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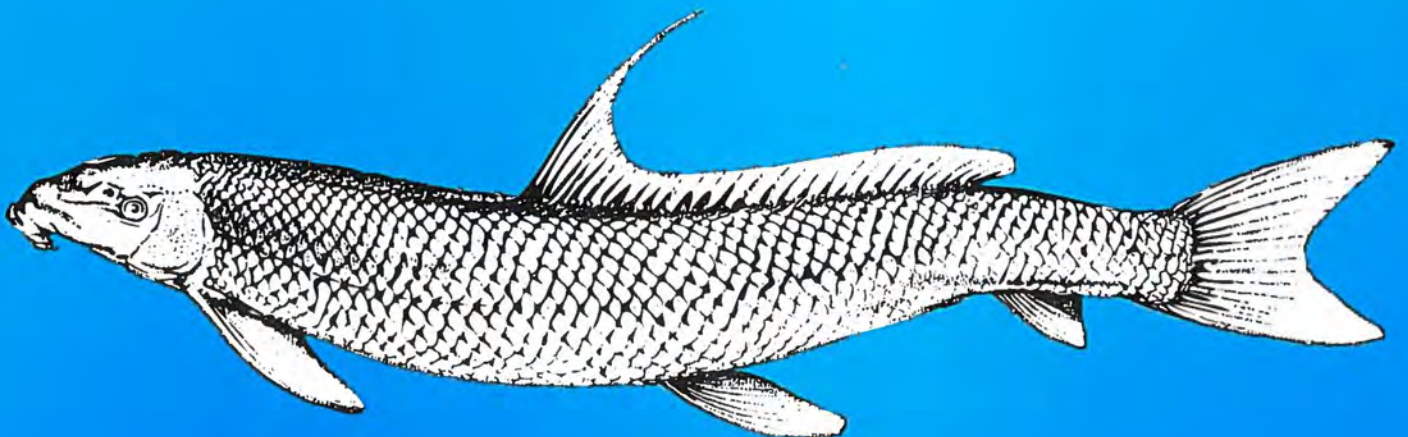
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TUSCALOOSA, ALABAMA

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The Loss of Free-flowing Streams in the Gulf Coastal Plain

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ABSTRACT: Shankman, David. 1999. The Loss of Free-flowing Streams in the Gulf Coastal Plain. *Bulletin of the Alabama Museum of Natural History*, Number 20:1-10, 1 table, 6 figures. The southeastern U.S. Coastal Plain contains high density stream networks and the largest area of alluvial wetlands in North America. Most of the major streams in this region have been modified by dams or other flood control-projects. A survey of rivers in the Gulf Coastal Plain indicates that 30 of the 41 major streams in this region have been dammed or channelized and one significantly affected by sand and gravel mining. Channel modifications, flow regulation, and changes in erosion and sediment transport associated with these river construction projects have significantly affected aquatic ecosystems. Also, a disruption of flood characteristics and sedimentation have altered critical river-floodplain interactions that have a direct effect on terrestrial ecosystems in adjacent bottomlands. The ten free-flowing streams are notable exceptions to the physically and ecologically altered rivers of this region. The free-flowing streams are increasingly viewed as important resources worthy of protection against further environmental degradation. All of the remaining free-flowing streams in the Gulf Coastal Plain, however, are presently subject to future damming or channelization.

Introduction

In recent years considerable attention has been given to the progressive loss of free-flowing streams in North America (Palmer, 1986; Benke, 1990; Doppelt et al., 1993, among others). Most stream alterations are attributable to large dams that result in upstream impoundment and downstream flow regulation. Major dam construction projects began in the 19th century and accelerated in the 1920s and 1930s. Proposals for large dams are now uncommon, but many of the remaining free-flowing streams are still threatened by flood control projects such as channelization and the building of flow diversion canals and levees. These floodplain and channel modifications, like dams, can significantly disrupt the natural hydrologic characteristics of a river and its floodplain. Many rivers are also threatened, although usually to a lesser extent, by land-use changes within their drainage basins,

including the expansion of urban fringes, deforestation, and land conversion for agriculture.

The concerns about the loss of free-flowing streams have often focused on degradation of aquatic and riparian terrestrial ecosystems and the loss of species diversity. The water quality of streams has notably improved since the 1960s. But human-induced geomorphic and hydrologic changes to rivers present more complicated problems that are now being recognized as possibly a greater threat to riverine systems. Flow regulation, changes in sediment transport, and direct or incidental channel modification will affect invertebrate and fish populations. Also, a disruption of the flooding regime and sedimentation can change critical river-floodplain interactions that degrade ecosystems in adjacent floodplains. Many aquatic and terrestrial species occurring in the riparian zone require a narrow range of physical conditions to survive

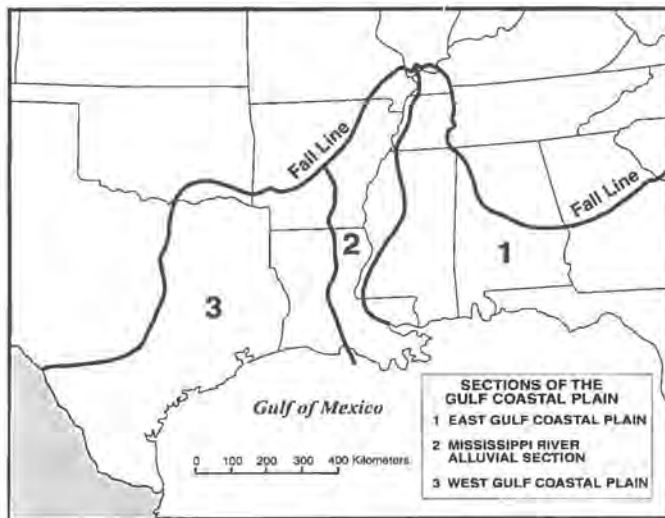


Figure 1: Location and subdivisions of the Gulf Coastal Plain.

and regenerate. The disruption of free-flowing streams will in many cases alter the conditions of these habitats so that they are no longer capable of supporting wetland species.

The southeastern U.S. Coastal Plain contains high-density stream networks and the largest area of alluvial wetlands in North America. The headwaters of most of the major Gulf Coastal Plain streams are located in the surrounding uplands (Figure 1). Stream gradients decrease as rivers flow into the relatively flat Coastal Plain, where they develop meandering patterns and broad floodplains. These alluvial valleys support high species diversity. Most of the major streams in this region, however, have been modified by dams or other flood control projects. In many cases these physical modifications have had a significant ecological impact.

The purpose of this paper is to inventory major rivers in the Gulf Coastal Plain to determine which remain free-flowing. Specific objectives are: (1) to identify the major rivers affected by dams or channelization on either the main channel or large tributaries, (2) to discuss the physical and ecological effects of channel modification and deforestation in river corridors or drainage basins, and (3) to review river protection in this region and prospects for the preservation of the remaining free-flowing streams.

River Evaluation

All streams in the Gulf Coastal Plain at least 150 km in length were selected for this investigation. These streams were surveyed to determine if they were free-flowing and maintain the ecological conditions necessary to continue supporting high species diversity. The determination of stream conditions were based on (1) the examination of streams on aerial photographs and 1:250,000 and 1:24,000 topographic maps, (2) consultations with the

U.S. Army Corps of Engineers and the U.S. Fish and Wildlife Service, and (3) site visits.

Rivers or river segments cannot always be easily classified as either a free-flowing stream of high natural quality or a highly modified stream with little natural value. The evaluation of the degree to which a stream is free-flowing is based on the presence of dams on the main stem of the river or major tributaries and channelization or diversion canals. Those rivers with no flow-control structures or major channel modifications are classified as free-flowing, but the channel morphology and hydrology of these streams can be altered by deforestation and land-use changes within the floodplain and watershed. However, land-use conversion in most cases has a relatively minor effect on riparian ecosystems when compared to major channel modifications.

The Gulf Coastal Plain and Its Major Rivers

The Coastal Plain is underlain by Cretaceous and Tertiary sediments exposed by falling sea levels, mostly during the mid-late Tertiary Period (>2 million years BP). Three generally recognized subdivisions of this region are the East and West Gulf Coastal Plain and the Mississippi River alluvial valley (Figure 1). The Fall Line is the uppermost boundary of the Coastal Plain and is a transitional zone separating it from the adjacent upland provinces which are generally areas of higher local relief. Rapids or waterfalls occur where streams cross from the older more resistant uplands into the less resistant rock of the Coastal Plain. The Fall Line marked the upper limits of navigation on most streams in this region before the construction of dams.

The major Coastal Plain rivers can generally be characterized as low gradient, meandering streams that carry high sediment loads. These streams flood most years during the winter and spring. Portions of the floodplain may be submerged for periods ranging from a few days to several weeks, and there is often more than one period of submergence. Rates of sedimentation in the adjacent floodplain are typically higher than that of any other region of North America. The active floodplains of many alluvial streams in this region are bounded by Late Pleistocene terraces (Dury, 1977; Alford and Holmes, 1985; Saucier, 1987). These surfaces are remnants of ancient floodplains formed during the interglacial periods of the last 2 million years, when average discharge, channel width, and meander wavelength were much greater than at present. Pleistocene river terraces encompass large parts of Coastal Plain alluvial river valleys. They rarely flood, however; and therefore support many upland plant species that are uncommon in modern floodplains.

The alluvial valleys in the Coastal Plain support diverse forest vegetation. Plant community patterns within the alluvial valleys are highly complex, depending on the hydroperiod (flooding, impoundment of surface water, and height of the water table), channel migration and

surface age, and complex disturbance regimes (White, 1979). A large portion of the bottomlands of many streams, however, has been deforested. Klopatek et al. (1979) estimated that 63 percent of the original southern floodplain forest has been lost. An even larger percentage of the lower Mississippi River alluvial valley, the largest contiguous wetlands area in North America, has been deforested (McDonald, et al. 1979).

Changing Hydrogeomorphic Conditions

On alluvial rivers there is a direct relationship between discharge, sediment load, and channel morphology. Changes of one of these variables will cause the adjustment of the others, and therefore there is a tendency toward long-term self-regulation, or a condition of equilibrium. All major rivers in the Gulf Coastal Plain have been altered to some extent by human activity. River adjustment begins immediately following disturbance. Achievement of a new equilibrium, however, may take many decades and perhaps centuries. Thirty of the 41 major streams in the Gulf Coastal Plain have been dammed or channelized and one significantly affected by sand and gravel mining (Table 1). The remaining ten rivers have had no major channel modifications and therefore are designated as free-flowing. Channel adjustment of free-flowing streams to human modifications has been relatively minor, but in some cases noticeable.

DAMS: Major dams have been built on the main channels or large tributaries of 25 of the 41 major Gulf Coastal Plain streams (Figures 2,3,4). Several of the rivers used for

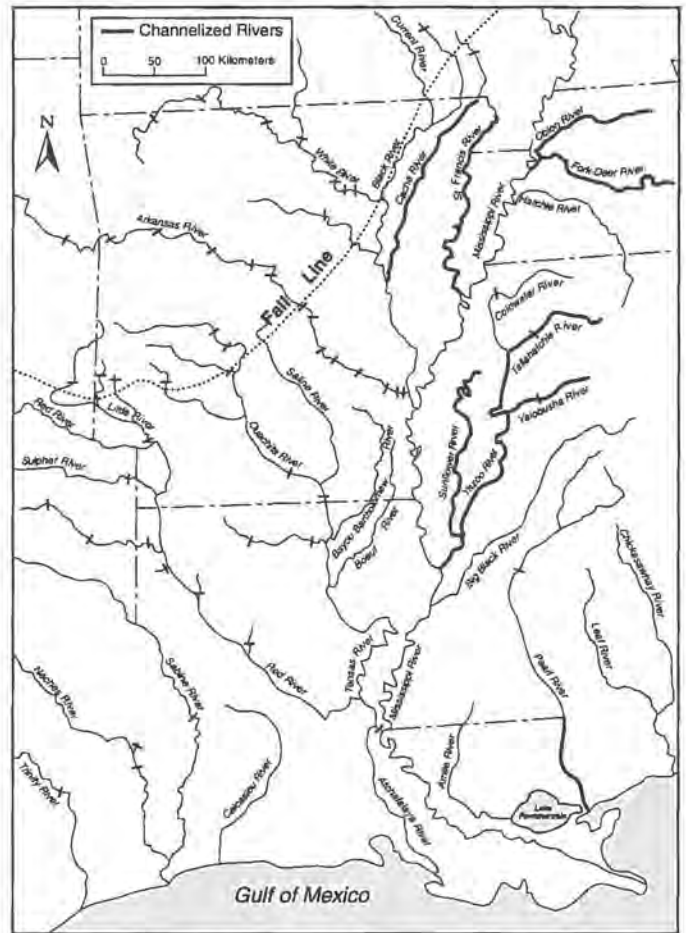


Figure 3: Major rivers in and adjacent to the Mississippi River alluvial valley. Locations of dams are shown.

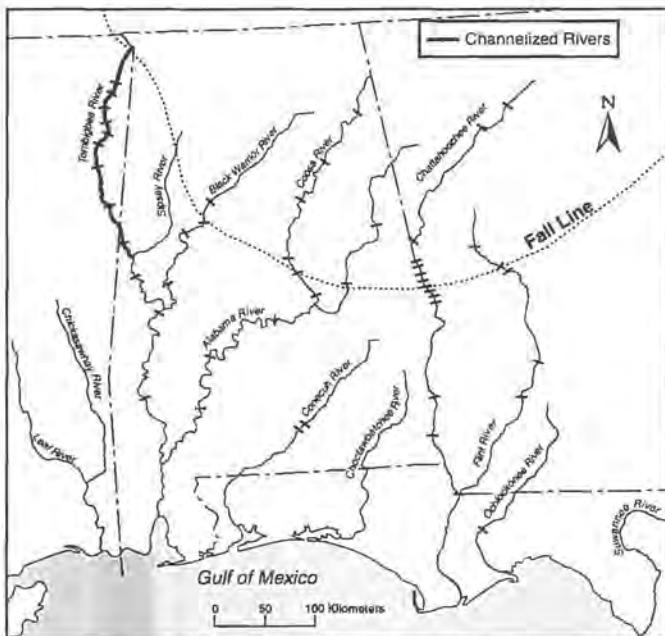


Figure 2: Major rivers in the East Gulf Coastal Plain. Locations of dams are shown.

navigation, such as the Chattahoochee, Black Warrior, and Tombigbee have a series of dams. Not all the dams are within the Coastal Plain; they are common on river segments upstream of the Coastal Plain, including the Arkansas, White, and Ouachita Rivers flowing out of the Ozark Mountains into the Mississippi River valley. Most of the rivers in the East Gulf Coastal Plain, and those in Texas also have dams upstream of the Coastal Plain. Dam construction on several Coastal Plain streams began in the late 1800s to improve river navigation and to allow commercial ships to move upstream of the Fall Line. Several large dams were built in the Gulf Coastal Plain during the first decades of this century for both navigation and flood-control. Major dam construction accelerated during the 1920s and 1930s, but has slowed in recent decades. The last large scale navigation/flood control project in this region was the development of the Tennessee-Tombigbee navigation canal that allowed barges to travel from the Tennessee River to the Gulf of Mexico by way of the Tombigbee, Black Warrior and Alabama Rivers. Ten dams with locks in addition to extensive levee systems were constructed.

Table 1. Dams and channelization on major rivers and their tributaries in the Gulf Coastal Plain.

Rivers	Dams		Channelization	
	main stream segment	upstream or tributaries	main stream segment	tributaries
East Gulf Coastal Plain				
Amite (MS-LA) ¹				
Pearl (MS)	x			x
Leaf-Pascagoula (MS)				
Chichasawhay (MS)				
Mobile-Alabama (AL)	x	x		
Tombigbee (MS-AL)	x	x	x	x
Black Warrior (AL)	x			
Sipsey (AL)				
Escambia-Conecuh (AL-FL)	x			
Choctahatchee (AL)				
Pea (AL-FL)	x			
Chattoahoochee (GA-FL)	x	x		
Flint (GA-FL)	x			
Ochlockonee (GA-FL)	x			
Suwannee (GA-FL)				
Mississippi River Tributaries				
Obion-Forked Deer (TN)			x	x
Hatchie (TN)				x
Yazoo (MS)	x	x	x	
Big Sunflower (MS)			x	x
Tallahatchie-Coldwater (MS)	x		x	x
Yalobuska (MS)	x		x	x
Big Black (MS) ²				
St. Francis (AR)	x		x	x
Arkansas (AR)	x	x	x	
White (AR)	x	x		
Black (AR)				x
Cache (AR)			x	x
Red (LA)		x		
Ouchita-Black (AR-LA)	x	x		
Saline (AR)				
Bayou Bartholomew (AR-LA)				
Boeuf (AR-LA)			x	
Atchafalya (LA)	x			
West Gulf Coastal Plain				
Calcasieu (LA)				
Sabine (LA-TX)	x	x		
Neches (TX)	x	x		
Trinity (TX)	x	x		
Brazos (TX)	x	x		
Colorado (TX)	x	x		
Guadalupe (TX)	x			
Nueces (TX)	x	x		

¹extensive gravel and sand mining in the lower floodplain.²some channel modifications for flood control, mostly channel cut-offs.

