrupted versus not interrupted (Figures 4B vs. 4A).

Moxostoma robustum—by having narrower lower lip angle (modally 117° vs. 164°); fewer supratemporal pores (modally 16 vs. 19); more dorsal-fin rays (modally 14 vs. 13), pectoral-fin rays (modally 17 vs. 16), lateral-line scales (modally 45 vs. 42), circumferential scales (34 vs. 30), circumferential scales above (modally 15 vs. 13) and

below the lateral line (modally 17 vs. 15), upper lip plicae (modally 33 vs. 30), infraorbital pores (modally 29 vs. 24) and preopercular-mandibular pores (modally 17 vs. 14); shorter lip length (2.7 vs. 4.6% SL); pharyngeal arch thin with comb-like teeth versus thick with molariform teeth (Figures 5A vs. 5B); breast scales modally 100% versus 50% embedded; lateral scale bases lacking pigmented crescents (Figure 8) versus having pigmented crescents; rear edge of lower lip moderately angled and indented in an inverted U-shape versus nearly straight (Figures 3D vs. 3F); lower lip corner abruptly thinning to junction with upper lip versus not thinning (Figures 3D vs. 3F); lower lip surface entirely deeply plicate and relatively smooth-surfaced, without midposterior fleshy extensions versus plicate with midposterior fleshy extensions (Figures 3D vs. 3F).

Moxostoma sp. Brassy Jumprock—by having fewer circumferential scales (modally 34 vs. 36), circumferential scales below the lateral line (modally 17 vs. 19), circumpeduncle scales (modally 12 vs. 16), gill rakers (modally 24 vs. 30), and narrower lower lip angle (modally 117° vs. 180°); more dorsal-fin rays (modally 14 vs. 12), pelvic-fin rays (modally 10 vs. 9), upper lip plicae (modally 33 vs. 30), supraorbital pores (20 vs. 18), infraorbital pores (modally 29 vs. 23), and preopercular-mandibular pores (modally 17 vs. 13 & 14); longer postorbital length (9.8 vs. 8.4% SL), body depth at dorsal-fin origin (27.5 vs. 23.7% SL), head width (16.8 vs. 15.1% SL), interorbital width (9.8 vs. 8.5% SL), and pectoral-fin length (21.8 vs. 18.1% SL); shorter lip length (2.7 vs. 3.9% SL); lower lip corner abruptly thinning to junction with upper lip versus not thinning (Figures 3D vs. 3G); lower lip surface entirely deeply plicate and relatively smooth-surfaced versus having some subplicae (Figures 3D vs. 3G).

Identification Key to Seven Species of *Moxostoma* Distributed Along the Atlantic Slope. The following dichotomous key can be utilized to identify the six other species of *Moxostoma* that are sympatric with *M. carolina* **sp. nov.** (Figure 10). This key has been adapted from Jenkins (1995), Jenkins & Burkhead (1994), and Tracy *et al.* (2024). Three species of *Moxostoma* also occurring only along the Atlantic slope are not included in the key: *M. ariommum*, *M. cervinum*, and *M. rupiscartes*. They differ from *M. carolina* **sp. nov.** in several ways: 1) all three species have modally 16 (range 14–6) circumpeduncle scales versus modally 12 circumpeduncle scale; 2) in *M. ariommum* the upper lip is papillose versus plicate; 3) in *M. cervinum* the dorsal and caudal fins have black tips versus black tips absent; and 4) in *M. rupiscartes* the lower lip plicae have numerous transverse grooves (subplicate) versus lower lip plicae without numerous transverse grooves (Jenkins and Burkhead 1994; Tracy *et al.* 2024).

- | | | |
|---|---|--|
| 1 | Circumpeduncle scales modally 16 (range 15–17) | Brassy Jumprock, <i>Moxostoma</i> sp. |
| - | Circumpeduncle scales modally 12 (range 11–14; rarely 14–16 (n=5 of 135 specimens for <i>Moxostoma macrolepidotum</i>) | |
| 2 | Lips papillose (Figure 3B) or semi-papillose (Figure 3A) | 2 |
| - | Lips plicate or subplicate (Figures 3C–G) | 4 |
| 3 | Upper and lower lips papillose, papillae rounded at edges, regularly arranged, small, and mostly equal in size. Lower lip with smoothly curved posterior margin, not abruptly thinned at its juncture with upper lip (Figure 3B). Dorsal-fin margin of large juveniles and adults almost always slightly to moderately falcate. Profile elongate, slightly or not at all elevated toward dorsal fin. Scale bases dark | V-lip Redhorse, <i>Moxostoma pappillosum</i> (Cope 1870) |
| - | Upper and lower lips semi-papillose. Plicae in lower lip deeply, transversely, and somewhat irregularly dissected, resulting in papillae-like subdivisions that are irregularly arranged and unequal in size. Lower lip abruptly thinned at its juncture with upper lip (Figure 3A). Dorsal-fin margin of large juveniles and adults convex, straight, or slightly concave. Profile moderate or highly elevated toward dorsal fin. Scale bases pale | Notchlip Redhorse, <i>Moxostoma collapsum</i> (Cope 1870) |
| 4 | Lower lip plicate (Figures 3C, D, & F) | 5 |
| - | Lower lip subplicate with deep transverse grooves (Figure 3E) | |
| | Shorthead Redhorse, <i>Moxostoma macrolepidotum</i> (Lesueur 1817) | |
| 5 | Lower lip V- or U-shaped (Figures 3C & D) | 6 |
| - | Lower lip not V- or U-shaped, almost completely straight with midposterior fleshy extension (Figure 6F) | |
| | Robust Redhorse, <i>Moxostoma robustum</i> (Cope 1870) | |
| 6 | Supratemporal canal usually interrupted medially (Figure 4B). Lateral-line scales modally 45 (range 43–47). Breast scales modally 100% (50–100%) embedded. Range restricted to middle Cape Fear River and lower Yadkin-Pee Dee basin (Figure 10B) | Carolina Redhorse, <i>Moxostoma carolina</i> sp. nov. |
| - | Supratemporal canal not interrupted medially (Figure 4A). Lateral-line scales modally 42 (range 39–45). Breast scales not embedded. Range restricted from Potomac basin in Maryland and Virginia south to Roanoke basin (Figure 6D) | |
| | Golden Redhorse, <i>Moxostoma erythrurum</i> (Rafinesque 1818) | |

Taxonomy

Moxostoma carolina Hogue, Tracy, Hughes, & Jenkins, new species

Carolina Redhorse

Figures 1, 3, 4, 7–9

Moxostoma n. sp., Carolina Redhorse Jenkins 1995; Jenkins 2011.

