A BRIEF ZOOGEOGRAPHIC HISTORY OF TONGUETIED MINNOW *EXOGLOSSUM LAURAE*

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Tonguetied Minnow *Exoglossum laurae* (Figure 1) inhabits the Great Miami, Allegheny, Genesee, and New rivers within the central Appalachian Mountains in western Pennsylvania and New York and the glacial till plains of western Ohio. The species is distributed throughout the upper reaches of these drainages, regions that are typically montane (Figure 2). Populations are thus separated by large distances, usually hundreds of river miles. Observational field data have also noted that Tonguetied Minnow is restricted to coldwater streams within its range (Trautman 1981). Fisheries management agencies have recognized the rarity of Tonguetied Minnow that has resulted from its limited and fragmented distribution. For example, the species is classified as Endangered in Ohio, Imperiled in West Virginia, Special Concern in North Carolina, and a Species of Greatest Conservation Need in New York. These characteristics first drew my attention to Tonguetied Minnow several years ago, and I wondered how it came to occupy this rather unusual distribution.

On one hand, Tonguetied Minnow's geography makes sense since the Allegheny, Genesee, and New rivers are located in the Appalachian Mountains. Thus, temperature profiles of these rivers are in line with the species' purported preference for cold water. On the other hand, the location of the Great Miami River is at odds with this explanation since the river cuts through the glacial till plains of western Ohio.

Tonguetied Minnow's geography also makes sense on another front. Three of its four native drainages, the Great Miami, Allegheny, and New rivers, are tributaries of the Ohio River. Perhaps the species evolved in the Ohio River and dispersed throughout the drainage over time. However, the Genesee River is problematic for this explanation since it flows into Lake Ontario, a component of the St. Lawrence River.

With generous and enthusiastic help from several fishery professionals and researchers (many of whom are NANFA members) and university students, I set out to find an explanation for Tonguetied Minnow's geographic distribution. We first collected multiple individuals from each of the four drainages that currently support Tonguetied Minnow. The DNA of these individuals was then extracted from their tissues and sequenced to uncover population-level patterns of genetic diversity. It was our hope that these genetic analyses would inform us about Tonguetied Minnow's evolutionary history and shed light on its distribution.

DNA sequence data revealed that the New River population has the highest level of genetic diversity and represents a unique evolutionary lineage within Tonguetied Minnow. Sequences also showed that the Great Miami, Allegheny, and Genesee rivers collectively comprise a second evolutionarily unique lineage, but one that is less genetically diverse than the New River. These genetic results revealed that the principal evolutionary "split" in Tonguetied Minnow is represented by an east-west axis lying to the north of the New River but to the south of all other populations. These results did not support either initial hypothesis, so how could they be explained?

The geological history of central Appalachian and Midwestern United States rivers, in combination with the genetics data, provided an answer to this question. The noted ichthyologist Charles Hocutt first proposed that Tonguetied Minnow's distribution has been a function of the ancient Teays and Pittsburgh rivers (Hocutt et al. 1978, 1986; Hocutt 1979; Figure 3). Prior to the beginning of the Pleistocene Epoch approximately 2.5 million years ago, the Teays River was the principal drainage of the central Appalachians and eastern Midwestern United States. The headwaters of the Teays River are preserved today by the New River, and from these headwaters, the Teays River flowed westward until terminating at the Mississippi River. The ancient Pittsburgh River was also extremely influential for Tonguetied Minnow. The Pittsburgh River was positioned north of the Teays River but flowed eastward

Figure 1. Tonguetied Minnow collected from the Mad River in Champaign County, Ohio, by the author and several ichthyology students from Ohio Northern University. Photograph taken October, 2018.

Photos by the author unless otherwise indicated.