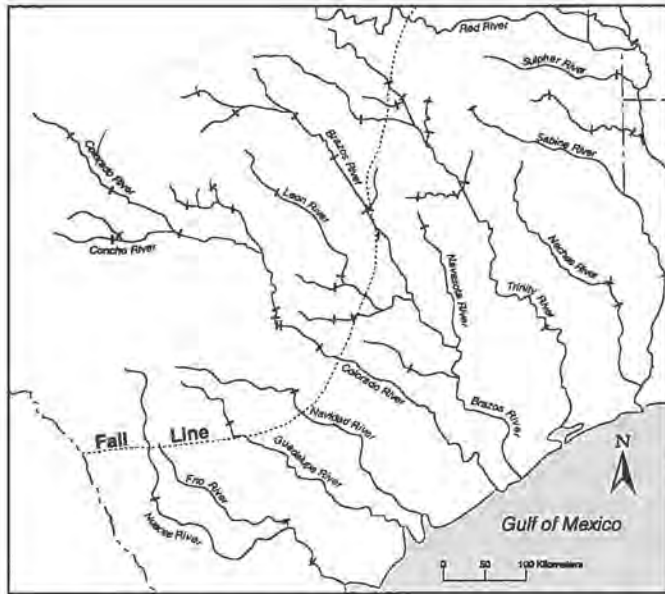


Figure 4: Major rivers in the West Gulf Coastal Plain. Locations of dams are shown.

The alluvial rivers of the Gulf Coastal Plain historically have had high sediment loads. The reservoirs created by dams, however, effectively trap almost all incoming suspended sediment, which can have a significant impact on downstream sediment loads and channel morphology. Water released from the dams has little sediment compared to pre-dam conditions, and sediment eroded below the reservoirs is not replaced. These effects of reservoirs are severe immediately below the dam, but decrease with distance downstream as tributaries join the main channel (Williams and Wolman 1984). There can be a

considerable distance below the dam (in some cases 100 km or more) before a stream regains a balance between erosion and deposition, although rates are highly variable depending on sediment transport and channel-bed material (Hales et al., 1970; Strand, 1977). Channel degradation is often associated with bank erosion and widening of the channel.

The reservoirs on the surrounding uplands trap sediment and the controlled releases disrupt natural seasonal water-level fluctuations. The downstream river segments well within the Coastal Plain are not necessarily highly degraded, however, and in many cases these streams carry high sediment loads and have at least near-normal seasonal water-level fluctuations. This is generally true for the lower White River in Arkansas and the Pearl and Yazoo Rivers in Mississippi that have dams located far upstream of their mouths. The distance downstream for a Coastal Plain river to recover to near normal pre-dam conditions is not known and certainly varies among streams. If large tributaries with unaltered hydrology and sediment loads enter the main channel, the recovery distance downstream may be small (Williams and Wolman, 1984). In contrast, the rivers that have a series of dams are the most severely degraded, both physically and biologically. Regularly spaced dams have transformed some rivers (including the Chattoohochee, Alabama, Black Warrior, and Tombigbee Rivers, all in the East Gulf Coastal Plain) into a series of pools with a relatively small annual change in stage and low sediment loads compared to pre-dam conditions (Figure 5).

CHANNELIZATION: Many of the major streams in the lower Mississippi River valley and adjacent alluvial valleys have

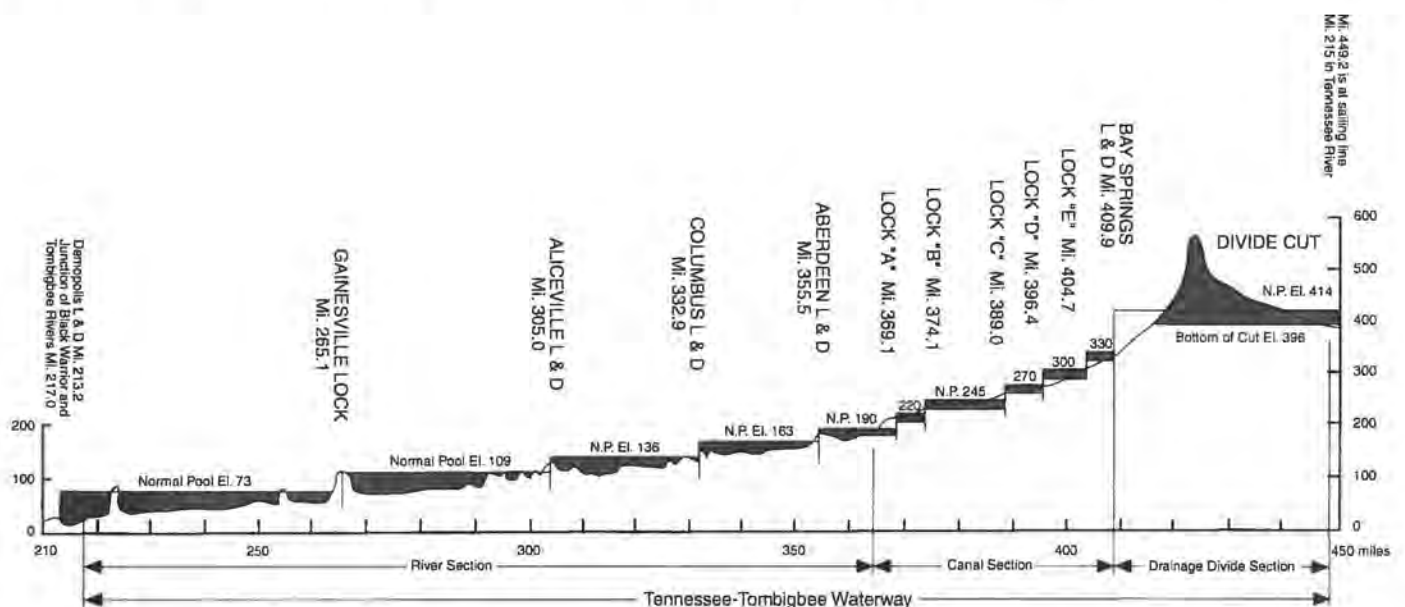


Figure 5: Latitudinal profile of the Tombigbee River after the construction of navigational locks and dams showing river elevations.

been channelized for flood control (Figure 3). These include the Obion and Forked Deer Rivers in western Tennessee, the Big Sunflower, Tallahatchie, Yalobuska, and Yazoo Rivers in Mississippi, and the Cache and St. Francis Rivers in Arkansas. Many of the smaller tributaries in this region have also been channelized (Figure 6). Channelization typically includes deepening and widening of the stream channel, and shortening its length by cutting off meanders. The purpose is to increase channel capacity and flow velocity so that water moves more efficiently downstream and flooding is reduced. Periodic dredging and maintenance are necessary to remove sediment that typically accumulates on the downstream sections of channelized rivers (Emerson, 1971; Schumm et al., 1984; Simon 1989) and to prevent the redevelopment of meanders.

Channelization by county or state governments became widespread in the early part of the century. Many of the first attempts at channelization had a relatively minor impact on the streams. Few meanders were cut off in most cases and channel enlargement was minimal. Also, the channelized sections of the rivers were usually not main-

tained and therefore they began reverting back toward a hydraulically inefficient, meandering channel. In recent decades, the U.S. Army Corps of Engineers and the Soil Conservation Service have been responsible for the channelization of most Gulf Coastal Plain streams. Plans are currently being developed to channelize or rechannelize several streams within the Mississippi River drainage, including the Big Sunflower River in Mississippi, and the upper sections of the Hatchie River, also in Mississippi, which is one of the few remaining free-flowing streams in the Gulf Coastal Plain.

Channelization effectively limits flooding on the upper reaches of streams by increasing channel capacity and flow velocity (Brookes, 1988). Ordinarily, floodwater is stored in soils and by surface impoundment (Hill, 1976). After channelization, however, the water is mostly contained within the channels. While channelization effectively decreases flooding upstream, the higher discharge increases flooding downstream. Channel enlargement reduces frictional resistance by creating a smoother perimeter and more uniform channel and by increasing the hydraulic radius (ratio of channel cross-sectional area to the wetted perimeter). Also, the straightened alignment increases the water-surface gradient. These changes in channel morphology result in an increase in water velocity. Runoff from the channelized portion of the drainage basin converges at downstream locations faster than the stream channel can accommodate, resulting in an increased flood frequency (Hillman, 1936; Lane, 1947; Emerson, 1971; Cambell et al., 1972; Little, 1973; Shankman and Pugh, 1992).

The faster flow velocity after channelization causes upstream channel degradation and accelerated erosion of tributaries. Stream-bed erosion results in high, oversteepened channel banks that are highly susceptible to erosion. Unstable banks composed of highly erodible sediment have in some cases retreated more than 1 m/year (Hupp, 1987). Downstream sediment deposition reduces the cross-sectional area of the channel, which further contributes to flooding (Yearke, 1971; Piest et al., 1977; Schumm et al., 1984). Increased sediment delivery from tributaries, caused by either channelization or deforestation, can aggrade streams. Because the alluvial valleys are areas of low relief, channel obstructions causing a small increase in water-surface elevation can flood large areas, in some cases thousands of hectares.

River Regulation and Ecosystem Degradation

In recent decades there have been numerous studies documenting declining aquatic and riparian populations and species diversity as a result of both dams and channelization (see reviews by Petts, 1985 and Brookes, 1988). The changes in channel morphology, hydrology, and water quality in Coastal Plain streams are often so severe that river ecosystems may be irreparably damaged (Swales, 1989). Impounded rivers, particularly those with

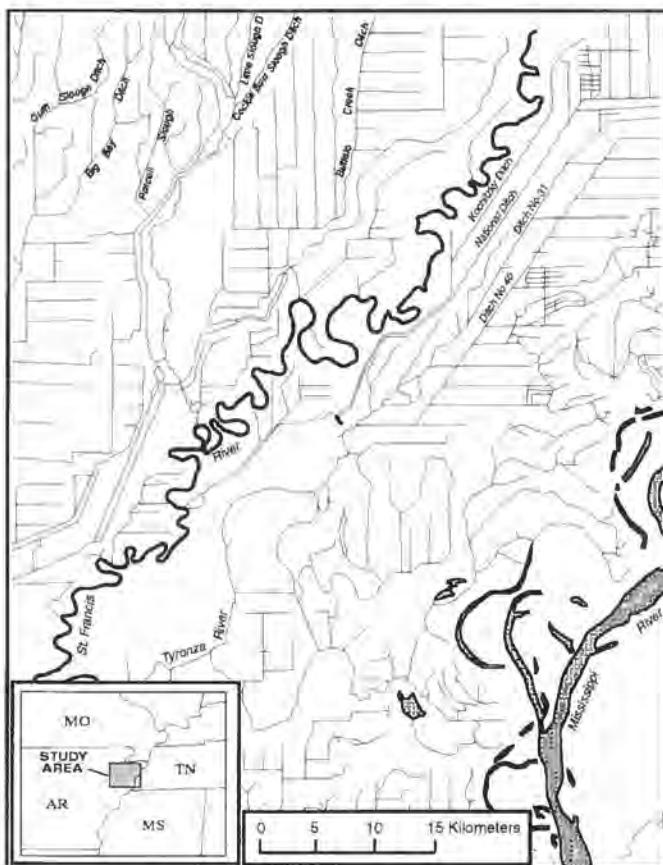


Figure 6: An area of the lower Mississippi River alluvial valley showing diversion canals and extensive tributary channelization along the St. Francis River in eastern Arkansas. Source: U.S. Geological Survey 7 1/2 minute topographic maps.

a series of dams such as the Black Warrior, Chattahoochie, and Tombigbee Rivers, have permanently altered channel conditions and cannot be expected to recover. Channelization, at least initially, will cause an even more severe biological impact than that caused by upstream dams. Natural hydrologic processes, however, will begin operating with the redevelopment of meanders and a pool-riffle sequence if the straightened channels are not maintained.

Aquatic Communities: Channel modifications can affect aquatic communities through the loss of habitat diversity, loss of instream cover, and changes in the flow regime and water quality (Simpson et al., 1982; Swales, 1982; 1989). As previously noted, these conditions are highly variable below dams depending on reservoir release patterns and the size of undammed tributaries entering the river. The regeneration of many aquatic organisms depends on undisturbed flow regime characteristics, and major hydrologic changes will result in a decline of some of the most abundant species. Changes in water quality, particularly temperature, dissolved oxygen, and suspended sediment will also have a detrimental affect on aquatic populations. Water released from dams has a lower sediment load than in free-flowing streams. Conversely, the greater velocity of channelized streams significantly increases the sediment loads. In both cases, the environmental changes of affected stream segments may exceed the physiological tolerance of some species (Bayless and Smith, 1967; Tarplee et al., 1971).

Channelized streams and those dredged for navigation lose channel heterogeneity that is essential for the regeneration of many species. Straightened channels disrupt the normal pool and riffle sequence occurring on most Coastal Plain streams (Keller, 1978). The loss of deep pools eliminates sheltered channel sites that normally provide cover for fish. Shallow sand and gravel beds that create riffles provide a necessary habitat for fish spawning and for many invertebrates. The dredging of these shallow beds and increased sediment deposition that typically occurs in channelized streams degrades potential spawning sites on the channel bottoms, decreases aquatic vegetation, and kills many benthic invertebrates causing a decline in fish that feed on these organisms (Brookes, 1988). Straightened and dredged channels also largely eliminate undercut banks and overhanging vegetation that provides shelter.

Lateral channel migration erodes banks causing trees to fall into the channel, and therefore, most Coastal Plain streams naturally contain a large quantity of woody debris. The western-most Coastal Plain streams in Texas typically contain less organic debris than rivers to the east because of the relatively sparse forest vegetation in the adjacent river bottoms. Downed trees are often removed from the large Coastal Plain rivers for improved navigation. Snags are also removed from channelized and sometimes

nonchannelized streams to reduce flooding. Most Coastal Plain streams probably have only a small portion of the snags they once contained. The removal of organic debris from channels in low gradient Coastal Plain rivers is highly destructive to aquatic ecosystems. Submerged woody debris is colonized by a large number of aquatic invertebrates (Wallace and Benke, 1984). Also, snags provide a major source of food for fish (Marzolf, 1978; Benke et al., 1985). Several of the most common fish species obtain a majority of their prey from snags. Without woody material there is a reduction in the abundance of fish.

Terrestrial Communities: The destructive effects of direct channel modification on water quality and aquatic ecosystems have been well documented. Until recently, however, there has been little attention given to the effects of damming and channelization on terrestrial bottomland ecosystems. Among the most significant impacts on terrestrial ecosystems is the altering of the magnitude and duration of flooding. This can result in a significant long-term change in floodplain plant community composition. Flood frequency and duration are greatest in the lowest bottomland sites adjacent to the channel. With increasing distance from the lower floodplain there is a decrease in flood frequency and a corresponding spatial gradient of plant communities composed of species with progressively lower flood tolerance (Penfound, 1952; Huffman and Forsythe, 1981; Wharton et al., 1982). A significant reduction in flooding will ameliorate the most important factor creating these cross-valley community gradients (Malanson, 1993; Bendix, 1994), and will result in a shift toward a homogeneous floodplain composed of later successional mesic species that previously occupied only the outer floodplain.

Many of the bottomland tree species are dispersed primarily by water and therefore are limited to the portion of the alluvial valley subject to flooding. However, along stream segments where a reduction in flood frequency and depth occurs, the potential distribution of these species is restricted to a narrower portion of the floodplain. Infrequent flooding also may allow the establishment and potential codominance of upland species that were precluded from floodplains by regular inundation. A decrease in flooding will lower overbank sedimentation and nutrient inputs into downstream bottomland habitats and the flow of bottomland nutrients back into stream channels. Reduced spring flooding causes drought stress on high floodplain surfaces and lowers floodplain sediment deposition that affects fertility and the creation of optimal seed bed conditions.

The complex vegetation patterns in the alluvial wetlands are not entirely attributable to gradients in the hydro-period. Finer scale vegetation patterns are attributable to the lateral movement of meandering streams. Channel migration results in complex patterns of new surfaces created by point-bar deposition and the filling in

of oxbow lakes. This process results in a mosaic of distinct forest communities whose composition depends largely on surface age and elevation (Shelford, 1954; Shankman and Drake, 1990; Shankman, 1993). The new surfaces are rapidly colonized by species of high flood tolerance that require flooding for seed dispersal and exposed sites and high light levels for successful establishment. Sediment deposited during flooding raises young surfaces, making them less susceptible to later inundation and more suitable for the establishment of less flood tolerant species that eventually replace the early arrivals. Therefore, the early colonizing species are uncommon on older surfaces that have been raised by verticle accretion. Stabilized channels preclude the formation of point-bars and oxbows, the primary regeneration sites for many species. Along many Coastal Plain rivers, a large-scale disturbance mechanism that is an important factor controlling spatial heterogeneity in the lower bottomland sites has been eliminated.

Changing Land-use and Deforestation

The alluvial valleys of the Coastal Plain are areas of fertile soils and low relief and therefore are among the most productive farmlands in the eastern U.S. The modified hydrology along some stream segments, in particular the lower peak discharges caused by dams and channelization, further encourages deforestation of bottomland forests and land-use conversion to agriculture. Large areas of many of the alluvial valleys along most of the major Coastal Plain streams have been deforested. This is most pronounced in the lower Mississippi River Valley including large sections of eastern Arkansas and Louisiana, and western Mississippi (Siniard, 1975; Hart, 1978). The lower segments of some of the largest Coastal Plain streams are within this valley, including the Yazoo, St. Francis, Arkansas, White, Red, and Ouachita Rivers. Greater than 90 percent of the land surface of many of the counties in this region is in cultivation (U.S. Department of Commerce, 1969-1987). Much of this region is protected from flooding by an extensive levee system.