Moxostoma sp. Carolina Redhorse Clements *et al.* 2012; Dixon 2005; Fernatt 2005; NCAC 2023; NCWRC 2015, 2021; Raley *et al.* 2004, 2007; Raley & Starnes 2007; Starnes 2004; Starnes *et al.* 2005.

Moxostoma Carolina Redhorse Rohde *et al.* 2009.

Moxostoma species, Carolina Redhorse Page & Burr 2011.

Moxostoma sp. cf. *erythrurum* “Carolina” Redhorse SCDNR 2015.

Moxostoma sp. “Carolina” Redhorse Tracy *et al.* 2020, 2024.

Moxostoma sp. 3 NCNHP 2022.

Holotype. NCSM 41138 (REJ 1980 & WCS-2518), adult male, 371 mm SL, 463 mm TL, 1190 g, North Carolina, Montgomery County, Little River, immediately below Smitherman Dam, 4.0 kilometers ESE center of Troy, 35.3438, -79.8531, Yadkin-Pee Dee River basin, 11 May 2005, William H. Dixon, Joseph P. Fernatt, Robert E. Jenkins, Wayne C. Starnes, and Bryn H. Tracy. [Note: Smitherman Dam was deconstructed in 2013.]

Co-occurring with the holotype that day were eight additional *Moxostoma carolina* (387–444 mm SL, 473–534 mm TL; six females and two males). These eight specimens (NCSM 41137) were measured, fin-clipped, and released.

Paratypes. All from the Yadkin-Pee Dee River basin. **North Carolina, Anson Co.:** NCSM 37251, 1, 107 mm SL, Mill Creek, ca. 1.5 miles S of Cairo, 34.86000, -79.93283, NCWRC Staff, 10 July 1961; **Anson-Richmond Cos.:** NCSM 30015, 1, 372 mm SL, Pee Dee River, upper Blewett Falls Lake, ca. 12.4 kilometers W center Ellerbe, 35.06000, -79.89690, J.M. Swing, V.F. Stancil, 15 August 2001; NCSM 30048, 1, 182 mm SL, Blewett Falls Lake, cove ca. 1 mile upstream of Blewett Falls Dam, ca. 8.0 miles WNW center Rockingham, 35.00000, -79.89095, J.M. Swing, J.U. Crutchfield, W.R. Garrett, V.F. Stancil, R.W. Lemonds, W. E. Partin, E.G. McGowan, 04 September 2001; NCSM 30049, 2, 77–239 mm SL, Blewett Falls Lake, cove ca. 0.5 miles downstream of Grassy Island complex, ca. 13.9 kilometers NW center Rockingham, 35.03000, -79.88055, J.M. Swing, J.U. Crutchfield, W.R. Garrett, V.F. Stancil, R.W. Lemonds, W. E. Partin, E.G. McGowan, 05 September 2001; NCSM 31134, 1, 64 mm SL, Blewett Falls Lake, cove ca. 0.5 miles downstream of Grassy Island complex, ca. 13.9 kilometers NW center Rockingham, 35.03000, -79.88058, J.M. Swing, T.E. Thompson, R.S. Hobbs., W.E. Partin., D.R. Pender, W.R. Garrett., C.R. Cofield., M.J. Chambers, 17 August 1999; NCSM 44084, 7, 79–94 mm SL, Pee Dee River, upper Blewett Falls Reservoir, Grassy Islands complex near mouth of Mountain Creek, 6.7 miles W of Ellerbe, 35.05000, -79.87860, W.C. Starnes, R.J. Heise, 11 October 2005; NCSM 44237, 3, 105–189 mm SL, Pee Dee River, Grassy Islands area and lower Mountain Creek (upper Blewett Falls Reservoir), ca. 6.8 miles W Ellerbe, 35.05000, -79.87880, W.C. Starnes, M.E. Raley, B.H. Tracy, 05 May 2006; NCSM 48269, 2, 306–310 mm SL, Pee Dee River, 2.8 mile reach from 0.5 mile below Blewett Falls Dam to US 74, ca. 6.1–5.5 miles WNW–W center of Rockingham, 34.98000, -79.86860, W.C. Starnes, J.U. Crutchfield, R.J. Heise, J.M. Swing, G.M. Hogue, B.K. Jones, J.M. Fisk, C. Sanders, J.E. Marsik, W.E. Stewart, E.A. Ozier, A.K. Hammers, T.J. Kwak, K.O. Sellers, D. Weaver, 08 May 2008; NCSM 59899, 1, 109 mm SL, Pee Dee River, (upper Blewett Falls Reservoir), island complex opposite and below mouth of Mountain Creek and lower 0.25 mile of creek, ca. 9.7 miles NW center Rockingham, 35.05000, -79.87700, W.C. Starnes, B.K. Jones, J.L. Griffin, 14 May 2010; **Montgomery Co.:** ANSP 211069, 2, 393–468 mm SL, Little River, at head of impoundment (of Hurley Dam), ca. 1.5 to 2 river miles N of Pekin Road (near confluence Big Creek), ca. 3.8–2.8 miles SSE center Troy, 35.31000, -79.87540, W.C. Starnes, G.M. Hogue, D.A. Hewitt, J.U. Crutchfield, J.M. Swing, V.F. Stancil, 23 April 2003; AUM 89625, 2, 359–436 mm SL, Little River, upper reach of Hurley Dam impoundment between Capelsie and Big Creek, ca. 1.5 to 2 river miles above Pekin Road, 3.4 miles S Troy, 35.32000, -79.86670, W.C. Starnes, R.E. Jenkins, J.M. Swing, V.F. Stancil, 29 April 2003; NCSM 35931, 3, 401–426 mm SL, Little River, upper reach of Hurley Dam impoundment between Capelsie and Big Creek, ca. 1.5 to 2 river miles above Pekin Road, 3.4 miles S Troy, 35.32000, -79.86670, W.C. Starnes, R.E. Jenkins, J.M. Swing, V.F. Stancil, 29 April 2003; NCSM 35947, 2, 402–439 mm SL, Little River, at head of impoundment (of Hurley Dam), ca. 1.5–2 river miles N of Pekin Road (near confluence Big Creek), ca. 3.8–2.8 miles SSE center Troy, 35.31000, -79.87540, W.C. Starnes, G.M. Hogue, D.A. Hewitt, J.U. Crutchfield, J.M. Swing, V.F. Stancil, 23