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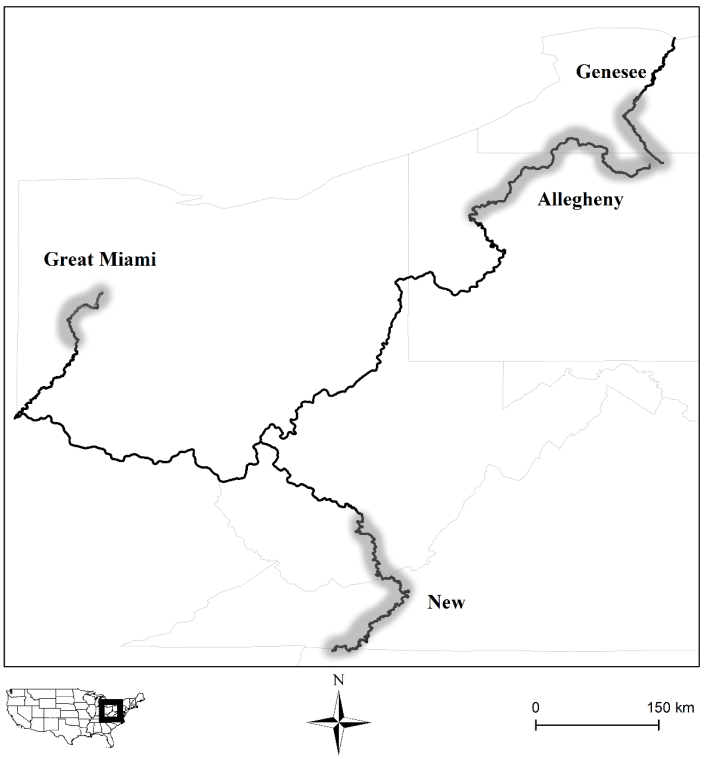

Figure 2. Present-day geographic range of Tonguetied Minnow. Populations inhabit regions shaded gray within each drainage.

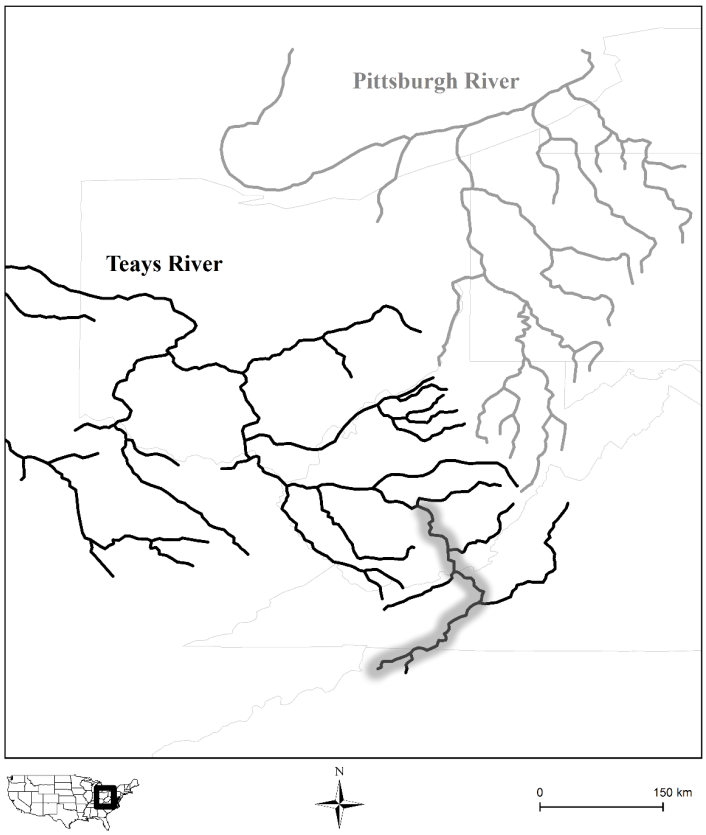

Figure 3. The ancient Teays and Pittsburgh rivers of the central Appalachian and Midwestern United States digitized and georeferenced in ArcGIS v.10 from the map of Hocutt et al. (1978). Glacially driven connections between these two systems during the Pleistocene likely permitted Tonguetied Minnow to invade areas to the north and west of its ancestral New River (shaded gray).

to the Atlantic seaboard. Connections between these two ancient systems during the Pleistocene appear to have been responsible for Tonguetied Minnow's distribution.