The removal of bottomland forest vegetation can have a significant effect on the magnitude of downstream flooding. There is a reduction in velocity as flood-water moves out of the channel and into the surrounding floodplain. The vegetative cover and surface organic debris in the forested bottoms increases the frictional resistance to overland flow (Gosselink et al., 1990a, b). Also, debris and beaver dams in gullies and small tributaries cause frequent surface impoundment in the lower bottomlands. Slower water velocity and impoundments enhance surface water infiltration which further increases bottomland water-storage capacity. Deforestation and the removal of organic matter on bottomland sites eliminates many of the impoundments and allows faster runoff, which contributes to higher downstream peak flows and a higher probability of flooding.

Because of the high water velocity in river channels during floods, Coastal Plain streams carry a large amount of sediment. The slowing of velocity as water moves from the channel to the bottomlands allows sediment deposition and gradual buildup of floodplain surfaces. Some sediment is carried back into the stream channels by receding flood water. However, faster runoff of bottomland sites caused by deforestation and removal of organic matter results in the development of gullies and increases the potential for erosion and transportation of sediment into river channels. This is particularly important if land is cultivated, in which case there is little surface organic material to hold the soils in place. The low gradient Coastal Plain streams are often unable to transport the additional sediment downstream. As a result, the river bed will aggrade, reducing the cross-sectional area of the channel. Stream channels that are shrinking because of high rates of erosion and sedimentation will have a higher water-surface elevation with an equal discharge, and therefore a greater probability of flooding. The higher peak flows caused by deforestation and rapid runoff from the previously forested floodplain may not be accommodated by the shrinking channels downstream.

Free-flowing Streams and Prospects for the Future

There are ten streams in the Gulf Coastal Plain that are still considered to be free flowing, here defined as streams that have not been channelized and are without dams or other significant channel construction on the major stream segments that would affect hydrology, geomorphic conditions, or water quality. These are the Hatchie, Big Black, Black, and Bayou Bartholomew Rivers in the Mississippi River drainage; the Sipsey, Choctahatchee, Leaf-Pascagoula, Chichasawhay, and Suwannee Rivers in the East Gulf Coastal Plain; and the Calcasieu River in the West Gulf Coastal Plain. These streams have escaped direct channel modifications that would have a significant affect on ecological conditions, and therefore are notable exceptions to altered rivers of this region. There has been no significant channel construction on the Amite River in Louisiana, but is not classified as free-flowing. There is extensive gravel mining on the mid and lower sections of this river that have altered sedimentation and channel morphology (Mossa and McLean 1997).

In the absence of channel construction, the free-flowing streams may appear to have undisturbed hydrology and geomorphology. But it is not likely that these streams function as they did before European settlement that began in the 1800s. All of these streams have been subjected to physical changes within the watershed. Probably the most important landscape modification affecting free-flowing streams is deforestation and land conversion to agriculture. Because these rivers continue to flood, a fairly large portion of the lower bottomlands of many of the free-flowing streams is still forested. However, extensive portions of the outer floodplain in addition to the

upland watershed have been converted to pasture or cultivation. So, although these streams have escaped direct channel modification, increased runoff from agricultural fields throughout the watershed has a direct effect on channel morphology and therefore hydrology and water quality.

Modification of tributaries can also significantly affect otherwise undisturbed streams. The Black River in central Arkansas and Hatchie River in western Tennessee are among the few streams in this region that has not been dammed or channelized. Both are classified as free-flowing and the Hatchie River was designated as a State Scenic River in 1968. For both, there have been only minor modifications of the main channels. But many of the major tributaries have been straightened which has resulted in increased discharge into the main stem of these rivers. Flooding on the downstream sections of the Hatchie River has increased significantly during the past decades, although it is not clear if this has been caused by tributary channelization, land-use conversion to agriculture, or a combination of both (Nabb and Shankman 1997). Channelization of any one or two tributaries would probably have only a minor effect on the main stem of the river. But small land-use or channel modification projects within the watershed incrementally alter how the main stream functions. The cumulative effect of disturbances present a potential problem for the few remaining free-flowing streams in the Gulf Coastal Plain. Any single construction project on tributaries may be justified for local flood control or other economic reasons if, when viewed in isolation, it has a negligible effect on the river. But the sum of channel construction projects or land-use changes within the watershed may have a significant impact on both the physical and ecological characteristics of the river.

The largest area of intact streams and forested alluvial wetlands now is along the tributaries of the major streams. These tributaries are not large enough for navigation or hydro-electric power generation. Still, they are highly vulnerable. Small streams are often channelized and transformed into drainage canals for flood control, a trend that has continued in recent years. Without the development of an appreciation for the connectivity of river networks and the effects of land-use and river modifications on downstream river segments, channelization of small tributaries may be erroneously viewed as inconsequential. As previously mentioned, channelization of small, low-order streams effectively decreases flooding in the adjacent floodplain, but at a cost to landowners downstream who are affected by worsening water quality and increased flooding.

The free-flowing streams in the Coastal Plain are increasingly viewed as an important resource worthy of at least some sort of protection against further environmental degradation. But this is not necessarily a prevailing view and in the Coastal Plain there are continuing efforts

for river modifications aimed at flood control and drainage of wetlands in adjacent bottomlands. Wetland protection laws, most notably Section 404 of the Clean Water Act that prohibits unauthorized filling of wetlands, are harshly criticized for restricting development. Also, proposals for new dams and river channelization, although much less common than in recent decades, have continued. The new proposals for flood control projects are usually for streams that are already dammed or channelized. Dredging and maintenance of channelized streams or the construction of new dams on rivers already dammed is probably more acceptable than major modifications on the few existing free-flowing. However, none of the designated free-flowing streams in the Gulf Coastal Plain have a protected legal status. It is possible that any or all of the remaining free-flowing streams in this region will be dammed or channelized. The greater threat, at least in the immediate future, comes from small incremental changes to the main river channel or tributaries, or to the floodplain or watershed surfaces.

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Allozyme Variation in the Longnose Shiner, *Hybopsis longirostris* (Teleostei, Cyprinidae)

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ABSTRACT: Titus, Thomas A., E.O. Wiley, and Mitchell Allen. 1999. Allozyme Variation in the longnose shiner, *Hybopsis longirostris* (Teleostei, Cyprinidae) Bulletin of the Alabama Museum of Natural History, Number 20:11-17, 2 tables, 3 figures. Allozyme variation was examined for 17 presumptive gene loci in 12 populations of *Hybopsis longirostris* from the southeastern United States. Nine loci were polymorphic. A hierarchical analysis of among-population genetic variation revealed that 79.9% of the variation was explained by differences between allopatric regions east and west of the Mobile Bay drainage, 16.4% of the variation was attributable to genetic differences among drainage systems within allopatric regions, and 3.7% was attributable to variation among populations within drainages. A cluster analysis based on Rogers' genetic distance indicates a relationship between genetic and geographic distance. A Distance Wagner tree and a parsimony tree based on allelic frequencies, both rooted with the closely related *Hybopsis ammophilus*, indicate that eastern and western populations of *H. longirostris* each form a monophyletic group. These data suggest that the eastern and western forms are highly divergent genetically, and that recurrent gene flow probably occurs among drainages within allopatric regions.

Introduction

The central Gulf Coastal region of the southeastern United States is inhabited by a diversity of freshwater vertebrates. Many sister species pairs exhibit geographic boundaries demarcated by the Mobile Bay drainage, with one member of the pair inhabiting drainages to the west of the Mobile and the other member occurring in drainages to the east (reviewed by Wiley and Mayden, 1985). Freshwater fish taxa exhibiting this pattern of distribution include *Ammocrypta beanii* and *A. bifascia* (Simons, 1988), the *Hybopsis winchelli* complex (Clemmer, 1971), *Eltheostoma chlorosomum* and *E. davisoni* (Page, 1983), and *Gambusia affinis* and *G. holbrooki* (Wooten et al., 1988). Wiley and Mayden (1985) suggested that this common distributional pattern resulted from a single vicariance event centered around the Mobile Bay drainage.

The longnose shiner, *Hybopsis longirostris*, is a common inhabitant of shallow, sandy streams in the Gulf Coastal region of Louisiana, Mississippi, Alabama, and Florida (Hubbs and Walker, 1942), and represents a possible exception to the taxonomically widespread pattern of speciation on either side of the Mobile Bay drainage. *Hybopsis longirostris* is replaced in the Mobile Bay drainage by a related species, *H. ammophilus* (Suttkus and Boschung, 1990), dividing the range of *H. longirostris* into two allopatric regions east and west of the Mobile system. Despite this geographic disjunction, populations of *H. longirostris* are morphologically similar and are thought not to have speciated as a result of the Mobile Bay vicariance event.

In a phylogenetic analysis of the *H. dorsalis* species group based on allozyme data, populations of *H.*

longirostris from east and west of the Mobile Bay formed a monophyletic group, and these populations were genetically distinct, sharing no electromorphs at three of the allozyme loci studied (Wiley and Titus, 1992). However, only a single population of each allopatric form of *H. longirostris* was examined, and additional data are needed to substantiate the limits of this genetic disjunction. The purpose of this investigation was to more thoroughly examine genetic variation within *H. longirostris* throughout its range to 1) more accurately characterize the pattern of genetic variation among allopatric forms, and 2) estimate genetic differentiation among drainages within each allopatric region.

Methods

Specimens were collected by seining from the following localities (numbers in parentheses correspond to those in Table 1):

(1) Pascagoula R. dr., Leaf R. 3 km S Moselle, Jones Co., Mississippi (KU 23051). (2) Pascagoula R. dr., Okatoma Cr. near Lux, Covington Co., Mississippi (KU 23052). (3) Escatawpa R. dr., Escatawpa R. at Rd. 96, Mobile Co., Alabama (KU 23053). (4) Biloxi R. dr., Biloxi R. at Big Biloxi Campground, Harrison Co., Mississippi (KU 23054). (5) Pearl R. dr., Beasha Cr. 7 km S Laurel Hill, Neshoba Co., Mississippi (KU 23049). (6) Jourdan R. dr., Hickory Cr. at Hwy. 43, Hancock Co., Mississippi (KU 23050). (7) Perdido R. dr., Hollinger Cr., Baldwin Co., Alabama (KU 23043). (8) Perdido R. dr., Styx R. at Hwy. 87, Baldwin Co., Alabama (KU 23044). (9) Escambia R. dr., Big Escambia Cr. at Rd. 17, Escambia Co., Alabama (KU 23045). (10) Yellow R. dr., Yellow R. at Hwy. 84, Covington Co., Alabama (KU 23046). (11) Choctawhatchee R. dr., Holley Mill Cr. at Hwy. 189, Coffee Co., Alabama (KU 23047). (12) Alabama R. dr., Little R. at Hwy. 59, Monroe Co., Alabama (KU 23048). (13) *Hybopsis ammophilus* (Alabama R. dr., Alabama (KU 22935); Tombigbee R. dr. (KU 22936, 22937)).

Voucher specimens were deposited in the Division of Ichthyology, Museum of Natural History, University of Kansas.

Specimens were immediately frozen in liquid nitrogen and stored at -70°C . Skeletal muscle and eye/brain were dissected and homogenized separately in a 1:1 (v:v) mixture of tissue and distilled water. Homogenates were centrifuged at 15,000 rpm for 10 min at 5°C . Within 72 h the supernatant fractions were electrophoresed at 5°C on horizontal starch gels composed of 12% hydrolyzed potato starch. Ten enzymes representing 17 presumptive gene loci were resolved on two buffer systems: Tris-citrate, pH 8.0 (Selander et al., 1971), skeletal muscle (mAcon-A, G3pdh-A, mMdh-A, sMdh-A, sMdh-B, sMdhp-A) and Tris-citrate, pH 7.0 (Whitt, 1970), eye/brain and skeletal muscle (Gpi-A, Gpi-B, Pgdh-A, Pgm-A, Tpi-A, Tpi-B¹, Tpi-B², Ck-A, Ck-B, Ck-C, and Ak-A). Enzyme nomenclature follows the recommendations of the International Union of Biochemistry Nomenclature

Committee (1992) and locus nomenclature follows the recommendations of Buth (1983). Electromorphs, herein referred to as alleles, were labelled a, b, c, etc. in order of increasing anodal mobility. Allelic designations are relevant to this study only.

Chi-square tests for conformation of genotypic frequencies to Hardy-Weinberg equilibrium and allelic heterogeneity among populations were performed. Significance values for Chi-square tests for Hardy-Weinberg equilibrium were adjusted for multiple comparisons by dividing 0.05 by the number of loci tested in each population and significance values for Chi-square contingency Tables were adjusted by dividing 0.05 by the number of loci tested in each group of populations. Three indices of within-population variation were calculated: mean heterozygosity by direct count (H); mean number of alleles per locus (A); and the percentage of loci polymorphic (P). Genetic variation among drainages was estimated for each allopatric region separately using the F-statistics of Wright (1978). Hierarchical F-statistics (Wright 1978) were computed at the level of populations (P), drainages (D), allopatric regions (A), and total (T). The following comparisons were made: population x total (F_{PT}), population x drainage (F_{PD}), drainage x allopatric region (F_{DR}), and allopatric regions x total (F_{RT}). Genetic similarity among pairwise comparisons of populations was estimated using Rogers' (1972) index of genetic distance (D_R). A UPGMA cluster analysis (Sneath and Sokal, 1973) using genetic distances was performed to compare genetic similarity with geographical proximity and to compare overall genetic differentiation with that reported for other species in this region. A Distance Wagner analysis was also performed and rooted with the combined data from two populations of *H. ammophilus*. Statistics were calculated only for polymorphic loci within *H. longirostris*. Indices of genetic variation, UPGMA clustering, and the Distance Wagner analysis were computed using BIOSYS-1 (Swofford and Selander, 1981). A parsimony analysis of the allelic frequency data was also performed following the algorithm of Swofford and Berlocher (1987) using the program FREQPARS, version 1.0.

Results

The following loci were monoallelic in all samples: mAcon-A, Gpi-A, Tpi-B¹, Tpi-B², and Ck-A. Three loci, Ak-A, Ck-B, and sMdh-A, exhibited only rare allelic variants and were excluded from further analyses because they did not meet the 95% polymorphic criterion.

Nine loci were polymorphic. Allelic frequencies, sample sizes, mean number of alleles (A), mean heterozygosity (H), and percentage of loci polymorphic (P) for polymorphic loci are summarized in Table 1. Mean number of alleles per locus ranged from 1.1 (PERDIDO 1, PERDIDO 2, and BILOXI) to 1.9 (PASCAGOULA 2). Percentage of polymorphic loci was from zero (BILOXI) to 33.3 (CHOCTAWHATCHEE, JOURDAN, and

Table 1. Genotype arrays, mean number of alleles per locus (A), percent loci polymorphic (P), and mean heterozygosity (H), for nine variable loci in *Hybopsis longirostris*.

Locus	Population												
	1*	2	3	4	5	6	7	8	9	10	11	12	13
Ck-C	bb(25)	bb(24) ab(1)	bb(27)	bb(13)	bb(15)	bb(21)	cc(16)	cc(30)	cc(16)	cc(36)	cc(32)	cc(30)	bb(10)
G3pdh-A	bb(32)	bb(25)	bb(27)	bb(21) bc(2)	bb(20)	bb(20)	aa(16)	aa(30)	aa(14)	aa(37) ac(3)	aa(32)	aa(30)	bb(21)
Gpi-B	cc(32)	cc(25)	cc(27)	cc(23)	cc(20)	cc(23)	cc(16)	cc(30)	cc(15) bc(1)	cc(32) cd(2) ac(1)	cc(17) cd(13) dd(2)	cc(30)	cc(21)
mMdh-A	aa(32)	aa(25)	aa(26)	aa(5) ab(11) bb(7)	aa(20)	aa(23)	aa(15)	aa(23) ab(4) bb(3)	aa(16)	aa(40)	aa(32)	aa(30)	aa(21)
mMdh-B	bb(32)	bb(25)	bb(10) ab(9) aa(5)	bb(7) ab(11) aa(5)	bb(11) ab(6) aa(3)	bb(20) ab(2) aa(1)	bb(15)	bb(3) ab(4) aa(23)	bb(3)	bb(38)	bb(29)	bb(30)	bb(21)
sMdhp-A	aa(30)	aa(25)	aa(16) ab(9)	aa(23)	aa(20)	aa(16) ab(5) bb(1)	aa(15)	aa(27)	aa(16)	aa(39)	aa(30)	aa(23)	aa(23)
Pgdh-A	cc(30)	cc(25)	cc(26) bc(1)	cc(23)	cd(3)	cc(22) bc(1)	cc(13)	cc(20)	cc(16)	cc(32) bc(6) ac(1) bd(1)	cc(21) bc(2) cd(7) dd(2)	cc(28)	cc(21)
Pgm-A	cc(18) ac(5) aa(3)	cc(20) ac(4) aa(1)	cc(27)	cc(23)	cc(19) ac(1)	cc(21)	cc(13) bc(2)	cc(24) ac(5)	cc(9) ac(3) cd(1) ce(1)	cc(12) ac(13) aa(12)	cc(7) ac(16) aa(9)	aa(30)	cc(21)
Tpi-A	bb(32)	bb(25)	bb(27)	bb(23) ab(5) aa(1)	bb(14) ab(5) aa(1)	bb(21) bc(2)	cc(16)	cc(30)	cc(16)	cc(39) cd(1)	cc(32)	cc(30)	cc(18) cd(2)
A	1.1	1.1	1.4	1.3	1.4	1.4	1.2	1.3	1.4	1.9	1.4	1.1	1.1
P**	11.1	11.1	22.2	22.2	33.3	22.2	22.2	33.3	11.1	22.2	33.3	0	11.1
H***	0.021	0.018	0.090	0.106	0.133	0.049	0.036	0.052	0.047	0.082	0.132	0.007	0.011

*1=Perdido 1, 2=Perdido 2, 3=Escambia, 4=Yellow, 5=Choctawhatchee, 6=Alabama, 7=Pearl, 8=Jourdan,

9=Pascagoula 1, 10=Pascagoula 2, 11=Escatawpa, 12=Biloxi, 13=*Hybopsis ammophilus*

**A locus is considered polymorphic if the frequency of the most common allele does not exceed 0.95.

***Mean heterozygosity calculated by direct count.

ESCATAWPA). Mean heterozygosity was lowest in BILOXI (0.007) and highest in CHOCTAWHATCHEE (13.3). An excess of heterozygotes was observed in two instances: at Pgm-A in PERDIDO 1 and at M-Mdh-A in JOURDAN.