April 2003; NCSM 44238, 1, 357 mm SL, Little River, ca. 1.0 mile reach from 100 m below NC 24/27 downstream to Smitherman Dam just above Troy-Candor Road, ca. 2.4–2.5 miles E-ESE of Troy, 35.36000, -79.85210, W.C. Starnes, M.E. Raley, B.H. Tracy, R.E. Jenkins, 04 May 2006; **Richmond Co.:** NCSM 35951, 2, 357–373 mm SL, Little River, ca. 5 mile reach from mouth to 200 m above NC 73, ca. 8.5–10.6 miles WNW–NW Ellerbe, 35.10000, -79.90860, W.C. Starnes, G.M. Hogue, D.A. Hewitt, J.U. Crutchfield, J.M. Swing, V.F. Stancil, 21 April 2003; NCSM 37249, 1, 43 mm SL, Little River, above and below SR 1148 (Grassy Island Road), ca. 1 mile above Pee Dee River, 8.3 miles WNW Ellerbe, 35.11000, -79.89810, W.C. Starnes, R.E. Jenkins, J.U. Crutchfield, J.M. Swing, E.F. Menhinick, 31 July 1996; NCSM 44081, 4, 153–192 mm SL, Mountain Creek, lower 0.3 mile from 200 m above Grassy Island Road to mouth, 6.6–6.8 miles W Ellerbe, 35.05000, -79.87580, W.C. Starnes, R.J. Heise, 11 October 2005; **South Carolina, Chesterfield-Marlboro Cos.:** NCSM 115360, 1, 243 mm SL, Pee Dee River, 4.1 miles S North Carolina state line, ca. 6.3 kilometers NNW Cheraw, 34.75000, -79.90620, Carolina Power & Light Staff, 24 April 1979; **Darlington-Marlboro Cos.:** NCSM 115361, 1, 159 mm SL, Pee Dee River, ca. 1 mile below US 15–401, ca. 1.9 kilometers ENE Society Hill, 34.52000, -79.83070, G. Grunzal, 17 October 1989.

Other Specimens Examined (Non-types catalogued). All from the Cape Fear River basin. **North Carolina, Chatham Co.:** NCSM 37255, 2, 120–142 mm SL, Indian Creek, on SR 2306 Goldston-Carbonton Road, ca. 6.1 kilometers S of Goldston, 35.54000, -79.33538, NCWRC staff, 09 August 1962; UT 45.790, 2, 223–232 mm SL, Deep River, lower Carbonton Reservoir, 35.519708, -79.348143, C. Saylor, D.A. Tomljanovich, 16 October 1988; UMMZ 243472, 1, 313 mm SL, Haw River, ca 0.25 river mile below Jordan Dam, 35.632196, -79.060976, R.E. Jenkins, *et al.*, 15 July 1997; **Chatham-Lee Cos.:** UMMZ 243473. 1, 321 mm SL, Cape Fear River, east channel of McKay's Island, 2.2 miles below junction of Deep and Haw rivers, 35.565402, -79.038242, R.E. Jenkins, *et al.*, 15 July 1997; **Harnett Co.:** NCSM 11532, 1, 366 mm SL, Cape Fear River, 0.8 kilometers below Daniels Creek, 5.5 miles NNW Mamers, 35.49000, -78.95340, R.J. Gilbert, G. Doxtater, 12 February 1974; **Lee-Moore Cos.:** NCSM 26908, 19, 197–369 mm SL, Deep River, 0.2 to 4.0 miles above Carbonton Dam, ca. 9.0 miles WNW Sanford, 35.51000, -79.34230, W.C. Starnes, T.L. Fullbright, R.E. Jenkins, M. Chambers, A.A. Coons, 17 July 1997; NCSM 29395, 2, 322–344 mm SL, Deep River, within 0.25 miles of Carbonton boat ramp, 0.25 miles above NC 42, 10.3 miles W Sanford, 35.52000, -79.35180, W.C. Starnes, G.M. Hogue, B.H. Tracy, T.L. Fullbright, M.E. Raley, R.M. Smit, 18 October 2000; NCSM 39873, 1, 322 mm SL, Deep River, Carbonton boat ramp and 200 meter reach upstream, ca. 15.9 kilometers WNW center Sanford, 35.52000, -79.34860, M.E. Raley, T.J. Kwak, E. Malindzak, J.M. Fisk, Y.Y. Huang, 09 June 2004; **Moore Co.:** NCSM 26844, 3, 314–346 mm SL, Deep River, at High Falls, at , NC 22, 4.8 miles NE Robbins, 35.48000, -79.52090, W.C. Starnes, K.D. Fitzpatrick, 18 May 1997; NCSM 29776, 1, 339 mm SL, Deep River, at NC 22 (High Falls), 4.8 miles NE Robbins, 35.48000, -79.51960, W.C. Starnes, G.M. Hogue, M.E. Raley, 27 April 2001; NCSM 30363, 6, 67–389 mm SL, Deep River, from shoal area and old mill site ca. 0.4 miles downstream of Glendon-Carthage Road (SR 1006) to railroad bridge ca. 2.3 miles downstream, 12–13 miles W Sanford, 35.49000, -79.41420, W.C. Starnes, G.M. Hogue, B.H. Tracy, M.E. Raley, N. Medlin, 13 September 2001; NCSM 37250, 1, 72 mm SL, Falls Creek, SR 1606 (River Road), ca. 8.5 kilometers NE center Robbins, 35.48000, -79.51611, B.H. Tracy, M. Hale, D. Lenat, N. Medlin, 05 May 1998; NCSM 39587, 2, 324–390 mm SL, Deep River, 3.8 miles impounded reach (river mile 50.7–54.5) from dam at High Falls to first shoal above, ca. 4.6–3.7 miles NE-NNE of Robbins, 35.48000, -79.52510, W.C. Starnes, B.H. Tracy, R.E. Jenkins, J.T. DeBerardinis, 22 October 2004; NCSM 52742, 1, 105 mm SL, Deep River, shoal/pool area just above mouth of Buffalo Creek, off end of Hallison-Highfalls Lane, off NC 22, ca. 5.8 miles NE of Robbins, 35.48000, -79.50590, W.C. Starnes, G.M. Hogue, B.H. Tracy, T.J. Kwak, B.K. Jones, J. Gray, K.K. Irvin, E.N. Buttermore, N. Beasley, J. Dycus, J. Brewster, H. Renninger, P.B. Cooney, B. Wallace, D. Weaver, 29 May 2008; NCSM 115322, 1, 78 mm SL, Deep River, at NC 22, at High Falls, 4.8 miles NE Robbins, 35.48000, -79.51960, W.C. Starnes, T.L. Fullbright, R.E. Jenkins, J. Bohlen, B-T. Lorper, G.B. Pottern, 11 April 1997; NCSM 115323, 5, 285–405 mm SL, Deep River, river mile 37.3–37.9, above railroad trestle near rocky bend, ca. 18.5 kilometers W Sanford, 35.49000, -79.38470, R.E. Jenkins, J.M. Fisk, T.J. Kwak, 25 May 2005; **Randolph Co.:** NCSM 17661, 1, 57 mm SL, Fork Creek, ca. ¼ mile W confluence with Deep River, 8.4 miles S Coleridge, 35.52000, -79.60380, A.L. Braswell, J.M. Alderman, R. Biggins, 22 September 1992; NCSM 44078, 5, 61–67 mm SL, Fork Creek, lower 1.55 mile reach from Riverside Road to mouth, ca. 6.5–5.8 miles NNW of Robbins, 35.52000, -79.61950, W.C. Starnes, J. Taylor, T.P. Walker, B.H. Tracy, 26 October 2005; NCSM 46045, 2, 77–78 mm SL, Deep River, just above Bennett Road (SR 1002), 7.7 miles N of Robbins, 35.54000, -79.58690, W.C. Starnes, B.H. Tracy, G.M. Hogue, P.E. Mascarelli, 06 September 2007.