Large-scale glaciations marked the beginning of the Pleistocene, and there were at least four rounds of glacial advance and retreat during this epoch. Repeated rounds of glaciations reconfigured river systems throughout the middle latitudes of eastern North America. Pleistocene glaciations also drove novel connections among previously autonomous river systems, including the ancient Teays and Pittsburgh rivers. For example, advancing glaciers would dam the Teays River creating enormous lakes, which often extended into other watersheds, thus creating ephemeral connections among them. The dynamic, glacially driven hydrogeology of the Pleistocene likely facilitated Tonguetied Minnow's ability to exploit connections between the Teays and Pittsburgh rivers and permitted northward and westward dispersal from its ancestral New River. Surface temperatures, including surface water temperatures, were considerably lower during glacial periods compared to interglacials, which also likely contributed to Tonguetied Minnow's ability to exploit these connections.

Patterns of genetic diversity support interdrainage connections between the ancient Teays and Pittsburgh rivers. Genetic diversity is highest within the New River, the ancestral drainage of Tonguetied Minnow, and lower in regions of more recent invasion, specifically, the Great Miami, Allegheny, and Genesee rivers. Recession of the last (i.e., most recent) glaciation left Tonguetied Minnow distributed as a collection of isolated remnant populations. In western Ohio, Tonguetied Minnow persists almost exclusively in the Mad River, a tributary of the Great Miami River (Figure 4). The majority of the Mad River's flow is sustained by large inputs of groundwater from the underlying aquifer, a hydrogeology that results in anomalously cool water temperatures compared to the surrounding fluvial systems within the region (Trautman 1981). Extensive dredging and channelization of the Mad River has facilitated drainage of row crops and controlled flooding and might have further contributed to infusion of groundwater.

Genetic analyses also uncovered somewhat unexpected results. Evidence for hybridization between Tonguetied Minnow and its only congener, Cutlip Minnow *E. maxillingua*, was detected in the New and Genesee rivers. Cutlip Minnow is native to several Atlantic slope drainages as well as the Genesee River below its Middle Falls whereas Tonguetied Minnow occurs only above the Genesee River's Middle Falls (Smith 1986). Therefore, the ranges of these species do not overlap. However, Jenkins and Burkhead (1994) first reported Tonguetied × Cutlip Minnow hybrids in the New River based on morphological data, so modest genetic evidence of hybridization detected in this drainage was not unexpected. However, hybridization between Cutlip and Tonguetied Minnow in the Genesee River was surprising and suggests that either the distribution of Cutlip Minnow in the Genesee River has been mischaracterized, or that Cutlip Minnow has been recently introduced above the Middle Falls.

Why would Cutlip Minnow be introduced into the range of Tonguetied Minnow? The answer to this question remains elu-

Figure 4. The Mad River of western Ohio, a tributary of the Great Miami River that supports Tonguetied Minnow. A. Much of the Mad River flows through land dedicated to cultivation of row crops, mainly corn and soy bean. Consequently, many sections, such as this one, have been channelized for agricultural drainage and flood control. B. Some sections of the Mad River maintain lush riparian zones and rapid flows. C. Searching for Tonguetied Minnow (foreground) and angling for Brown Trout (background) in the Mad River. All photographs taken June, 2020.

sive, but anecdotally, every population of Tonguetied Minnow is (or has been) stocked with large numbers of Brown Trout *Salmo trutta* for sport fishing. Could it be that Cutlip Minnow has been introduced into the New and Upper Genesee rivers as bait for Brown Trout? Regardless of the reason, hybridization with Cutlip Minnow likely represents a significant threat to the persistence of Tonguetied Minnow. The Great Miami River population is therefore of great importance since it is a pristine genetic reservoir for the species which is located far from the native (and introduced) range of Cutlip Minnow.

Preliminary research of Tonguetied Minnow genetics has provided at least some tentative answers to our initial questions regarding the geography of this species (Oswald et al. 2020). However, more questions than answers arose from this research. For example, how extensive is hybridization between Tonguetied and Cutlip Minnow and for how long has it been occurring? Is it possible to reintroduce Tonguetied Minnow into drainages from which it has been extirpated (namely, the Little Miami River and possibly, the Monongahela River)? Do non-native Brown Trout introduced for sport fishing exert appreciable impacts on Tonguetied Minnow? Is "Tonguetied Minnow" actually a collection of multiple species? Hopefully, all of these questions will be answered with further research into this rare North American native to ultimately assist in its conservation.

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