Qualitatively, the nine polymorphic loci can be divided into three classes. One class includes loci sharing virtually no alleles between allopatric regions (Ck-C, G3pdh-A, and Tpi-A). The second class of loci displayed widespread polymorphism in samples from both regions (sMdh-B, Pgdh-A and Pgm-A). The third class of loci exhibited allelic variants that are common only within a single sample (mMdh-A, sMdhp-A, and Gpi-B).

Statistically, all nine polymorphic loci displayed highly significant allelic heterogeneity among samples. Within allopatric regions, F_{ST} ranged from 0.015 (Ck-C) to 0.618 (Pgdh-A) in the eastern samples and from 0.010 (Tpi-A) to 0.464 (Pgm-A) in the western populations (Table 2). Mean F_{ST} was similar in both regions, being 0.335 for eastern samples and 0.320 in western samples. In the hierarchical analysis of genetic variation, F-statistics and variance components for the comparisons population x total, population x drainage, drainage x region, and region x total were combined for all loci. The variance component associated with total genetic variation among samples was 1.845. The variance component explained by genetic variation among regions was 1.474 (79.9% of the total) resulting in a value of 0.717 for F_{RT} . A variance

component of 0.302 (16.4% of the total variation) is explained by comparing drainages within a region, resulting in a value of 0.301 for F_{DR} . The smallest variance component was 0.067 (3.7% of the total variation), and was explained by comparing populations within drainages, resulting in a value of 0.099 for F_{PD} .

The average D_R across all populations was 0.280. Overall genetic divergence among populations is illustrated by the UPGMA phenogram (Fig. 1). The eastern and western populations are clearly differentiated into two clusters. Far less differentiation has occurred within each of these clusters. In the eastern cluster, the two populations within the Perdido River drainage (PERDIDO 1 and PERDIDO 2) were most similar to one another, whereas in the western cluster, the two populations within the Pascagoula drainage (PASCAGOULA 1 and PASCAGOULA 2) do not cluster together. PASCAGOULA 1 clusters with the JOURDAN and PEARL samples, whereas PASCAGOULA 2 is most similar to ESCATAWPA, and is within a cluster that also contains BILOXI.

The Distance Wagner analysis (Fig. 2) indicated that the eastern and western populations form two well-differentiated groups. Based on the rooting established by *H. ammophilus*, slightly more genetic divergence has accumulated along the branch representing the ancestor of the western populations relative to the ancestor of the eastern populations of *H. longirostris*. Distance Wagner relation-

Table 2. F-statistics for eastern and western populations of *H. longirostris*.

Populations	Locus	F_{IS}	F_{IT}	F_{ST}
Eastern	Ck-C	-0.019	-0.003	0.015
	G3pdh-A	-0.045	-0.007	0.036
	mMdh-A	0.036	0.516	0.498
	sMdh-B	0.188	0.410	0.274
	sMdhp-A	-0.044	0.082	0.120
	Pgdh-A	-0.364	0.479	0.618
	Pgm-A	0.322	0.400	0.115
	Tpi-A	0.094	0.205	0.122
	Mean	0.074	0.384	0.335
Western	G3pdh-A	-0.039	-0.006	0.031
	Gpi-B	-0.039	0.141	0.174
	mMdh-A	0.520	0.589	0.143
	sMdh-B	-0.091	-0.014	0.070
	Pgdh-A	0.049	0.118	0.073
	Pgm-A	0.048	0.490	0.464
	Tpi-A	-0.013	-0.002	0.010
	Mean	0.065	0.364	0.320

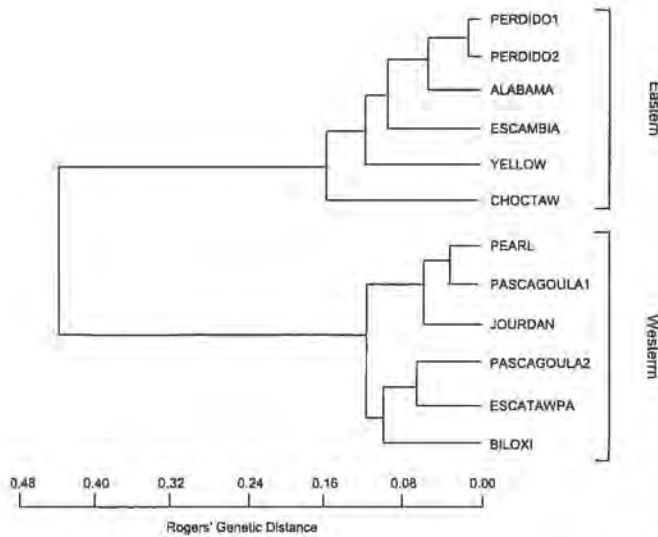


Figure 1. UPGMA phenogram based on Rogers' genetic distance among pairwise comparisons of 12 *H. longirostris* populations.

ships among populations within each allopatric region differ from those indicated by the UPGMA phenogram and indicate very short internal branches supporting relationships among populations.

Parsimony analysis of allelic frequencies for each locus produced a tree of length 18.207 and also indicates two distinct groups corresponding to the eastern and western populations (Fig. 3). The topology of the parsimony tree differed in many respects from that of the UPGMA phenogram and the Distance Wagner tree, but was similar in showing short branches among populations within the eastern and western groups and somewhat more divergence along the lineage leading to the western populations.

Discussion

The allopatric distribution of the eastern and western *H. longirostris* populations should preclude the possibility of gene flow between these two regions. Within allopatric regions, the opportunities for gene flow among drainages are probably restricted to periods of extreme flooding in the lower reaches of these rivers or via stream capture. In both cases, this intermittent gene flow would be more likely between rivers in close geographical proximity, leading to the prediction that genetic differentiation should be less among geographically proximate river systems. Gene flow among populations within a stream is not constrained by geography or physiography, and should result in relatively less genetic differentiation among populations within a drainage than that observed among drainages or allopatric regions.

The data show that the most extensive genetic divergence observed in this study has occurred at the level of allopatric regions. This is indicated by the hierarchical F-

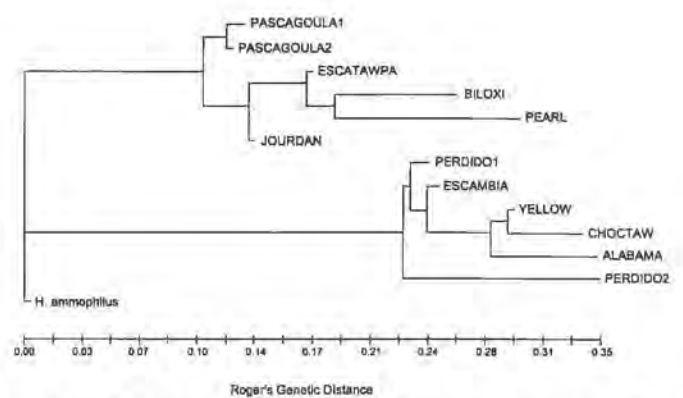


Figure 2. Distance Wagner tree based on Rogers' genetic distance among pairwise comparisons of 12 *H. longirostris* populations and rooted with *H. ammophilus*.

statistics in which 79.9% of the allelic variation among populations is explained at the level of allopatric regions, and the UPGMA cluster analysis, in which populations from these two regions form two very divergent clusters (Fig. 2). This regional variation is primarily attributable to three loci, Ck-C, G3pdh-A, and Tpi-A, at which almost no alleles were shared by populations east and west of the Mobile Bay drainage.

Of the three loci displaying marked regional differences in allelic composition, the only one exhibiting shared alleles between allopatric regions was Tpi-A; two heterozygotes were observed for the common western allele in the sample from the Alabama River. The Alabama drainage is the westernmost drainage of the eastern form of *H. longirostris* and the only river system sampled in which *H. longirostris* is syntopic with *H. ammophilus*, a closely related species (Suttkus and Boschung, 1990). The rare Tpi-A allele in Alabama drainage *H. longirostris* is the

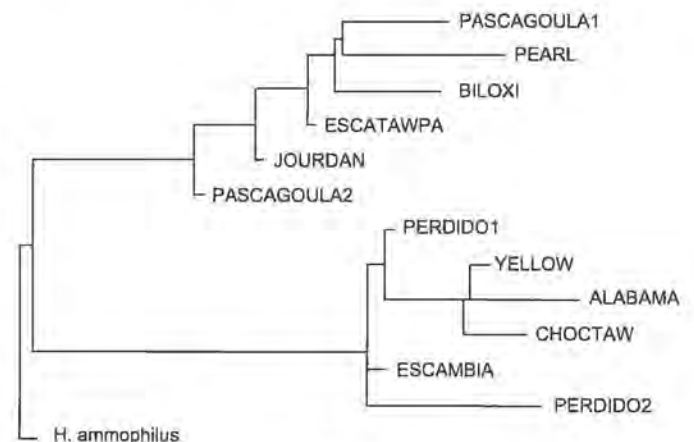


Figure 3. Modified Distance Wagner tree based on parsimony analysis of allelic frequency differences among 12 *H. longirostris* populations and rooted with *H. ammophilus*. Branch lengths are proportional.

common allele in syntopic *H. ammophilus*, and the common allele in *H. longirostris* is present in low frequency in the Alabama drainage *H. ammophilus* (Wiley and Titus, 1992). Either limited hybridization has occurred between these species in this drainage, or this rare allelic variant has been maintained at low frequency over one or two speciation events. The Tpi-A heterozygotes in Alabama River *H. longirostris* were not F_1 hybrids with *H. ammophilus* as indicated by the absence of heterozygote genotypes at several other loci distinguishing these two species. This suggests that if hybridization has occurred it is introgressive. These data indicate the need for further study of this potential contact zone between *H. longirostris* and *H. ammophilus* in the Alabama River drainage.

Genetic variation among drainages within allopatric regions explained 16.4% of the variation in *H. longirostris*. In addition, the average F_{ST} for populations within allopatric regions was very similar, indicating that the same amount of genetic differentiation among populations in western and eastern regions has occurred. In general, geographic distance was a good predictor of genetic similarity among populations. This was particularly evident in the eastern populations; the westernmost samples were from the Perdido and Alabama drainages and are most similar to one another, with increasing genetic divergence found in samples from progressively more eastern drainages. Although the headwaters of the Alabama and Escambia drainages are extensive and in close proximity, the Perdido drainage is between these two systems. The Alabama and Perdido samples were more similar genetically than the Alabama and Escambia samples. This pattern is consistent with the hypothesis that gene flow among drainages occurs when high water results in contact at river mouths, rather than as a result of continuity between headwater streams, a possible outcome of stream capture. In the western samples, the relationship between geographic proximity and genetic distance is less clear. Samples from the two most western drainages, the Pearl and Jourdan, clustered together, and the more eastern drainages, the Escatawpa and Biloxi, were within a cluster. However, populations from within the Pascagoula system do not cluster together.

Replicate populations sampled within the Perdido drainage in the east and the Pascagoula drainage in the west accounted for only 3.7% of the total genetic variation. Overall genetic distance shows that the two Perdido samples were most similar to one another, but the two samples from within the Pascagoula drainage did not cluster together; PASCAGOULA 1 clustered with a more western cluster that includes the Jourdan and Pearl drainages and PASCAGOULA 2 clustered with the more eastern Escatawpa and Biloxi populations. Differentiation between these populations was apparently the result of frequency differences at one locus, in particular a higher frequency of the Pgdh-A "d" allele in PASCAGOULA 2 relative to PASCAGOULA 1. The Pascagoula localities are

in close proximity, with one from Leaf River and the other from Okatoma Creek near its confluence with Leaf River, suggesting that the apparent lack of genetic similarity between these samples was the result of sampling error. In addition, Stein et al. (1985) found three populations of *Lythurus roseipinnis* from widely separated localities within the Pascagoula system to be genetically most similar to one another, indicating no taxonomically widespread pattern of genetic discontinuity within this drainage. Because our sampling design was intended primarily to elucidate genetic variation among allopatric regions, we have examined few replicate samples within drainages, and the differentiation exhibited by the Pascagoula samples suggests that patterns of genetic variation within drainage systems should be evaluated further for *H. longirostris*. More extensive sampling within drainages may also provide a better estimate of the genetic relationships among drainages within allopatric regions.

The average D_R among *H. longirostris* populations is 0.280. This value is comparable to that observed among populations of *Gambusia* (average $D_R = 0.39$) from the southeastern United States (Wooten et al., 1988), but is considerably higher than the average D_R of 0.08 for the *Lythurus roseipinnis* complex (Stein et al., 1985). Preliminary data for the *Hypopsis winchelli* complex (Shaw et al., 1995) suggest that in the central Gulf coast region *H. longirostris* populations are far more differentiated allozymically than are populations of *H. winchelli*. Also, members of the *L. roseipinnis* and *H. winchelli* complexes are morphologically distinct (Clemmer, 1971; Snelson, 1972), whereas populations of *H. longirostris* are not distinguishable based on traditional scalation and morphometric characters (K. Wollter, unpublished data). Thus, based on the lack of morphological variation *H. longirostris* was previously thought to be an exception to the vicariant pattern exhibited by other species pairs along the central Gulf Coast. However, the allozyme data indicate that populations of this species have developed considerable genetic differentiation as a result of the Mobile Bay vicariance event. The taxonomic status of eastern and western *H. longirostris* should be reevaluated.

Acknowledgements

We thank R. Cashner and S. Stevensen (University of New Orleans), D. Etnier (University of Tennessee), H. Bart (Auburn University), and F. Cross, T. Schmidt, K. Shaw, A. Simons, and D. Siegel-Causey (University of Kansas) for assistance with field work. K. Wollter made valuable comments on the manuscript. Funding was provided by University of Kansas General Research Fund Grant #3365 to E. O. Wiley and National Science Foundation Grant #BSR8722562 to E. O. Wiley and D. Siegel-Causey.

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A New Species of *Cycleptus* (Cypriniformes: Catostomidae) from Gulf Slope Drainages of Alabama, Mississippi, and Louisiana, with a Review of the Distribution, Biology, and Conservation Status of the Genus

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ABSTRACT: Burr, Brooks M. and Richard L. Mayden. 1999. A New Species of *Cycleptus* (Cypriniformes: Catostomidae) from Gulf Slope Drainages of Alabama, Mississippi, and Louisiana, with a Review of the Distribution, Biology, and Conservation Status of the Genus. *Bulletin of the Alabama Museum of Natural History*, Number 20:19–57, 8 tables, 11 figures. The blue sucker was described originally by C. A. Lesueur (as *Catostomus elongatus*) in 1817 from a 2-foot long dried specimen obtained from the Ohio River. The species was subsequently transferred to *Cycleptus* and the name has remained stable since that time. *Cycleptus*, a North American endemic, occupies large rivers in the Mississippi River basin; it also occurs in Gulf Slope drainages from the Mobile basin, Alabama, to the Rio Grande basin, New Mexico, Texas, and Mexico. External examination of over 390 museum specimens revealed significant variation in dorsal fin ray number, scale number, body shape, and lip morphology; these features are geographically concordant and permit allocation into recognizable taxonomic units. A new species, *Cycleptus meridionalis*, herein described, is restricted to Gulf Slope drainages from the Mobile basin, Alabama, to the Pearl River drainage, Louisiana. It has usually 25–29 (vs. usually 28–34 in *C. elongatus*) dorsal-fin rays, usually 16 (vs. usually 19–20) caudal-peduncle scale rows, usually 37–40 (vs. usually 41–49) body-circumferential scale rows, usually 49–53 (vs. usually 53–58) lateral-line scales, a shorter (vs. longer) snout, and a shorter (vs. longer) dorsal fin base. Samples from the Rio Grande basin are divergent in a few characters including: 1) elongate lip papillae, 2) vague striping on sides of body, and 3) a somewhat brassy or golden body color. Elongate lip papillae occur also in samples from the Red and Arkansas rivers where water conditions are historically turbid, similar to those of the lower Rio Grande. The striping pattern is not consistent among hundreds of individuals examined alive from the Rio Grande, and the brassy golden colors occur also in other populations of *C. elongatus* depending on water conditions and season. We allocate samples from the Rio Grande to *C. elongatus*, recognizing that after further study other characters may be found to support recognition of a new taxon in that region.