Non-types (uncatalogued, likely destroyed). Cape Fear River basin. **North Carolina, Moore Co.:** REJ 1489, 8, 198–374 mm SL, Deep River Carbondon Reservoir and above, ca. 3–9 river miles above Carbondon boat ramp, R.E. Jenkins, W.C. Starnes, K.W. Ashley, R.T. Rachels, S.L. Bryant, D.A. Besler, 08 May 1996.

Diagnosis. *Moxostoma carolina* can be separated from *M. albidum* (Girard 1856), *M. ariommum*, *M. austrinum* Bean 1880, *M. cervinum*, *M. congestum* (Baird and Girard 1854), *M. hubbsi* Legendre 1952, *M. lachneri* Robins and Raney 1956, *M. mascotae* (Regan 1907), *M. milleri* Robins & Raney 1957, *M. rupiscartes*, *M. valenciennesi* Jordan 1885, and the undescribed *M. sp.* Brassy Jumprock by having 11–13 circumpeduncle scales (vs. greater than 13, usually 16) (Akin *et al.* 2025; Page *et al.* 2023); from *M. anisurum*, *M. collapsum*, and *M. pappillosum* by having deeply plicate lower lips (vs. papillose or semi-papillose lips); from *M. antelunare* by having males with cephalic breeding tubercles (vs. males lacking cephalic breeding tubercles) and by lacking dark and light stripes laterally along the body (vs. having dark and light stripes laterally along the body) (Akin *et al.* 2025); from *M. breviceps* (Cope 1870), *M. carinatum* (Cope 1870), *M. macrolepidotum*, *M. pisolabrum* Trautman & Martin 1951, *M. robustum*, and *M. ugidatli* by having a lower lip angle generally less than 120° (vs. lower lip angle ca. 180°); from *M. duquesnei* (Lesueur 1817) by having males with cephalic breeding tubercles (vs. males lacking cephalic breeding tubercles); from *M. erythrurum* by having embedded breast scales (vs. breast scales not embedded) and by having an interrupted supratemporal canal (vs. a not interrupted supratemporal canal); from *M. lacerum* (Jordan & Brayton 1877) by lacking a unique mouth with cleft lower lip (vs. unique mouth with cleft lower lip) (Akin *et al.* 2025); and from *M. poecilurum* Jordan 1877 by lacking a conspicuous black stripe on the lower lobe of the caudal fin (vs. black stripe present) (Page *et al.* 2023).



FIGURE 7. Photographs of the holotype of *Moxostoma carolina* sp. nov., NCSM 41138 (371 mm SL). Photographs by J.L. Bissette and S.A. Smith.

Description. Meristic, morphometric, and descriptive characteristics of *Moxostoma carolina* are presented in Table 4. A medium-size, moderately elongate to very robust redhorse sucker; head length moderate; snout rounded or nearly blunt; body thick dorsoventrally. Fins medium size; dorsal-fin distal margin moderately or slightly concave, S-shaped, or straight, most frequently straight in adults, tips not distinctly rounded; caudal-fin lobes about equally long, tips acuminate or lower lobe slightly rounded. Lateral line multi-pored with as many as five pores per scale. Vertebrae modally 39 (38–39), dorsal-fin rays 14 (13–17); pectoral-fin rays 17 (16–19); pelvic-fin rays 10 (9–10); anal-fin rays 7 (7); caudal-fin rays 18 (18); lateral-line scales 45 (43–47); circumferential scales 34 (32–36); circumferential scales above lateral line 15 (13–15); circumferential scales below lateral line 17 (16–19); circumpeduncle scales 12 (11–13); predorsal scales 15 (13–18); gill rakers 24 (22–27) [not recorded for holotype due to destructive technique required to remove the arch]; upper lip plicae 33 (19–38); lower lip plicae 18 (14–24); supratemporal pores 16 (4–29); postorbital pores 7 (5–11); supraorbital pores 20 (13–27); infraorbital pores 29 (21–43); and preopercular-mandibular pores 17 (14–28). Breast modally 90% (70–100%) scaled; embedded scales on the breast, modally 100% (50–100%).