Myxocyprinus, the sister group of *Cycleptus*, is restricted to the Yangtze River basin, China, a general geographic pattern repeated among other aquatic vertebrates including the paddlefishes, *Polyodon* + *Psephurus* clade, the giant salamanders, *Cryptobranchius* + *Amblyops* clade, and two sister species of *Alligator*, one restricted to southeastern United States, and another in Chinese fresh waters. This is apparently an ancient pattern also repeated in some tree species and other plants.

The U. S. Fish and Wildlife Service and numerous state natural resource agencies have listed both species of *Cycleptus* (as *C. elongatus*) as rare, threatened, or endangered. Recent data from the Mississippi and Ohio rivers and the Rio Grande basin demonstrate that *C. elongatus* is reproducing and showing evidence of recruitment at many localities throughout its range. It is, for example, the most abundant “large” species in the Rio Grande basin in the vicinity of Big Bend National Park. Studies of the distribution and abundance of *C. meridionalis* by Mark Peterson, Gulf Coast Research Laboratory, on the Pearl and Pascagoula rivers, and by M. F. Mettee, Geological Survey of Alabama, on the Mobile basin populations, strongly indicate that this species continues to participate in massive spring spawning migrations. Details of reproduction and recruitment are not yet accurately known, but formal protection is probably unwarranted. Both species are long-lived (up to 30+ years of age), reach large sizes (>800 mm SL), congregate in huge numbers during the spawning season, and are of considerable commercial value. Because of the unique phylogenetic, biogeographic, and life history significance of *Cycleptus*, we recommend that its population numbers, spawning sites, and recruitment patterns be carefully monitored in an effort to maintain viable populations.

Introduction

Cycleptus elongatus (Catostomidae) was described originally by Charles Alexander Lesueur (as *Catostomus elongatus*) in 1817 from a 2-foot long dried specimen obtained by Thomas Say from the Ohio River. The species was subsequently transferred to the subgenus *Cycleptus* (sensu Rafinesque, 1820), which was later elevated to generic rank by Agassiz (1854, 1855). In an early series of papers, Jordan (1876, 1878a,b) helped promote the higher classification of Agassiz and the name has remained stable since that time. Recently, fossilized teeth were used to describe (Sytchevsjaya, 1986) a new Asian species, *Cycleptus robustus*, but according to Smith (1992) the teeth are misidentified. *Cycleptus* is therefore considered endemic to North America and occupies large rivers in the Mississippi River basin extending from Pennsylvania to central Montana, and south to Louisiana; it also occurs in Gulf Slope drainages from the Mobile basin, Alabama, to the Rio Grande basin, New Mexico, Texas, and Mexico (Page and Burr, 1991). Although seasonally sporadic in most streams, it is locally common in the middle Rio Grande; relatively few specimens are vouchered in research collections.

Cycleptus occupies a special position in the Catostomidae, having been regarded as both a basal taxon and as the sister genus to *Myxocyprinus*, the sucker complex indigenous to China (Smith, 1992). One of the most phenotypically distinct catostomids, *Cycleptus* has been the subject of an in-depth osteological account (Branson, 1962a), a detailed genealogical analysis (Smith, 1992), and a few studies on aspects of its life history (e.g., Hogue et al., 1981; Rupprecht and Jahn, 1980; Moss et al., 1983; Yeager and Semmens, 1987). *Cycleptus elongatus* had Federal Category 2 Status, but does not receive legal protection. It receives some level (i.e., threatened, endangered, watch list, special concern) of recognition as a protected species in several of the midwestern and southern states.

In 1970, Robert E. Jenkins reported results of examination of 27 specimens of *Cycleptus* from the Mississippi, Missouri, Mobile, and Rio Grande basins for number of scales around the caudal peduncle; his counts revealed a bimodal frequency distribution (i.e., a trenchant difference in scale number) and convinced one of us (BMB) to pursue a more detailed account of geographical variation in a number of phenotypic characters of *Cycleptus*.

It is our purpose to present evidence here for a second species of *Cycleptus*, endemic to Gulf Slope drainages from the Pearl River, Louisiana and Mississippi, to the Mobile basin, Alabama. Differences in scale number, body shape, fin-ray number, and morphology of lip papillae seem sufficient to diagnose a new species and demonstrate significant character modification in populations occupying the Rio Grande basin of New Mexico, Texas, and Mexico. Additionally, we provide a range map for *Cycleptus* based on specimens vouchered in collections, color drawings of adults,

and add commentary on general conservation status, abundance, and probable spawning areas.

Methods

Methods of making counts and measurements follow Hubbs and Lagler (1974) except as follows. Measurements less than 150 mm were taken with dial calipers (nearest 0.1 mm); those greater were taken with a meter stick. Slightly curved specimens were straightened for measurement. Moderately or sharply curved specimens were not measured. Body circumferential scale counts were made in a vertical line just anterior to the dorsal fin origin. Caudal peduncle scale rows are the least circumferential count. Unless otherwise indicated lengths are standard length (SL), although total length (TL) is used in reference to larval and post-larval material.

Gill rakers were counted on the lateral (or anterior) surface of the first right arch. Pharyngeal arches and teeth were studied from skeletonized specimens. Extensive use was made of color descriptions and photographs of living and freshly preserved specimens by others. Sex was determined by examination of gonads. Variable means and modes were examined for geographic variation. When significant variation was absent, samples were successively amalgamated into major drainages.

The truss-geometric protocol (Strauss and Bookstein, 1982; Bookstein et al., 1985) was used in part to archive body form and included 28 measurements distributed among two sagittal truss cells with appended anterior and posterior triangles (Fig. 1). Among the 28 measurements were several straight-line measures used to assess body depth, body width, caudal peduncle depth, head depth, and other "traditional" body shape comparisons. Because it was evident early on that variation existed in head and snout shape and their comparative proportions we included additional measurements (Fig. 2) of the head, snout, and lip region in an effort to capture subtle differences not detected by those measures made in Fig. 1. Principal components were factored from the covariance matrix of log-transformed morphometric characters following the recommendations of Bookstein et al. (1985). Multivariate analysis of the morphometric data was accomplished using sheared principal components analysis (PCA) (Humphries et al., 1981; Bookstein et al., 1985) to eliminate overall size effects. Because of presumed sexual dimorphism, males and females were subjected separately to sheared PCA. Multivariate analyses were conducted on the University of Alabama and Southern Illinois University at Carbondale mainframe computers using programs available in the Statistical Analysis System (SAS Institute Inc., 1982) and as modified by David L. Swofford, National Museum of Natural History.

The synonymy for the Southeastern Blue Sucker includes published (i.e., non-grey literature, sensu Collette [1990]) references known to us; that for the genus *Cycleptus* and *C. elongatus* includes only those references

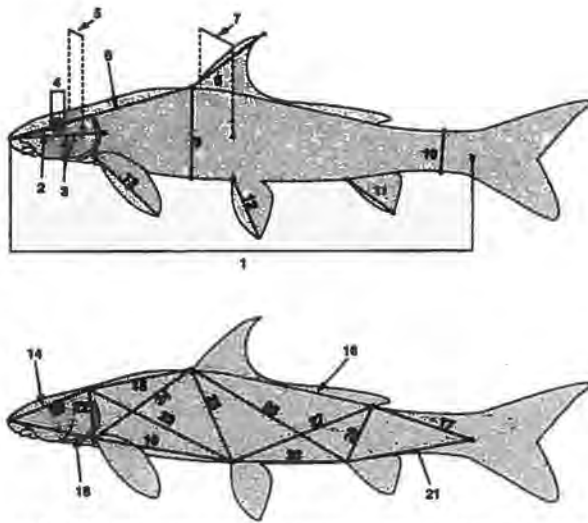


Figure 1. Diagrammatic representation of truss-network distance measures applied to *Cycleptus*. Numbers refer to measurements made between homologous landmarks or traditional straight-line measurements.

that contain substantial historical, biological, distributional, or systematic information. Literature references to *Cycleptus* are generally summarized in Bruner's (1991) bibliography of the Castostomidae, although his listings are far from exhaustive. All references to the Southeastern Blue Sucker have been under the name *C. elongatus* and consequently include general information for the now restricted *C. elongatus*. Symbolic codes for fish collections follow those recommended by Leviton et al. (1985) and Leviton and Gibbs (1988), with some modifications from Poss and Collette (1995), except that OSUM (not OSM) refers to the Ohio State University Fish Collection and GSA refers to the Geological Survey of Alabama, Tuscaloosa, Alabama.

We consider the formal description and naming of a species to represent a hypothesis, but that the named unit(s) corresponds to an actual entity in nature (Brothers, 1985). We follow Mayden (1997) in viewing the Evolutionary Species Concept (ESC; sensu Wiley, 1978; Frost and Hillis, 1990) as the most process-free conceptualization of species as taxa. As such, we consider species to be individuals (Ghiselin, 1974; Hull, 1976). Unlike other concepts developed for species, the ESC does not knowingly exclude elements of biological diversity thought to be species. However, as operational guidelines or tools, other concepts (e.g., Morphological, Taxonomic, and Phylogenetic Species Concepts) serve a fundamental role for the discovery of species in nature that are consistent with the theoretical ESC (Mayden, 1997).

Cycleptus Rafinesque

Cycleptus Rafinesque 1819:421 (original description; *Cycleptus nigrescens*, type by monotypy; also treated in Rafinesque 1820:355). Agassiz 1854:354 (valid genus;

"*Catostomus elongatus* belongs also to this genus *Cycleptus*"). Jordan 1878c:186–189 (detailed description). Jordan and Evermann 1896:168 (description). Jordan 1917:110 (valid genus). Jordan 1923:139 (in classification of world fishes). Hubbs 1930:8–9 (genus and subfamily characters). Nelson 1948:236, 240, 241 (Weberian apparatus). Nelson 1949:560, 564 (opercular bones). Miller 1959:199–203 (monotypic, closest relative of *Myxocyprinus*). Ferris and Whitt 1978:197, 199, 201 (phylogeny from duplicate gene loss). Fuiman 1985:834, 838 (phylogeny of adults and larvae). Eschmeyer and Bailey in Eschmeyer 1990:113, 447 (valid genus; in classification of world fishes). Burr and Mayden 1992:22 (in list of North American genera). Smith 1992:778, 800, 810, 840 (phylogeny and biogeography; sister taxon to Asian *Myxocyprinus*). Nelson 1994:137 (characters; monotypic). Eschmeyer in Eschmeyer 1998:1908, 2458 (valid genus; in classification of world fishes). Gilbert 1998:20 (nomenclatural status).

Rhytidostomus Heckel 1843:1023 (original description; *Catostomus elongatus*, type by subsequent designation of Jordan and Evermann 1896:168; synonym of *Cycleptus*).

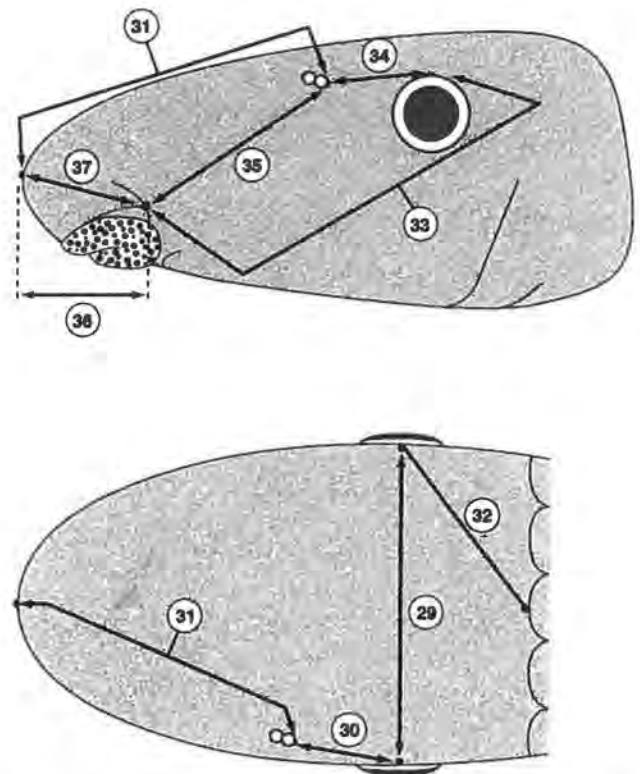


Figure 2. Detail of measurements made on the head region of representative specimens of *Cycleptus*. Numbers refer to measurements made between homologous landmarks or traditional measurements.

DIAGNOSIS.—A large (to at least 825 mm), relatively elongate (body depth going about 4–5 times into SL) sucker with a small head (length of head going 5 or more times into SL); dorsal fin long-based and falcate anteriorly, usually with 25–34 rays, 1st and 2nd principal rays long, rays rapidly shortening to about 7th or 8th ray, remaining rays all short; caudal fin large, widely forked; anal fin small, with 7–8 rays; pectoral fins elongate and falcate; mouth small, horizontal, and distinctly overhung by snout; lips covered by numerous papillae; lateral line complete, nearly straight, usually with 49–58 lateral line scales; lower lobe of caudal fin black in juveniles and subadults; back and sides tan, olive, or copper to blue-black, fins dusky to black; males (and females, less so) in spring densely covered with white, epidermal breeding tubercles; pharyngeal arch moderately stout, symphysis short, with about 32–45 teeth per arch (Eastman, 1977; original data); swim bladder with 2 chambers; chromosomes $2n = 96–100$ (Uyeno and Smith, 1972).

BIODIVERSITY.—Genus presumed to be monotypic for 175 years, but here considered to comprise two species, *C. elongatus* from the Mississippi and Rio Grande basins, and a few coastal drainages in Texas, and a new species described here from Gulf Slope drainages of Alabama, Mississippi, and Louisiana.

RANGE.—Endemic to North America, in Mississippi, Mobile, and Rio Grande basins, and some Gulf Slope drainages between Mobile and Rio Grande basins. Distribution of *Cycleptus* + *Myxocyprinus* clade similar to the *Polyodon* + *Psephurus* clade (see Grande and Bemis, 1991). Geographic pattern also repeated, for example, among giant salamanders (*Cryptobranchus* + *Andrias* clade), and two species of *Alligator*.

ETYMOLOGY.—*Cycleptus*, round and slender (Jordan and Evermann, 1896). The author of the name, C. S. Rafinesque, apparently meant it to mean “small round mouth.”

Cycleptus elongatus (Lesueur)

Blue Sucker
Figure 3, top

Catostomus elongatus Lesueur 1817:103–104; unnum. fig. [opposite page 103] (original description; Ohio River). Kirtland 1838:169 (Ohio River, Ohio). DeKay 1842:203 (near New York). Cuvier and Valenciennes 1844:455 (description). Storer 1846:422 (description). Kirtland 1845:267 (Ohio River, Ohio). Kirtland 1851:349 (Ohio River at Cincinnati). Eschmeyer et al. in Eschmeyer 1998:524, 2238 (review of type; valid as *Cycleptus elongatus*; in classification of fish species of the world). Gilbert 1998:181 (status of type; nomenclatural review; original description date 7 November 1817).

Cycleptus nigrescens Rafinesque 1819:421 (original description; Ohio River).

Sclerognathus elongatus: Günther 1868:23 (description; range)

Cycleptus elongatus: Agassiz 1854:354 (resurrection of Rafinesque's genus; *Catostomus elongatus* belongs in *Cycleptus*). Agassiz 1855:197 (description and clarification). Jordan 1875:222 (in Indiana list). Jordan 1876:298 (in manual of vertebrates). Nelson 1876:50 (in Illinois list). Jordan 1877:38 (description and clarification of name). Jordan 1878a:420 (in North American catalog). Jordan 1878b:100, 189–190 (synonymy; description). Jordan 1878c:64 (in Illinois list). Jordan and Brayton 1878:80 (Cumberland River at Nashville). Hoy 1883:434 (Baraboo River, Wisconsin). Jordan and Gilbert 1883:121 (description; Mississippi Valley). Forbes 1884:81 (in Illinois list). Cragin 1885:107 (Kansas River between Manhattan and Topeka, Kansas). Graham 1885:72 (Kansas River, Kansas). Jordan 1885:17 (in North American list). Evermann 1886:4 (Whitewater River at Brookville, Indiana). Jordan and Evermann 1886:160 (Ohio and lower Wabash rivers, Indiana). Jenkins 1887:94 (Wabash River at Terre Haute, Indiana). Henshall 1888:77 (not common in Ohio River). Meek 1890:72 (not common in Iowa). Herrick 1891:236 (description of optic lobes). Meek 1892:221 (not common in Mississippi River, Iowa). Woolman 1892:262, 287 (Cumberland River just south of Kuttawa, Kentucky). Eigenmann and Beeson 1894:83 (Indiana records). Garman 1894:55 (Ohio and Cumberland rivers, Kentucky). Call 1896:15 (Falls of Ohio [River]). Evermann and Cox 1896:389, 426 (not taken often in Missouri River). Jordan and Evermann 1896:168–169 (description; range; etymology; synonymy). Cox 1897:23 (description; Minneapolis specimen presumably destroyed in fire). Evermann 1902:286 (Falls of the Ohio). Large 1903:12 (in Illinois list). Forbes and Richardson 1908:65–66 (description; Illinois distribution). Meek 1908:154 (Río Salado, Nuevo León, México). Fowler 1913:45 (St. Louis, Missouri, and Kiskiminetas River, Pennsylvania). Shira 1917:11 (successful hatching of eggs). Evermann 1918:336, 366 (Kentucky and Tennessee records). Fowler 1919:62 (Kiskiminetas River, Pennsylvania). Forbes and Richardson 1920:65–66 (description; Illinois distribution). Jordan 1929:61 (description; range). Coker 1930:182–184 (spring and fall migrations in upper Mississippi River). Jordan et al. 1930:102 (synonymy; range). Greene 1935:57 (Wisconsin records). O'Donnell 1935:478 (Illinois distribution). Fowler 1945:11, figs. 39–40 (listed and figured). Gerking 1945:40 (Wabash and Ohio rivers, Indiana). Eddy and Surber 1947:117, 127–128 (in key; description; Minnesota distribution). Fowler 1948:16 (Pennsylvania). Nelson 1948:245, 246 (Weberian apparatus

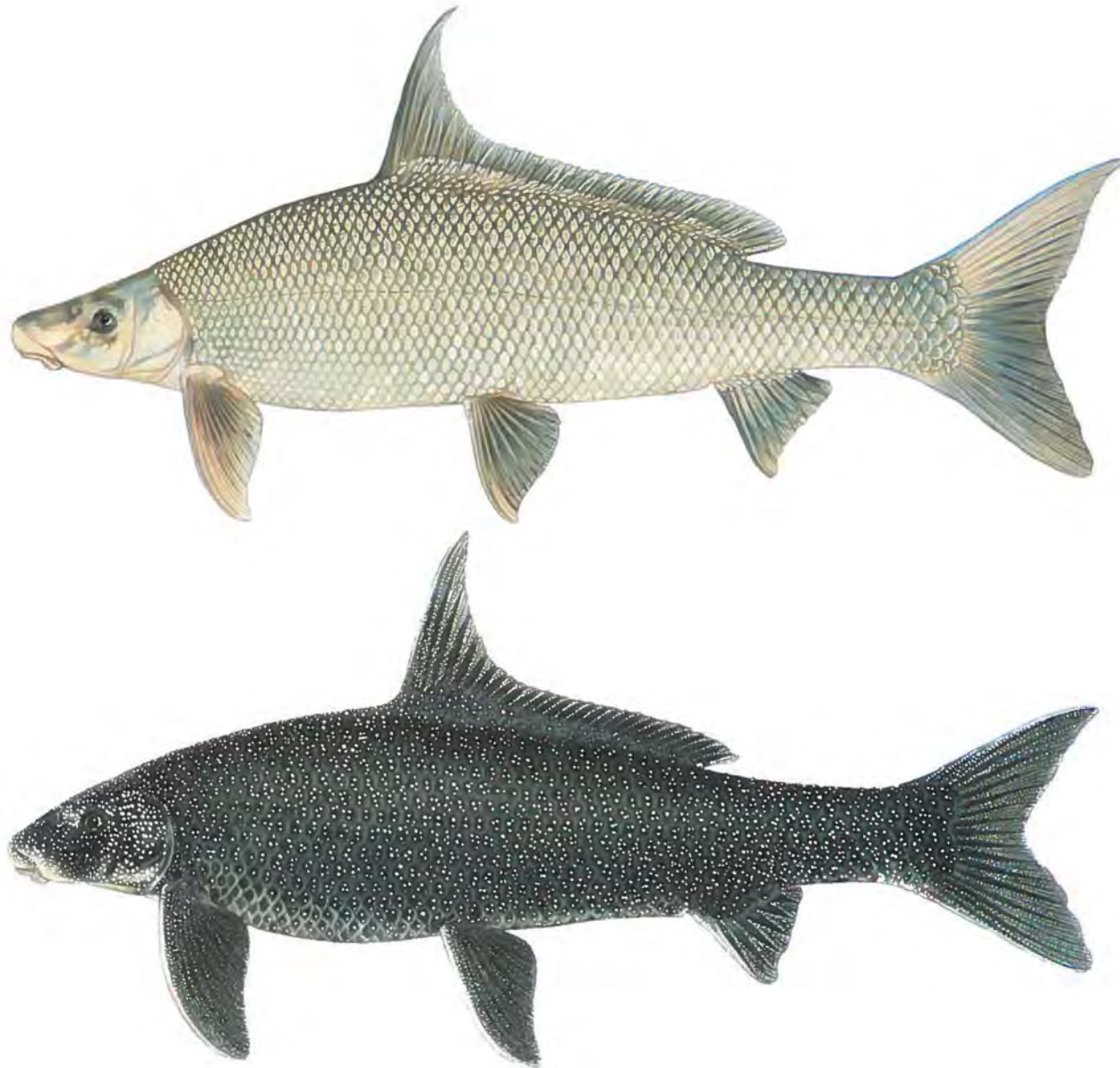


Figure 3. Top. *Cycleptus elongatus*, about 508 mm SL, Missouri River, Andrew County, Missouri, July 1994 (UAIC 12110.01). Bottom. *Cycleptus meridionalis*, paratype male, 485 mm SL, Tallapoosa River, Elmore County, Alabama, May 1980 (UAIC 11973.01). Illustrations, by Joseph R. Tomelleri, are copyrighted.

- figured and described). Alvarez 1950:40 (in key to Mexico fishes; Río Bravo). Moore and Cross 1950:139 (adults from Lake Texoma, young from Grand Lake, Oklahoma). Barnickol and Starrett 1951:282, 292–293 (records and decline in upper Mississippi River). Harrison and Speaker 1954:515 (Big Sioux River, Iowa). Lewis 1955:23 (Big Muddy River, Illinois). Bailey 1956:330, 352 (list; in Iowa key). Cleary 1956:283 (Iowa distribution map). Harlan and Speaker 1956:71–72 (description; Iowa range; biology). Hubbs 1957:100 (large rivers, Texas). Koster 1957:37, 39–40 (in key; description; Pecos River, New Mexico). Trautman 1957:34, 80, 221–223, 226, 229, 232, 253 (in key; description; Ohio distribution). Clarke et al. 1958:167 (Lyon Co., Kansas). Hubbs and Hubbs 1958:306 (Río Salado, Nuevo León, México). Cook 1959:32, 74, 77–78 (in key; description; Mississippi distribution). Metcalf 1959:393 (Neosho River, Kansas). Underhill 1959:100 (Missouri River, at mouth of Vermillion River). Minckley 1959:416 (Blue River, Kansas). Riggs and Bonn 1959:162 (Lake Texoma, Oklahoma). Bailey et al. 1960:17 (in U.S. and Canada list). Breukelman 1960:20, 21, 33 (identification in Kansas). Gehlbach and Miller 1961:2, 6–7 (bones from Bandelier National Monument, New Mexico). Bailey and Allum 1962:78–79 (South Dakota records). Branson 1962a:81–150 (detailed osteological study). Branson 1962b:360–362 (tubercle description). Clay 1962:47–49 (in key; description). Fisher 1962:428 (Missouri River, Missouri). Clemens and Johnson 1964:390, 391, 393, 395 (pituitary extract donor study). Miller and Evans 1965:470–471, 483 (functional brain and lip morphology). Smith 1965:8 (Illinois distribution). Breder and Rosen 1966:235 (spawning dates). Metcalf 1966:139 (Kansas River, Kansas). Smith 1966:13 (osteologically aberrant). Cross 1967:164, 166–168 (in key; description; Kansas distribution; biology). Moore 1968:91 (description; range, in part). Carlander 1969:486–487 (age and growth data from grey literature). Bailey et al. 1970:24 (in U.S. and Canada list). Brown 1971:110, 114–115 (in key; description; Montana distribution; biology). Elrod and Hassler 1971:27, 29, 30, 31, 32, 38 (age, growth, abundance in Lake Sharpe, South Dakota). Pflieger 1971:378, map 90 (Missouri distribution). Phillips and Underhill 1971:2, 4–5, 19 (in key; Minnesota distribution). Smith et al. 1971:7–8, 16 (widely distributed but uncommon in upper Mississippi River). Walburg et al. 1971:454, 457, 459, 462 (abundance and biology in Lewis and Clark Lake tailwater). Miller 1972:243 (threatened in six states). Contreras-Balderas and Rivera T. 1972:47–48 (Río Bravo, Coahuila, México). Uyeno and Smith 1972:644 (chromosome number). Buchanan 1973:41, map 91 (in key; Arkansas distribution map). Hubbs and Wauer 1973:376, 377, 378 (Tornillo Creek, Texas). Leiby et al. 1973:777–779 (gill parasites from Missouri River, North Dakota). Miller and Robison 1973:115, 120–121 (in key; description; Oklahoma distribution; biology). Smith 1973:24 (in Illinois key). Christenson 1974:1–7 (common in lower Chippewa and Red Cedar rivers, Wisconsin). Douglas 1974:181, 190–191, 417 (description; Red and Sabine rivers, Louisiana; color plate). Eddy and Underhill 1974:275, 279–280 (in key; description; Minnesota distribution). Pigg and Hill 1974:126 (Kiamichi River, Oklahoma). Platt et al. 1974:102 (rare in Kansas). Robison et al. 1974:139, 140, 142 (rare in Oklahoma). Clay 1975:90–91, 400 (description; Kentucky records; biology). Cross and Collins 1975:8, 88 (description; biology; Missouri, Kansas, and Neosho rivers, Kansas; state threatened). Pflieger 1975:179, 187 (in key; description; Missouri distribution; biology). Randolph and Lindsay 1975:55–56 (review of Oklahoma records). Hubbs and Pigg 1976:116 (threatened in Oklahoma). Lundberg and Marsh 1976:334 (evolution and function of pectoral fin rays). Miller 1976:6 (Río Salado, Nuevo León, México). Eastman 1977:72, 80–81 (pharyngeal teeth figured; in key). Ferris and Whitt 1977:259 (tetraploid that has returned to a functionally diploid state). Hubbs et al. 1977:94, 95, 96 (Rio Grande, Texas). Pigg 1977:76 (Muddy Boggy River, Oklahoma). Bussjaeger and Briggs 1978:534 (bile salts as possible indicators of phylogeny). Curry and Spacie 1978:185 (Wabash River, Tippecanoe County, Indiana). Eddy and Underhill 1978:111 (in key; range). Ferris and Whitt 1978:196, 197, 198, 199, 201, 202, 205 (phylogenetic and phenetic relationships). Guillory et al. 1978:706 (conservation status in southern states, in part). Etnier et al. 1979:1 (Tennessee River at Decatur, Alabama). McReynolds et al. 1979:170 (threatened in Indiana). Smith 1979:148–149 (description; Illinois distribution). Burr 1980:68 (Kentucky range). Eastman 1980:134 (caudal skeleton). Ferris and Whitt 1980:652, 654, 656 (same level of genetic variability as diploid teleosts). Gilbert 1980:396 (spot distribution map; systematics; biology). Robinson and Jahn 1980:209 (infected with *Myxotrema cyclepti*). Robins et al. 1980:26 (in U.S. and Canada list). Rupprecht and Jahn 1980:323–326 (biology in upper Mississippi River). Starnes and Etnier 1980:B-19–B-20 (threatened in Tennessee). Branson et al. 1981:81 (threatened in Kentucky). Hogue et al. 1981:585–587 (description and illustrations of larval stages). McGuire 1981:1, 5, 6 (in larval key; characters). Smith 1981:166 (Holocene record). Trautman 1981:40, 87, 403–405 (in key; description; Ohio distribution). Guillory 1982:112 (lower Mississippi River, Louisiana). Phillips et al. 1982:153–154 (Minnesota range). Warren and Cicerello 1982:[3] (Green River, Kentucky). Becker 1983:37, 47, 130, 186, 552, 611–614, 622, 636, (color plate; in key; description; Wisconsin distribution; biology; threatened status). Boschung et al. 1983:459–460 (description; range, in part). Buth 1983:387 (polyp-

- loidy confirmed). Cooper 1983:128 (description; Pennsylvania distribution; biology; extirpated status). Lindsay et al. 1983:44 (Poteau River, Oklahoma). Moss et al. 1983:15–21 (life history in Neosho River, Kansas). Pennington et al. 1983:204–211 (near revetted banks on lower Mississippi River, Mississippi). Retzer et al. 1983:22–23 (Green River, Kentucky). Fago 1984:11, map 44 (lower Red Cedar River, Wisconsin; threatened). Ferris 1984:64, 74, 80 (tetraploidy). Pearson and Krumholz 1984:233–234 (Ohio River records). Ramsey et al. 1984:7 (Tennessee drainage, Alabama). Fuiman 1985:837, 838 (phylogeny based on larval characters). Gilbert in Cooper 1985:168, 244–245 (color plate; formerly in Kiskiminetas River, Pennsylvania; probably extirpated in state). Williams et al. 1985:23 (reduced in the Rio Grande system). Burr and Page 1986:305, 307, 310, 317, 321 (range reduction; member of big river faunistic group). Burr and Warren 1986:149, 366, 373, 382 (Kentucky distribution; habitat). Cincotta et al. 1986:101, 108 (Ohio River, West Virginia). Conner and Suttkus 1986:420, 439, 454 (Gulf Coast tributaries, Texas and Louisiana). Cross et al. 1986:393, 403 (Missouri River). Hocutt et al. 1986:167 (probable in upper Ohio River tributaries). Miller 1986:134 (Rio Grande, México). Robison 1986:274 (member of “Old Fauna”). Sandheinrich and Atchison 1986:189–190 (Missouri River, Iowa-Nebraska). Smith and Miller 1986:461 (rios Grande and Conchos, Pecos River, México, Texas, and New Mexico). Starnes and Etnier 1986:342 (Tennessee and Cumberland rivers). Baker and Armstrong 1987:96 (Spring River, Arkansas). Cowley and Sublette 1987a:411–412 (food habits in Black River, New Mexico). Cowley and Sublette 1987b:215 (Black River, New Mexico). Harlan and Speaker 1987:64–65, 199 (description; Iowa distribution; biology; color plate). Johnson 1987:10, 28, 29, 30, 31, 33, 34, 35, 36, 37, 38, 39 (protected status in United States). Propst et al. 1987:410 (questionable from lower Rio Grande, New Mexico). McNerny and Held 1988:69–70 (larvae from upper Mississippi River, Wisconsin). Robison and Buchanan 1988:256, 266–267 (in key; description; Arkansas distribution; biology; color photograph of juvenile). Pearson and Froedge 1989:189–190 (556 individuals stranded below McAlpine Dam on the Ohio River). Williams et al. 1989:6 (in part, special concern status throughout range). Tomelleri and Eberle 1990:97, plate 69 (range; status; biology; color plate). Hubbs et al. 1991:23, 24 (in key; Texas range). Etnier and Starnes 1991:130 (jeopardized in Tennessee). Page and Burr 1991:167, map 183 (description; range; habitat). Robins et al. 1991:25 (in U.S. and Canada list). Ross and Breneman 1991:211–212 (Yazoo, Big Black, and Mississippi rivers, Mississippi). Sublette et al. 1991:10, 191, 215–217, color plate 25 (in key; description; New Mexico distribution; biology; color plate). Fago 1992:75, map 81 (figured; Wisconsin spot distribution map). Mayden et al. 1992:840 (in list of North American native fishes). Smith 1992:786–787, 789–792, 800, 814–815 (genealogical relationships; sister taxon of *Myxocyprinus*; evolution of large-river suckers). Anonymous 1993:48–49 (young-of-the-year in Mississippi River side channels, Illinois). Berry et al. 1993:73, 80 (James River, South Dakota; special concern in Dakotas). Burr and Warren 1993:192, 200 (extirpated from Big Muddy River, Illinois). Espinosa et al. 1993:23 (“ríos del NE de México, entre los ríos Pánuco y Bravo”). Etnier and Starnes 1993:260, 268, 270 (in key; description; Tennessee distribution; biology; color photograph of juvenile). Fago and Hatch 1993:38, 43, 52 (St. Croix River; threatened). Gammon 1993:154 (Wabash River). Holman et al. 1993:273–276 (Big Black River, Mississippi). Jackson et al. 1993:259–260, 265 (in commercial fishery, Yazoo River, Mississippi). Limbird 1993:290 (Arkansas River). Larimore and Fritz 1993:223, 226 (rare in Kaskaskia River, Illinois). Ruelle et al. 1993:463, 466 (White, Bad, Cheyenne, Moreau, and Grand rivers, South Dakota). Sanders et al. 1993:316 (rare in Kansas River, Kansas). Schmulbach and Braaten 1993:64, 65 (Vermillion River, South Dakota). White and Bramblett 1993:402 (common in Yellowstone River, Montana). Brown and Coon 1994:720, 724 (Lamine River, Missouri). Jenkins and Burkhead 1994:111 (possible occurrence in Virginia). Kay et al. 1994:114–121 (principal account on these pages, many comparisons throughout volume, in part; in key; description of eggs and larvae; illustrations; original descriptive material based largely on *C. meridionalis*). Nelson 1994:137 (monotypic; subfamily Cycleptinae). Contreras-Balderas et al. 1995:75 (Nuevo León, México; vulnerable). Cross and Collins 1995:15, 122–123, 271, plate 17 (in key; description; Kansas distribution; biology; color plate). Stauffer et al. 1995:172, 181–182 (in key; description; West Virginia distribution; biology). Burr et al. 1996:169, 176 (new Illinois records for larvae and adults). Mettee et al. 1996:321, 334–335 (in key; description, in part; Alabama distribution, in part; biology; color map). Pflieger 1997:168, 179–180 (in key; description; Missouri distribution; biology).
- HOLOTYPE.**—Apparently not extant; dried two-foot specimen, collected by Thomas Say from Ohio River, said to be in ANSP collection (Lesueur, 1817:104). Neither Fowler (1913) nor Böhlke (1984) mentioned any ANSP types, and E. B. Böhlke (pers. comm.) informs us the specimen is presumed to be lost or discarded. According to Gilbert (1998), an illustration of the type accompanies some copies of the journal containing the original description, although these figures apparently were not present originally. Hubbs (1930:29) stated that these figures were not