Lips entirely plicate, relatively smooth-surfaced, except for plication. Lower lip ridges (and grooves) are distinctly wider than upper lip ridges. All lower lip ridges, except in small triangular anteromedial area, are angled medio-posteriorly from the mid-longitudinal axis. Lower lip unnotched posterolaterally, thinning to junction with upper lip occurring along anterolateral area of lower lip. Posterior margin of lower lip moderately angled, lower lip indented in an inverted U-shape; the halves forming modally 117° (98–140°) angle. Circumlabial tissue often variously folded in small area near junction of upper and lower lips. Surficially prominent, large semicircular gular pad between the halves of the lower lip and posteriorly present. Pharyngeal arch thin, teeth comb-like [not examined on the holotype due to destructive technique required to remove arch]. Supratemporal canal interrupted.

TABLE 4. Meristic, morphometric, and descriptive characters of *Moxostoma carolina* sp. nov. Gill raker counts are not recorded for holotype due to destructive techniques required to remove them. SD = standard deviation.

Meristic Character (No.)	Mode	Range	n	Holotype (NCSM 41138)
Post-Weberian Vertebrae	39	38–39	7	39
Dorsal-Fin Rays	14	13–17	82	15
Pectoral-Fin Rays	17	16–19	83	17
Pelvic-Fin Rays	10	9–10	80	10
Anal-Fin Rays	7	7	76	7
Caudal-Fin Rays	18	18	76	18
Lateral-Line Scales	45	43–47	82	43
Circumferential Scales	34	32–36	80	33
Circumferential Scales above Lateral Line	15	13–15	80	14
Circumferential Scales below Lateral Line	17	16–19	80	17
Circumpeduncle Scales	12	11–13	82	12
Predorsal Scales	15	13–18	77	15
Gill Rakers	24	22–27	75	No data
Lower Lip Angle (°)	117	98–140	67	121
Upper Lip Plicae	33	19–38	72	28
Lower Lip Plicae	18	14–24	72	14
Supratemporal Pores	16	4–29	77	22
Postorbital Pores	7	5–11	77	7
Supraorbital Pores	20	13–27	77	23
Infraorbital Pores	29	21–43	77	33
Preopercular-Mandibular Pores	17	14–28	77	28

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TABLE 4. (Continued)

Morphometric Character (standardized to % SL)	Mean ± SD	Range	n	Holotype (NCSM 41138)
Total Length (mm)	N/A	138–566	80	463
Standard Length (mm)	N/A	105–468	84	371
Snout Length	10.0 ± 0.5	8.9–11.0	74	40 mm (10.8)
Postorbital Length	9.8 ± 0.5	8.6–11.1	74	38 mm (10.2)
Head Length	23.6 ± 0.6	22.1–25.0	74	89 mm (24.0)
Caudal Peduncle Length	13.0 ± 0.6	11.6–14.4	74	48 mm (12.9)
Caudal Peduncle Depth	10.8 ± 0.7	9.2–14.5	74	37 mm (10.0)
Body Depth at Dorsal-Fin Origin	27.5 ± 1.2	25.2–30.9	74	96 mm (25.9)
Head Depth at Occiput	18.1 ± 0.5	16.8–19.5	74	68 mm (18.3)
Body Width	18.1 ± 1.1	16.0–21.1	74	73 mm (19.7)
Head Width	16.8 ± 0.5	15.6–18.2	74	60 mm (16.2)
Interorbital Width	9.8 ± 0.4	8.4–10.7	74	36 mm (9.7)
Orbit Length (Diameter)	34.2 ± 0.5	3.5–6.0	74	14 mm (3.8)
Lip Width	5.9 ± 0.4	5.0–6.9	71	23 mm (6.2)
Lip Length	2.7 ± 0.3	2.0–3.3	71	4 mm (1.1)
Dorsal Fin Height at Longest Ray	20.0 ± 2.3	16.4–25.1	69	67 mm (18.1)
Caudal-Fin Lower Lobe Length	25.7 ± 2.0	23.0–30.9	67	95 mm (25.6)
Pectoral Fin Length	21.8 ± 1.2	18.0–25.4	74	81 mm (231.8)
Pelvic Fin Length	16.7 ± 1.3	14.8–22.8	72	60 mm (16.2)
Anal Fin Length	23.7 ± 1.5	21.1–28.3	74	97 mm (26.1)
Descriptive Character	Description			
Body Shape	Body moderately elongate to very robust; body and caudal peduncle moderately stout			
Head Size & Shape	Moderate			
Interrupted Supratemporal Canal	Yes, interrupted medially; 98% of specimens (n=81)			
Snout Shape	Rounded or nearly blunt			
Distal Dorsal-Fin Margin Shape	Slightly to moderately concave, S-shaped, or straight			
Caudal Fin Shape	Lobes about equally long			
Pigmentation of Lateral Scale Bases	Minute to small amount of pigment at scale base (n=12)			
Breast Scales—% Scaled	(70–100) modally 90 (n=83)			
Breast Scales—Embedded	Yes (n=30)			
Breast Scales—% Embedded	(50–100), modally 100 (n=30)			
Nuptial Tubercles—Males	Small to medium tubercles on snout, cheek, lower jaw, gular pad, branchiostegals, operculum, and often on dorsal area of head; tiny to small on lateral body, one to several per scale; small to large on anal and caudal fins			
Nuptial Tubercles—Females	No tubercles present (n=7)			
Gular Pad	Surficially prominent, large semicircular gular pad between the halves of the lower lip and posteriorly			
Pharyngeal Arch & Teeth	Pharyngeal arch lightly built, with thin and comb-like teeth on the lower edge; 86–96 teeth (n = 3; SL: 296–343 mm)			
Upper Lip Surface	Small lips often tucked under adjacent tissue; lips entirely plicate, plicae thin, numerous; relatively smooth-surfaced, most grooves quite oblique to longitudinal axis			

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TABLE 4. (Continued)

Lower Lip Surface	Entirely and deeply plicate; few in number; relatively smooth-surfaced, plicae ridges and grooves distinctly wider than upper lip ridges; ridges much angled from mid-longitudinal axis
Lower Lip Corner	Abrupt thinning to junction with upper lip; unnotched posterolaterally
Shape of Rear Edge of Lower Lip	Posterior margin moderately angled; lower lip indented in an inverted U-shape

Sexual Dimorphism. No mean differences between males and females across 19 morphometric characters (see Supplemental file S6). Statistical difference found between males and females in mean length of anal fin (male = 24.4% SL \pm 1.5, n = 40 vs. female = 22.8 \pm 0.9% SL, n = 34; unpaired t test, $p < 0.001$), as was hypothesized in Jenkins 2011. No modal differences between males and females across 20 meristic characters and percentage of breast scalation (Table 6). Sexual dimorphism noted in nuptial tuberculation patterns. Males with few tubercles on head–orbital area; anterior snout and lower opercular region densely tuberculate from upper lip to nostrils, except directly below eye. Internasal, interorbital, and occipital areas bear scattered tubercles. Ventral head, including branchiostegal area, heavily tuberculate. Dorsal, pectoral, and pelvic fins lack tubercles; anal and caudal fins have tubercles on rays. Tubercles vary from small to large; on body minute and irregularly scattered, one to several per scale (Jenkins 2011; Page & Burr 2011, Figure 8). Females lack nuptial tubercles.

Coloration. In life (Figure 9), body of large juveniles and adults laterally dominantly golden with brassy sheen, or individual scales graded silvery to brassy. Lateral body occasionally golden-brown or olive-toned in adults, silvery in juveniles. Scales two to four rows below lateral-line scale row with one to three golden or brassy, short to medium, horizontal stripes extending posteriorly from uniformly patterned, non-striped anterior area; mid-height of stripes centered at approximate mid-height of scales. Body bicolored, golden brassy laterally grading to pale white below lateral line, including the belly. Belly white, creamy, and/or silvery, sometimes with slight golden sheen. Snout and cheek laterally with upper dark area dark olive or brown, usually sharply demarcated in large juveniles and adults from often distinctly yellowed lower area, yellowish sometimes paling to white in lower opercular, gular, and branchiostegal areas. Iris silvery in inner half or nearly entirely, inner edge narrowly silvery- or brassy-rimmed. Lips white, cream, or slightly pink-tinted, occasionally rusty- or orange-stained, or with blackish areas. Scale-pocket crescents usually black dorsally to dusky olive in lateral line area, posterior edge of crescents above lateral line are usually moderately well defined; posterior margin of dorsal and lateral scales often silvery, grading to brassy toward crescents.

Dorsal and caudal fins olive or hyaline (occasionally red-orange), darkest in membranes; pectoral and pelvic fins mostly orange to orange-red, pectoral fin the brightest. Anal fin usually slightly or moderately dusky in juveniles, usually moderately to strongly hyaline, darkest in membranes, rays tending olive in adults; anal fin of some adults suffused pale orangish. Nuptial males with long, wide, uniformly moderately dusky or hyaline, mid-lateral stripe on body, in peak being black, encircling snout and extending to tail base; bordered dorsally by wide pale stripe that encircles the occiput. Females tend towards lesser development of the pattern.

In alcohol (Figures 7, 8), specimens lack chromatic coloration in body and fins; bicoloration greatly diminished. Specimens lacking distinct posterior horizontal stripes just beneath lateral-line scale row. For specimens with nuptial tuberculation, tubercles visually much more pronounced (Figure 8), as well as lateral line and cephalic pores.

Distribution. *Moxostoma carolina* is endemic to lower Piedmont streams and inshore areas of mainstem rivers and reservoirs in the Cape Fear and Yadkin-Pee Dee basins of North Carolina and South Carolina (Jenkins 2011; Rohde *et al.* 2009; Starnes 2004; Starnes *et al.* 2005; Tracy *et al.* 2020, 2024; Figure 10). In North Carolina, adults and juveniles have been found in the mainstem of the Pee Dee River downstream from Blewett Falls Dam to the state line; in the mainstem of the Cape Fear River downstream from mouth of Daniels Creek to just downstream from Buckhorn Dam; the mainstem of the Deep River; in run-of-river reservoirs with spawning shoals upstream of the impoundments along the Deep and Little rivers; and in inshore areas of the upper reaches of Blewett Falls and Tillery reservoirs. Young-of-year and juveniles have been collected from tributaries to the Pee Dee River, Blewett Falls Reservoir, and Deep River such as Mill Creek in Anson County, Mountain Creek in Richmond County, McClendons and Falls creeks in Moore County, Indian Creek in Chatham County, and Fork Creek in Randolph

County. In the Cape Fear River basin there are no records from the mainstem of the Cape Fear River downstream from Lillington, NC; from the Haw River system upstream from Jordan Reservoir, including Jordan Reservoir; or from the Rocky River system. In the Yadkin-Pee Dee River basin there are no records upstream from Narrows Dam or from the Rocky River watershed. In South Carolina, *M. carolina* occurs only in the mainstem of the Pee Dee River from the state line downstream to Florence, SC (Rohde *et al.* 2009). In North Carolina or South Carolina there are no records of collections from the upper Santee River basin (i.e., Catawba, Congaree, Wateree, and Broad rivers; Jason Bettinger, pers. comm., 01 July 2024) or the Coastal Plain.



FIGURE 8. Photographs of the nuptial tuberculation patterns of *Moxostoma carolina* **sp. nov.**, holotype, NCSM 41138 (371 mm SL). Photographs by J.L. Bissette and S.A. Smith.



FIGURE 9. Photograph of *Moxostoma carolina* **sp. nov.** in life, holotype, NCSM 41138 (371 mm SL). Photograph by B.H. Tracy.