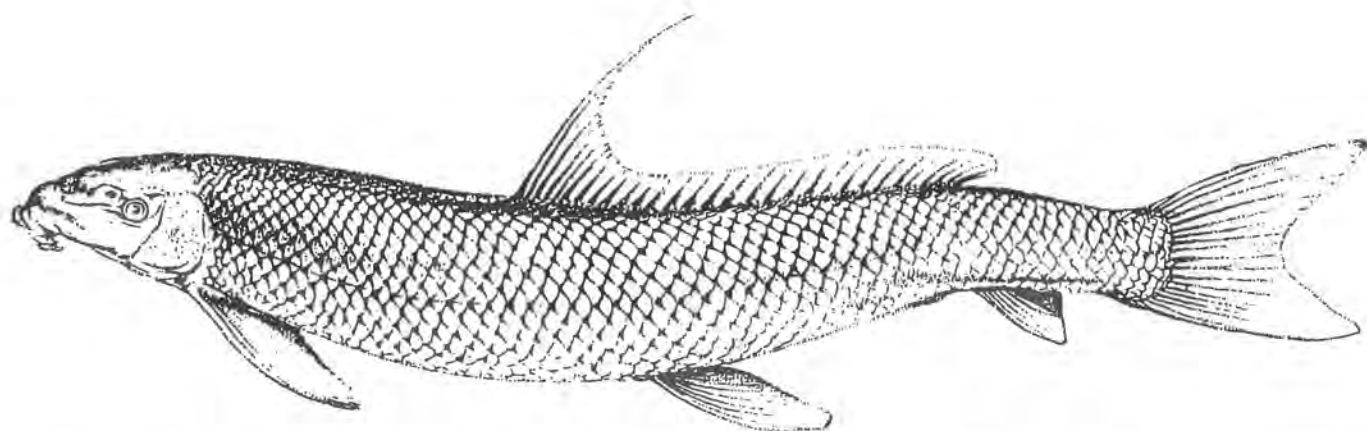


Figure 4. Copy of presumed original drawing of *Catostomus elongatus* Lesueur (1817) as reproduced in some copies of the Journal of the Academy of Natural Sciences of Philadelphia. See discussion under "Holotype."

made available until 1822, and were evidently inserted later in individual copies of the journal. Reproduction of Lesueur's original drawing (Fig. 4) leaves no doubt that the fish he was describing is indeed the species we know today as *Cycleptus elongatus*.

MATERIAL USED FOR COUNTS AND MEASUREMENTS.—Numbers in parentheses are numbers of specimens examined followed by range in length of specimens in mm SL. **MISSISSIPPI RIVER BASIN. Mississippi River Drainage. WISCONSIN:** KU 4956 (1, head only), St. Croix River, in Kettle River rapids, Burnett Co., 26 August 1959. MPM 8550 (1, 505 mm SL), Red Cedar River, T26N, R13W, Sec. 3(4), Dunn Co., 8 July 1975. MPM 16340 (1, 395 mm SL), Chippewa River, T23N, R14W, Sec. 2SW, Pepin Co., 20 May 1977. MPM 19041 (1, 610 mm SL), Black River, Station 2, T19N, R6W, Sec. 27SE, Jackson Co., 2 May 1978. MPM 16669 (1, 540 mm SL), 16670 (1, 540 mm SL), both from Wisconsin River, T8N, R4E, Sec. 30NE, Sauk Co., 25 May 1977. MPM 17851 (1, 530 mm SL), Wisconsin River, T8N, R5E, Sec. 6SE, Sauk Co., 25 July 1977. MPM 17641 (415 mm SL), Wisconsin River, T9N, R6E, sec. 31SW, Dane Co., 24 May 1977. MPM 17687 (1, 444 mm SL), Wisconsin River, above Sauk City, T9N, R6E, Sec. 6SW, Dane Co., 10 May 1977. MPM 17774 (1, 429 mm SL), Wisconsin River, T8N, R2E, Sec. 11SW, Iowa Co., 13 June 1977. MPM 11679 (1, 480 mm SL), Mill Creek of Wisconsin River, T8N, R4E, Sec. 29NW, Iowa Co., 28 May 1975. MPM 29938 (1, 460 mm SL), Kickapoo River, T7N, R4W, Sec. 8NW, Crawford Co., 30 April 1980. **MINNESOTA:** JFBM 24441 (1, 390 mm SL), Minnesota River, Carver Rapids RR Bridge, T115N, R23W, Sec. 20, Carver Co., 25 July 1989. JFBM 16584 (1, 525 mm SL), Mississippi River, at Homer, Winona Co., July 1948. **IOWA:** JFBM 9844 (1, 325 mm SL), 9845 (1, 330 mm SL), 9846 (2, 350–425 mm SL), all from Mississippi River, at Guttenberg, Clayton Co., 28 November 1938. **ILLINOIS:** INHS 23150 (1, 390 mm SL), Mississippi River, RM 364, at Hamilton, T5N, R8W, Sec. 30, Hancock Co., 3 August 1970. SIUC 3753 (2, 285–

430 mm SL), UAIC 10768.01 (1, 450 mm SL), all from Mississippi River, at Keokuk bridge and dam, Hancock Co., 8 October 1981. SIUC 18162 (1, 395 mm SL), Mississippi River, Quad Cities nuclear power station (impingement), Cordova, Rock Island Co., 30 October 1990. SIUC 14466 (1, 157 mm SL), Mississippi River, Pool 14, near Cordova, Rock Island Co., July 1975. INHS 24773 (1, 131 mm SL), Mississippi River, RM 505, 2 mi. N of Cordova, T20N, R2E, Sec. 18, Rock Island Co., 23 September 1968. INHS 85040 (1, 78 mm SL), Green River, at Cleveland, Henry Co., August 1900. INHS 26845 (1, 450 mm SL), Illinois River, near Havana, RM 120.5, mouth of Spoon River, T4N, R4E, Sec. 20, Fulton Co., 6 May 1976. INHS 25795 (1, 315 mm SL), Illinois River, RM 123.6, 2 mi. N of Havana, T22N, R8W, Sec. 30NW, Mason Co., 19 May 1967. INHS 14437 (1, 400 mm SL), Illinois River, RM 123, 2 mi. N of Havana, T22N, R8W, Sec. 30NW, Mason Co., 9 May 1974. INHS 20457 (1, 124 mm SL), Kaskaskia River, 7 mi. NNE Vandalia, T7N, R1E, Sec. 12, Fayette Co., 11 August 1964. INHS 16444 (1, 288 mm SL), 16447 (1, 135 mm SL), both from Kaskaskia River, 1.5 mi. SE of Carlyle, T2N, R2W, Sec. 19, Clinton Co., 18 August 1960, 6 September 1968. INHS 24313 (1, 450 mm SL), Mississippi River, near Rockwood, T8S, R5W, Sec. 18, Randolph Co., 10 December 1969. **MISSISSIPPI:** USNM 129717 (1, 490 mm SL), Mississippi River, at Greenville, Washington Co., 25 May 1933. PSU 1852 (1, 162 mm SL), Mississippi River, near Vicksburg, Warren Co., April 1973. **MISSOURI:** KU 9770 (1, 430 mm SL), Current River, at Doniphan, T23N, R2E, Sec. 27, Ripley Co., March 1965. **Missouri River Drainage. SOUTH DAKOTA:** SIUC 19098 (2, 370–410 mm SL), Missouri River, near Vermillion, Clay Co., 1973. JFBM 18961 (1, 59 mm SL), Vermillion River, at mouth, Clay Co., 24 July 1956. UMMZ 166960 (2, 500–520 mm SL), Missouri River, below Fort Randall Dam, Charles Mix Co., 29 August 1952. UMMZ 167781 (1, 231 mm SL), Fort Randall Reservoir, near Old Wheeler Bridge, Charles Mix Co., 21 July 1954. **NEBRASKA:** UNSM ZM-03221 (1, 145

mm SL), Missouri River, at mile marker 615.8, Sarpy Co., January 1976. UNSM ZM-02094 (1, 107 mm SL), Bow Creek, near Wynot NE, T32N, R2E, Sec. 11SW, Cedar Co., 18 September 1985. **KANSAS:** KU 21603 (1, head only), Blue River, below Rocky Ford Dam, Pottawatomie Co., 23 April 1986). KU 19699 (1, 350 mm SL), Kansas River, D3 pit, Wyandotte Co., 8 March 1981. KU 20761 (1, 392 mm SL), Kansas River, T11S, R24E, Sec. 28, Wyandotte Co., 8 March 1981. KU 18831 (1, 355 mm SL), Kansas River, T12S, R23E, Sec. 7, Leavenworth Co., 6 September 1980. KU 18829 (1, 315 mm SL), Kansas River, T12S, R23E, Sec. 18, Johnson Co., 5 August 1980. KU 12642 (1, 214 mm SL), 22170 (1, 189 mm SL), both from Kansas River, below dam at Lawrence, T12S, R20E, Sec. 19, Douglas Co., 2 May 1967, 16 September 1988. KU 23889 (1, 468 mm SL), KU 23890 (6, 495–538 mm SL) all from Kansas River, at Lawrence, below Bowersock Dam, Douglas Co., 13 April 1992. KU 17928 (1, 320 mm SL), Missouri River, mile 463–475, Doniphan Co., 6 October 1978. **MISSOURI:** KU 9026 (1, 497 mm SL), Osage River, at Tuscumbia, T40N, R14W, Sec. 10, Miller Co., 22 August 1962. TU 53824 (1, 27 mm SL), Missouri River, from Hwy. 54 at Jefferson City upstream 1 mi., Callaway Co., 21 June 1968. **Ohio River Drainage. OHIO:** UMMZ 107266 (1, 520 mm SL), Scioto River, Scioto Township, Pike Co., 25 May 1930. OSUM 1159 (1, 375 mm SL), 1873 (1, 375 mm SL), [both from] Scioto River, Rush Township, Scioto Co., October 1939, 14 June 1940. OSUM 1429 (1, 175 mm SL), Scioto River, Station #1, Scioto Co., 18 October 1939. OSUM 67955 (1, 465 mm SL), Scioto River, at Rushtown Falls, Scioto Co., 19 September 1985. OSUM 9534 (1, 410 mm SL), OSUM 9535 (2, 380–430 mm SL), all from Muskingum River, Dam 2, Muskingum Township, Washington Co., 28 & 29 June 1930. **KENTUCKY:** UL 7634 (1, 395 mm SL), Licking River, at Myers, Nicholas Co., June 1956. UL 2338 (1, 377 mm SL), Ohio River, at Falls, Jefferson Co., 11 May 1982. SIUC 8402 (4, 370–430 mm SL), UAIC 10767.01 (2, 410–430 mm SL), all from Ohio River, at Falls, Louisville, Jefferson Co., 15 June 1983. SIUC 11791 (1, 410 mm SL), Ohio River, at Falls, Louisville, Jefferson Co., 29 July 1982. UL 12840 (1, 286 mm SL), Ohio River, below Dam # 43, Meade Co., 3 October 1959. UL 7215 (1, 323 mm SL), Ohio River, at Lock # 50, Crittenden Co., 11 June 1957. **INDIANA:** INHS 65244 (2, 112–355 mm SL), White River, near Petersburg, Pike Co., 1985–1986. BMNH 84.7.7:143 (1, 470 mm SL), White River. UAIC 10330 (1, 540 mm SL), Wabash River, at Cayuga, just downstream public service of Indiana Cayuga Power Plant, Vermillion Co., 10 June 1992. INHS 27892 (1, 505 mm SL), Wabash River, 3.5 mi. SE of New Haven, at island, T8S, R15W, Sec. 2, Posey Co., 16 April 1992. **ILLINOIS:** INHS 64198 (1, 450 mm SL), Embarras River, 2.5 mi. SE of Charleston, T12N, R9E, Sec. 25, Coles Co., 12 July 1988. INHS 2813 (1, 245 mm SL), Wabash River, at Old York, T9N, R11W, Sec. 34, Clark Co., 11 August 1967. INHS 7715 (1, 360 mm SL), Wabash River, at Rochester, T2S, R13W, Sec. 14, Wabash Co., 4 August 1967. INHS 9348 (1, 360 mm SL), Wabash River, 2 mi. S of Russellville, T4N, R10W, Sec. 10, Lawrence Co., 19 August 1970. INHS 9275 (1, 475 mm SL), Wabash River, 5 mi. S of Russellville, T4N, R10W, Sec. 34, Lawrence Co., 3 August 1967. INHS 4586 (1, 550 mm SL), Wabash River, at New Haven, T7S, R10E, Sec. 27, Gallatin Co., 20 March 1971. INHS 61138 (1, 346 mm SL), Ohio River, at Shawneetown, Gallatin Co., 22 May 1935. UL 9007 (1, 356 mm SL), Cache River, Pulaski Co., 10 June 1957. **Cumberland River System. TENNESSEE:** UT 45.245 (1, 340 mm SL), Cumberland River, at Cumberland River Steam Plant, Stewart Co., Summer 1976. **Tennessee River System. TENNESSEE:** UMMZ 103771 (1, head only), Clinch River, below Norris Dam, Anderson Co., 16 May 1939. TU 28498 (1, 490 mm SL), Clinch River, at mi. 33, ca. 8 mi. SW of Oak Ridge, Anderson Co., 7 February 1963. TU 36996 (1, 530 mm SL), Clinch River, ca. 8 mi. S of Oak Ridge, Anderson Co., February–April 1963. UT 45.410 (1, 558 mm SL), Ft. Loudon Reservoir, cove at Lenoir City Park, Loudon Co., 10 April 1982. UT 45.1010 (1, 470 mm SL), Duck River, mile 22.5, at HYTE Ford, Maury Co., 15 July 1992. **ALABAMA:** UMMZ 200919 (1, 355 mm SL), Tennessee River, in Pickwick Reservoir, at 7 Mile Island, just below Florence, 5 mi. below Wilson Dam, Colbert/Lauderdale Co., April 1939. **Arkansas River Drainage. KANSAS:** KU 16468 (1, 515 mm SL), 16469 (1, 578 mm SL), 16471 (1, 267 mm SL), 16479 (1, 540 mm SL), 16551 (1, 408 mm SL), 16552 (1, 517 mm SL), 16553 (1, 505 mm SL), 16554 (1, 480 mm SL), all from Neosho River at Neosho Falls, Woodson Co., 24 April 1976, 27 May 1976, 9 June 1976. KU 2595 (1, 540 mm SL), 2596 (1, 65 mm SL), both from Neosho River at Neosho Falls, T23S, R17E, Sec. 28–33, Woodson Co., 12 July 1952. KU 2545 (4, 55–89 mm SL), 2546 (1, 540 mm SL), all from Neosho River, near Neosho Rapids, T19S, R13E, Sec. 29, Lyon Co., 11 July 1952. KU 14239 (3, 355–460 mm SL), Neosho River, just below Redmond Dam, Coffey Co., 22 June 1970. KU 2578 (1, 590 mm SL), 2579 (1, 64 mm SL), 3477 (1, 550 mm SL), all from Neosho River, at Burlington, T21S, R15E, Sec. 26, Coffey Co., 12 July 1952, 4 April 1955. KU 16328 (1, 608 mm SL), Neosho River, at Humboldt, T26S, R18E, Sec. 4, Allen Co., 15 July 1974. KU 23007 (1, 505 mm SL), Neosho River, T26S, R18E, Sec. 4SW, Allen Co., 12 August 1991. KU 4277 (1, 518 mm SL), 4278 (1, 485 mm SL), 4279 (1, 558 mm SL), all from Neosho River, at Erie, T28S, R19E, Sec. 35, Neosho Co., 9 August 1957. KU 22396 (2, 137–163 mm SL), Neosho River, W of St. Paul on Ks. Rt. 57, Neosho Co., 3 September 1988. KU 18411 (2, 127–182 mm SL), Neosho River, at Chetopa, Labette Co., 8 September 1978. **OKLAHOMA:** OSUS 20259 (1, 300 mm SL), Neosho River, above mouth of Russell Creek, T29N, R21E, Sec. 21, Ottawa/Craig Co., 22 July 1991. OSUS 15144 (1, 365 mm SL), tailrace of Pensacola Dam (Lake Hudson), Mayes Co., 21 July 1988. **ARKANSAS:** TU 184023 (5, 27–31 mm SL), Arkansas River, below Dardanelle Lock & Dam, Pope/Yell Co., 24