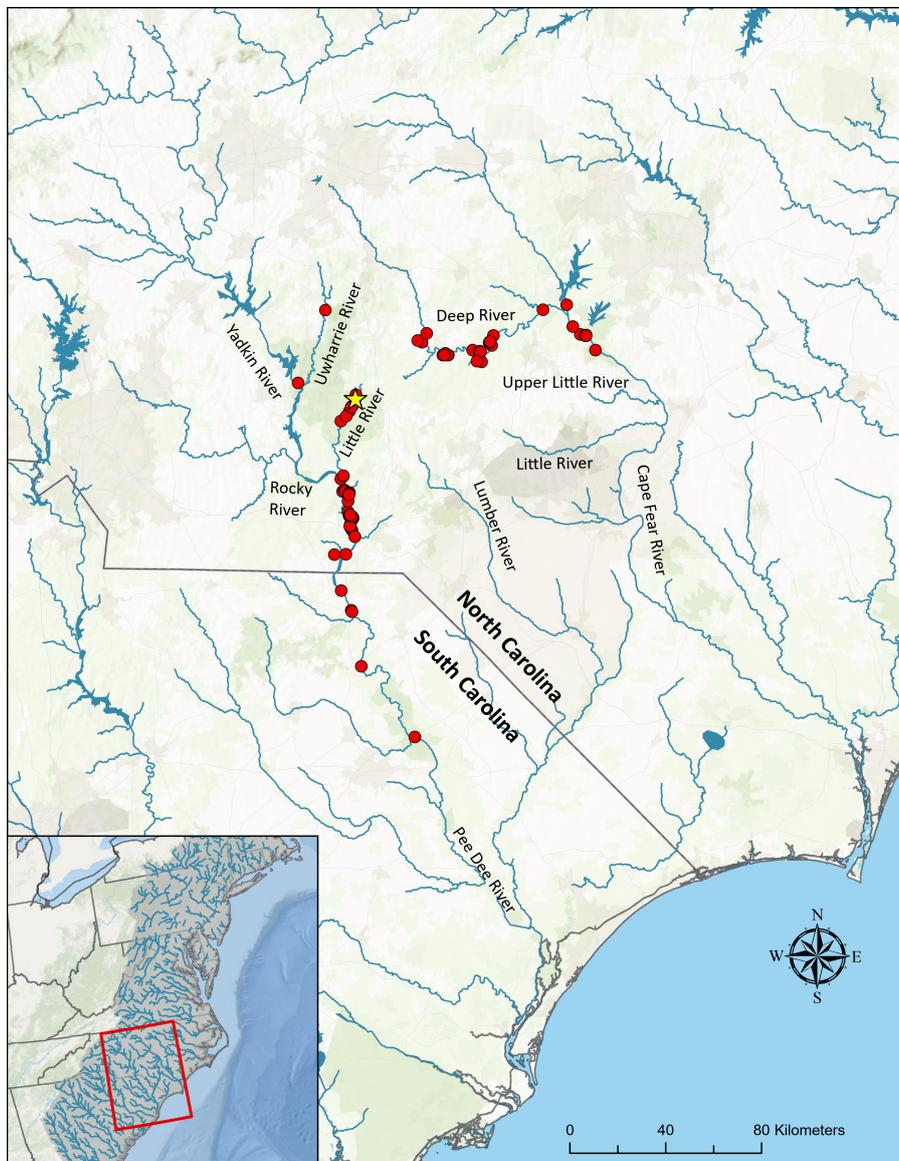


FIGURE 10. Distribution of *Moxostoma carolina* **sp. nov.** in North Carolina and South Carolina, USA. Yellow star indicates type locality. Red dots indicate localities based upon vouchered specimens (Data in Supplemental Files).

Historically, the distribution of *Moxostoma carolina* was possibly much more widespread. Tracy and Jenkins (2021) speculated that in 1869, Edward Drinker Cope did encounter this species in the Yadkin River at the Koontz Plantation in Rowan County based on unclearly described nominal species of redhorses (e.g., *Ptychostomus albus* Cope 1870 and *P. thalassinus* Cope 1870, both synonyms of *M. collapsum*), a description of an unnamed species (Cope 1870, p.474, last paragraph under *P. erythrurus*), and because of another species sympatric with *M. carolina*, which is widely distributed in the middle Yadkin River system, *M. sp.* Brassy Jumprock. *Moxostoma carolina* might have been more widely distributed in the upper Cape Fear River basin (i.e., the Haw River subbasin) prior to water quality degradation from the cities of Greensboro and Burlington, effluent from textile mills, and the creation of Jordan Reservoir in the late 1970s. The creation of the Yadkin-Pee Dee River Chain of Lakes in the middle and lower Yadkin River basin between 1917–1928 would also have fragmented its distribution. Currently, populations of *M. carolina* are fragmented by a series of run-of-river impoundments along the Deep and Little rivers and by hydroelectric dams along the mainstem of the Yadkin-Pee Dee River.

Life History. Much of the life history information of *Moxostoma carolina* was accumulated by Dr. Jenkins and undergraduate students at Roanoke College in Salem, VA. Unpublished age and growth data calculated by Dr. Jenkins can be found in the Supplemental file S1H. Based on aging of the opercles, the maximum age of *M. carolina* was determined to be 17 years and from scales it was determined to be a maximum of 13 years. These two ages were calculated from a female specimen (ANSP 211069), 468 mm SL, 566 mm TL, 2512 g, collected on 23 April 2003 from the Little River, in the upper reaches of Hurley Reservoir, Montgomery County, NC. The maximum weight of *M. carolina* was reported to be 3000 g from a 585 mm TL fish netted and released on 23 April 2003 from the Little River, in the upper reaches of Hurley Reservoir, Montgomery County, NC (Starnes 2004). The maximum weight that Dr. Jenkins recorded was 2512 g (ANSP 211069).

The diet of *M. carolina* was studied by undergraduate students, William H. Dixon and Joseph P. Fernatt, at Roanoke College in Salem, VA. The stomach contents of six fish from the Deep, Pee Dee, and Little rivers, collected in April, May, and October, were found to contain primarily chironomid larvae, microcrustaceans (cladocerans and copepods), and detritus. Typical habitat of food items indicated that *M. carolina* usually feeds in littoral depositional areas rather than lotic erosional areas (Dixon 2005; Fernatt 2005).

Moxostoma carolina inhabits well-flowing and slow sections of streams and at least inshore areas of a few small (run-of-river) to large reservoirs and seems to prefer slow current and lacustrine habitats (Jenkins 2011). During most of the year, except during spawning, *M. carolina* can be found in deeper pools of warm, moderate-gradient creeks to major rivers, mainstem reservoirs, and small run-of-river reservoirs. Many lotic sites where this species has been found have rocky to sandy to considerably silted substrate.

Based on tubercle and gonad development, spawning is suspected to occur in the spring (late April–early May) for a short period of time on gravelly shoals in larger streams similar to other redhorse suckers, although no one has observed actual spawning. It is also postulated that upon hatching, the young-of-year migrate into the smaller creeks to grow until they reach Age 1 or 2 before returning to the mainstem of rivers or impoundments (Jenkins 2011; Starnes 2004; Starnes *et al.* 2005).

No estimates of population size have been made for the Yadkin-Pee Dee or Cape Fear River populations of *M. carolina*. However, based upon targeted surveys and those who have collected specimens, it is rare in collections and rare when encountered. It is often difficult to collect due to the deep, non-wadeable pools it inhabits, which can only be sampled by a boat electrofisher. Competition with nonindigenous species such as *Ictiobus bubalus* (Rafinesque 1818) in the Yadkin-Pee Dee River and predation by the nonindigenous *Pylodictis olivaris* (Rafinesque 1818) in the Yadkin-Pee Dee River and Cape Fear River may also be limiting its numbers. Most adult specimens encountered by researchers are measured, PIT (Passive Integrated Transponder) tagged, and released rather than being preserved. Young-of-year (i.e., those < 100 mm TL) are rare in collections because they are thought to inhabit small, rocky-bottomed streams, which can be difficult to sample.

Etymology. *Carolina* is derived from the Latin version of King Charles I of England's name, *Carolus*, and means the "Land of Charles", originally called Carolana in 1629. The species epithet, a noun in apposition, was found written in Dr. Jenkins' handwriting on his 11 May 2005 field data sheet (REJ 1980) and we concur with this name. The species epithet and common name reflect the fact that the Carolina Redhorse is the only species of *Moxostoma* endemic to both North Carolina and South Carolina.

Conclusion

Moxostoma carolina is genetically, phenotypically, and geographically distinguishable from all other described and undescribed species of *Moxostoma*. Phylogenetic analysis of the COI mitochondrial gene supports *M. carolina* as a distinct evolutionary lineage, with no close relationship to *M. erythrurum* (Figure 2). Similar to the results of Clements *et al.* (2012) based on cytochrome b and GH intron 3 sequences, the most closely related sequences to *M. carolina* are from *M. collapsum* and *M. anisurum*. However, unlike their findings, we did not detect a close relationship to *M. ariommum*. Also in contrast, *M. erythrurum* was found to be sister to a clade containing *M. pappillosum* with our COI data (Figure 2), rather than sister to *M. carinatum* (Clements *et al.* 2012). Morphologically, *M. carolina* can be distinguished from the other 24 species of *Moxostoma* by the number of caudal peduncle scales, the texture of the lower lip, the lower lip angle, and pigmentation and tuberculation patterns. *Moxostoma carolina* is rare, localized, and endemic to lower Piedmont streams and inshore areas of mainstem Yadkin-Pee Dee River reservoirs in North Carolina and South Carolina (Figure 5).

The southeastern United States is considered a biodiversity hotspot, and this is evident in the number of species of *Moxostoma* within this region. With the recent descriptions of *M. antelunare* and *M. ugidatli* (Akin *et al.* 2025; Jenkins *et al.* 2025), along with *M. carolina*, there are now 17 described species of *Moxostoma* known from this region with 9 of those species occurring along the Atlantic slope (Page & Burr 2011). Within this rich diversity of *Moxostoma* are found many that are imperiled and facing serious threats. Threats to these species include habitat fragmentation by hydroelectric dams, point and nonpoint source pollution, waste runoff from confined animal feeding operations, minimal minimum flow regimes below dams, introduction of nonindigenous species, and increasing urbanization (e.g., see Cooke *et al.* 2005; Cooke *et al.* 2012). The localized distribution of *Moxostoma carolina*, known from only two disjunct and isolated populations, and subject to these threats, is one of these imperiled species. *Moxostoma carolina* is classified as State Threatened and a Species of Greatest Conservation Need in North Carolina (NCWRC 2015, 2021) and is considered a Species of Greatest Conservation Need in South Carolina (SCDNR 2015). Therefore, the need for further work on its conservation status in both North Carolina and South Carolina is warranted.

Acknowledgments

The authors are profoundly indebted to Dr. Robert E. Jenkins, not only for his contribution to this publication, but to his love of North American catostomids. It was that love that propelled him to measure and study thousands of specimens in his lifelong quest to know all about these wonderful and under-appreciated species. The data that he collected helped to form the basis for this and other studies and will continue to help in illuminating their evolutionary relationships, life histories, and conservation needs.

The authors gratefully acknowledge the following people with Duke Energy, the North Carolina Wildlife Resources Commission, and the South Carolina Department of Natural Resources for providing distributional data of *Moxostoma carolina*: Jason Bettinger, Justin Dycus, Brena K. Jones, Casey G. Joubert, Kevin Kubach, Jason Marsik, and Mark Scott. We are indebted to Jesse L. Bissette and Scott A. Smith for their photographic expertise, which made the images in this publication possible, and to Dr. Daniel Dombrowski and Shane Christian of the North Carolina Museum of Natural Sciences for conducting X-ray imaging of *M. carolina*, *M. collapsum*, *M. erythrurum*, and *M. sp.* Brassy Jumprock specimens. We thank Ashlee Somol for assisting in the molecular lab. We also thank Chris Scharpf for verifying the etymology of *M. carolina*. Finally, we extend our sincere appreciation to Dr. Jonathan W. Armbruster, Professor and Curator of Fishes at the Auburn University Museum of Natural History, for providing Dr. Jenkins' original data sheets, digital field notes, and electronic files for the seven species of *Moxostoma* studied herein.

Contributions

G.M. Hogue was responsible for study design, acquisition and archiving of specimens and tissues, meristic and morphological measurements, analyses and interpretation, and manuscript preparation. B.H. Tracy was responsible

for study design, meristic and morphological measurements, analyses and interpretation, and manuscript preparation. J.A. Raine was responsible for preparation of the distributional maps. L.C. Hughes was responsible for genetic data generation and analysis. R.E. Jenkins began this project and was responsible for acquisition of specimens, meristic and morphological measurements, analyses, and interpretation. All authors contributed edits to the final submitted manuscript.

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Supplementary Materials. The following supporting information can be downloaded at the DOI landing page of this paper:

S1A–G—Dr. Jenkins’ original data for the seven species discussed in this study. Considerable effort was made to decipher the abbreviations used by Dr. Jenkins within each of his data files. While we were able to decipher many of them, some are still unknown because we did not have the “Jenkins’ Rosetta Stone”.

S1H—Dr. Jenkins’ original data for age and growth for *Moxostoma carolina*.

S2—Definitions of meristic, morphometric, and descriptive characters.

S3—Dataset of meristic, morphometric, and descriptive characters.

S4—Literature review of meristic, morphometric, and descriptive data for the seven species discussed in this study.

S5—Dataset for distributional maps.

S6—Comparisons of the meristic and morphometric characters between male and female *Moxostoma carolina*.