July 1974. TU 184022 (1, 308 mm SL), Arkansas River, mi. 289.1, Sebastian/Crawford Co., 17–18 August 1974. **MISSOURI:** UMMZ 135895 (2, 240–250 mm SL), Elk River, above bridge on Hwy. 43, S of Tiff City, T22N, R34W, Sec. 23, McDonald Co., 22 July 1942. **Yazoo River Drainage.** **MISSISSIPPI:** NLU 65581 (3, 45–57 mm SL), 65576 (5, 45–54 mm SL), all from White Lake Backwater, Yazoo, approximately 3 mi. N of Hwy. 32, T25N, R1E, Sec. 21, Tallahatchie Co., 22 May 1991. TU 85211 (1, 135 mm SL), O'Neal Creek, 6.6 mi. NE of Satartia, Hwy. 3, Yazoo Co., 9 November 1973. **Red River Drainage.** **OKLAHOMA:** OSUS 2073 (3, 346–371 mm SL), Lake Texoma, Hickory Creek Arm, Marshall Co., 28 February 1948. OSUS 24350 (2, 343-ca. 400 mm SL), Muddy Boggy River, 5 mi. N of Lane on rd. to McGee Creek Lake, T3S, R13E, Sec. 6, Atoka Co., 20 June 1988. TU 83166 (9, 370–435 mm SL), Kiamichi River, at Hugo Dam, Choctaw Co., June 1973. OSUS 10669 (1, 445 mm SL), Red River, Choctaw Co., 15 December 1977. **LOUISIANA:** NLU 5048 (1, 160 mm SL), Red River, at Coushatta, Red River Par., 11 August 1966. TU 47600 (1, 515 mm SL), Red River, at RM 78, Rapides Par., 25 August 1967. **Ouachita River System.** NLU 54217 (1, 436 mm SL), Ouachita River, 0.25 mi. N of Bayou Bartholomew, Ouachita Par., 20 February 1983. NLU 55113 (1, 57 mm SL), Bayou Bartholomew, 1.1 mi. W of FM 1107 of Hwy. 165, 1.2 mi. N of Perryville, Morehouse Par., 11 July 1984. NLU 32646 (1, 425 mm SL), Bayou Bartholomew, 3 mi. N of La. 592, Pt. Pleasant, T21N, R5E, Sec. 45, Morehouse Par., 23 October 1985. **Gulf of Mexico Basin. Sabine River Drainage.** **LOUISIANA:** TU 36977 (3, 380–425 mm SL), Sabine River, 8 mi. S of Toro, Sabine Par., 26–27 June 1963. TU 36979 (6, 345–435 mm SL), Sabine River, 8 mi. S of Toro, Sabine Par., 13–14 July 1964. TU 36983 (1, 345 mm SL), Sabine River, at Anthony's Ferry, 8 mi. SW of Toro, Sabine Par., 5–6 July 1963. TU 37079 (1, 373 mm SL), Sabine River, at Anthony's Ferry, 8 mi. SW of Toro, Sabine Par., 13–14 July 1963. TU 36987 (5, 365–425 mm SL), Sabine River, at Anthony's Ferry, 8 mi. SW of Toro, Sabine Par., 14–15 July 1964. TU 37038 (1, 400 mm SL), Sabine River, 7.5 mi. SE of Toro, at Anthony's Ferry Landing, 1 July 1963. NLU 5214 (14, 98–176 mm SL), Sabine River, at Rapid Zwolle Landing, Sabine Par., 5 September 1966. NLU 3513 (2, 395–440 mm SL), NLU 3514 (3, 420–430 mm SL), [both from] Sabine River, Pindleton Crossing, 1.5 mi. above river, Sabine Par., 14 April 1966. **Neches River Drainage.** **TEXAS:** TU 72685 (1, 350 mm SL), Neches River, at FM 1013 bridge (public boat ramp), 4.9 mi. W Mount Union, Tyler Co., 21 October 1971. **Colorado River Drainage.** **TEXAS:** TNHC 23602 (2, 501–523 mm SL), Colorado River at Smithville from about 50 m below St. Hwy. 95 to 400 m below St. Hwy. 71, Bastrop Co., 29 June 1996. TNHC 24964 (2, 510–519 mm SL), Colorado River at Smithville from Hwy. 95 downstream to lower Riverbend Park, Bastrop Co., 19 July 1997. **Rio Grande Basin. Pecos River Drainage.** **NEW MEXICO:** MSB 7000 (5, 177–262 mm SL), Pecos River, Avalon Dam Spillway, Eddy Co., 2 November 1989. INHS 81990 (4, 177–204 mm SL), Pecos River, Eddy Co., 1963–1964. **TEXAS:** TU 38672 (1, 435 mm SL), Pecos River, 30 mi. SE of Sheffield, Terrell Co., 12 July 1965. **Rio Grande Drainage.** **TEXAS:** NLU 17189 (1, 75 mm SL), Rio Grande, 4 mi. W of Lajitas on Hwy. 2462, Presidio Co., 18 July 1970. MSB 9985 (2, 425–430 mm SL), Rio Grande, ca. 14 mi. downstream of Redford, between RM 925–924, Presidio Co., 13 April 1991. MSB 10025 (2, 181–201 mm SL), Rio Grande, between RM 925.0–922.8, Presidio Co., 13 April 1991. MSB 10032 (3, 167–285 mm SL), Rio Grande, between RM 922.8–918.5, Presidio Co., 13 April 1991. MSB 9988 (1, 568 mm SL), Rio Grande, ca. 20.5 mi. downstream of Redford, between RM 918.5–916.5, Presidio Co., 14 April 1991. MSB 9989 (1, 405 mm SL), Rio Grande, ca. 26.5–32.3 mi. downstream of Redford, between RM 912.5–906.7, Presidio Co., 14 April 1991. MSB 10045 (2, 211–224 mm SL), Rio Grande, between RM 912.5–906.7, Presidio Co., 14 April 1991. MSB 10050 (1, 211 mm SL), Rio Grande, between RM 906.7–904.0, Presidio Co., 15 April 1991. MSB 9992 (1, 415 mm SL), Rio Grande, Big Bend National Park, 2 mi. downstream of Lajitas, RM 902, Brewster Co., 16 April 1991. TNHC 8927 (1, 255 mm SL), Rio Grande, Colorado Canyon, 1 km E of Conterbando Creek, Presidio Co., 14 January 1978. MSB 9994 (2, 430–435 mm SL), Rio Grande, Big Bend National Park, ca. 5.5 mi. downstream of Lajitas, between RM 898.5–896.3, Brewster Co., 16 April 1991. MSB 10070 (2, 205–218 mm SL), Rio Grande, between RM 877.0–833.0, Brewster Co., 18 April 1991. MSB 9997 (1, 530 mm SL), Rio Grande, Big Bend National Park, ca. 8.7 mi. downstream of Castolon, between RM 868.3–867.5, Brewster Co., 19 April 1991. MSB 9999 (1, 320 mm SL), Rio Grande, Big Bend National Park, ca. 12.9 mi. downstream of Castolon, between RM 864.1–862.8, Brewster Co., 19 April 1991. MSB 10001 (1, 432 mm SL), Rio Grande, Big Bend National Park, ca. 18.8 mi. downstream of Castolon, between RM 858.2–855.8, Brewster Co., 20 April 1991. MSB 10003 (1, 313 mm SL), Rio Grande, Big Bend National Park, ca. 34.7 mi. downstream of Castolon, between RM 842.3–841.2, Brewster Co., 21 April 1991. MSB 10005 (1, 478 mm SL), Rio Grande, Big Bend National Park, 0.4 mi. upstream of Boquillas, between RM 808.4–805.4, Brewster Co., 26 April 1991. MSB 10010 (1, 528 mm SL), Rio Grande, Big Bend National Park, ca. 22.5 mi. downstream of Boquillas, between RM 785.5–783.4, Brewster Co., 28 April 1991. MSB 10007 (1, 545 mm SL), Rio Grande, Big Bend National Park, ca. 12.6 mi. downstream of Boquillas, between RM 795.4–793.8, Brewster Co., 27 April 1991. MSB 10011 (1, 453 mm SL), Rio Grande, ca. 24.8 mi. downstream of Boquillas, between RM 783.2–781.6, Brewster Co., 28 April 1991. MSB 10016 (1, 550 mm SL), Rio Grande, ca. 67.6 mi. downstream of Boquillas, between RM 740.4–740, Brewster Co., 30 April 1991. MSB 10020 (1, 410 mm SL), Rio Grande, ca. 16.1 mi. upstream of Brewster/Terrell Co. line, between RM 726.6–725.6, Brewster Co., 2 May 1991.

TNHC 1992-9 (5, 185-235 mm SL), Rio Grande, 0.5 mi. above to 2 mi. below Dryden crossing, Terrell Co., 7 January 1992. TU 73670 (1, 46 mm SL), Rio Grande, and Goodenough Spring Run, 14 mi. W of Comstock, Val Verde Co., 11 April 1968. **MEXICO:** TNHC 4055 (1, 210 mm SL), Río Conchos, 1 km from mouth of Rio Grande, Chihuahua, 13 June 1954. UAZ 95-62 (1, 116 mm SL), Río Conchos drainage, 11 mi. W Ojinaga at El Acon, Chihuahua, 23 July 1972.

SKELETONS EXAMINED.—UMMZ 176973 (1), [Red River], draft tubes of service generators of Denison Dam, [Grayson] Co., Texas, 8 July 1959. SIUC 26826 (1), Mississippi River, RM 116.5, just below mouth of Kaskaskia River, Randolph County, Illinois, 24 October 1996.

VOUCHERED SPECIMENS USED FOR RANGE MAP, NOT FOR COUNTS OR MEASUREMENTS (duplications excluded).—Numbers in parentheses are numbers of specimens vouchered. **Mississippi River Basin. Mississippi River Drainage. Mississippi River System. ILLINOIS:** CU 25513 (1), Mississippi River, vicinity of Oquawka, Henderson Co., January. ANSP 159677 (1), Kaskaskia River, 1 mi. below Carlyle, Clinton Co., no date. SIUC 23892 (1), Pool 24, RM 296.1 at Cincinnati Landing (T5S, R7W, Sec. 26SE), Pike Co., 10 June 1993; SIUC 23935 (1), Pool 24, RM 280.5 at Delair Access (T7S, R5W, Sec. 20), Pike Co., 10 June 1993; SIUC 23931 (1), Pool 24 about 7.5 mi. SW Pleasant Hill [in Pike County], Calhoun Co., 11 June 1993; SIUC 24948 (1), RM 244.7, 3 mi. NW Batchtown (T12S, R2W, Sec. 6), Calhoun Co., 10 June 1992; SIUC 25460 (1), at Piasa Harbor, RM 209.5, Jersey Co., 17 June 1994; SIUC 23923 (1), RM 125.2 at Little Rock Ferry, Randolph Co., 11 June 1993; SIUC 24945 (1), at rock dikes, 4 mi. NW Chester (T7S, R7W, Sec. 15SE), Randolph Co., 29 August 1995; SIUC 24886 (1), at Grand Tower aerial pipeline (T10S, R4W, Sec. 23SE), Jackson Co., 16 June 1994; SIUC 23934 (1), RM 43.9 at Thebes Public Access (T15S, R3W, Sec. 8SE), Alexander Co., 11 June 1992. **MISSOURI:** ANSP 6658 (1), [Mississippi River], St. Louis, [St. Louis Co.], no date. **TENNESSEE:** UT 45.411 (4), Mississippi River, at Randolph boat access, Tipton Co., 17 May 1982. UT 45.480 (1), Mississippi River, ca. 0.5 mi. above I-40, Shelby Co., 12 June 1983. **ARKANSAS:** UF 28438 (1), Mississippi River, just SE of Millwood, Phillips Co., June 1988. **MISSISSIPPI:** UT 45.757 (5), Big Black River, at Miss. 80, Bovina, Hinds Co., 20 May 1988. USNM 201486 (1), Short Creek, tributary to Yazoo River, 3.1 mi. W of Yazoo City, Yazoo Co., 10 June 1964. **LOUISIANA:** UT 45.760 (7), Mississippi River, west bank at La. 80, Point Coupee Par., 18 May 1988. **Missouri River Drainage. MONTANA:** MSUB uncat., Missouri River, dredge cuts below Ft. Peck Dam, 15 July 1963. MSUB uncat., Ft. Peck Reservoir, 22 August 1949. MSUB uncat., Tongue River, 2 mi. above mouth, [Custer Co.], 24 April 1974. **NORTH DAKOTA:** UMMZ 178955 (1 skeleton), [Missouri River]

tailrace of Garrison Dam, [McLean Co.], 25 June 1960. **SOUTH DAKOTA:** JFBM 18977 (15), Missouri River, at Elk Point, Union Co., 26 June 1956. **NEBRASKA:** UT 45.685 (27), Missouri River, RM 660, Herman, Washington Co., 13 June 1979. **Ohio River Drainage. PENNSYLVANIA:** ANSP 22109 (1), 23789 (1), Kiskiminetas River, western Pennsylvania, [probably 1860s]. **OHIO:** USNM 12278 (1), [Ohio River], at Cincinnati, [Hamilton Co.], no date. **INDIANA:** SIUC 25857 (4), Wabash River, RM 38-42, from Old Dam to Mink Island, Posey County, 12 April 1996. UF 78540 (2), Wabash River, RM 181-182, downstream from Breed Power Plant, near Riverview, Sullivan Co., September 1988. UF 78625 (2) Wabash River, RM 178, near York, Sullivan Co., Sept. 1988. UF 78702 (2), Wabash River, RM 218-222, just upstream from Terre Haute, near Wabash River Power Plant, Vigo Co., 1988. CAS-SU 10309 (1), [White River], at Gosport, [Owen Co.], no date. USNM 69001 (3), [Wabash River], at New Harmony, [Posey Co.], 1899-1900. USNM 66937 (1), Wabash River, at Bonebank, [no county], 12 August 1890. **Cumberland River System. KENTUCKY:** USNM 63856 (1), [Cumberland River], at Kuttawa, [Lyon Co.], 26 July 1890. Tennessee River System. **TENNESSEE:** UT 45.283 (1), Nolichucky River, RM 20, Greene Co., 18 July 1975. **Tennessee River System. ALABAMA:** GSA 3122 (1), Bear Creek on Natchez Trace (T5S, R15W, SEC. 9), Colbert Co., 22 July 1997. **Red River Drainage. OKLAHOMA:** OKMNH 26145 (1), [Red River, now Lake Texoma], 2 mi. E Willis, Marshall Co., 18 March 1951. OKMNH 26147 (1), Lake Texoma, near University of Oklahoma Biological Station, Marshall Co., 18 March 1951. OKMNH 35229 (1), Denison Lake, Denison Dam Draft Tubes, Bryan Co., 13 January 1958. **LOUISIANA:** TU 125956 (2), Red River, along right bank, at RM 94, Rapides Par., 23 June 1982. TU 121658 (1), Red River, along right bank at RM 90, Rapides Par., 15 June 1981. TU 125913 (1), Red River, along right bank at RM 105, Rapides Par., 23 June 1982. **Rio Grande Basin. TEXAS:** OSUS 76 (2), Rio Grande, near Laredo, [Webb Co.], 7 April 1939. OSUS 5494 (22), Rio Grande, at Big Bend National Park, 5 mi. above Boquillas, [Brewster Co.], 17 April 1960. OSUS 11854 (1), Rio Grande, at mouth of Terlingua Creek, Brewster Co., 16 April 1960. **MEXICO:** FMNH 5575 (3), [Río Salado], Rodriguez, Nuevo Leon, no date.

DIAGNOSIS.—A species of *Cycleptus* as diagnosed above and distinguished from its congener by having more numerous scales, usually 19-20 caudal-peduncle scale rows (Table 1), usually 41-49 body-circumferential scale rows (Table 2), usually 53-58 lateral-line scales (Table 3), and usually 95-104 lateral-line scales plus body-circumferential scale rows (Table 4); more numerous dorsal-fin rays, usually 28-34 (Table 5); a longer snout and a more elongate dorsal fin base (Table 6, Figs. 5-6).

DESCRIPTION.—Morphometry. Body usually elongate, oval in cross section, body depth 19 to 31% SL; body width 11 to 18% SL; head width 11 to 14% SL. Caudal peduncle elongate, its length averaging 23% SL. Head moderately long, averaging 18% SL in adults over 157 mm SL; snout lateral profile declivous to slightly bulbous, projecting anterior to upper lip; snout length averaging 49% of head length (Table 7). Orbit small, its diameter 12 to 17% of head length in specimens 157–540 mm SL. Most adults are 325–737 mm SL. Largest Kansas specimen is 763 mm (Cross and Collins, 1995). Trautman (1981) notes that rivermen give maximum total lengths (TL) of 36 to 40 inches (91.4 to 102 cm), weights of 12 to 15 lbs (5.4 to 6.8 kg). TL = 1.24 SL. The species reaches a maximum SL of about 825 mm. Fish up to 20 lbs (9.1 kg) were formerly common in the Missouri River (Pflieger, 1975) and Coker (1930) noted that some may reach 25 lbs (11.3 kg) in the upper Mississippi River. Largest specimen examined here is 610 mm SL (largest from Rio Grande is 568 mm SL).

Lips. Mouth relatively small. Posterior margin of lips ranging from a rounded or slightly emarginate edge to deeply indented and nearly dividing the lower lip into halves. Surfaces papillose, ranging from short, blunt, and rounded papillae to elongate, fleshy, almost barbel-like projections (Fig. 7A-F). The latter condition especially evident in samples from southwestern rivers, e.g., Rio Grande, Red River. Papillae on upper lip generally longer than those of lower lip.

Fins. Dorsal fin margin falcate anteriorly, 1st and 2nd developed rays long, rapidly shortening to about 8th ray, remaining rays all short. Pectoral and pelvic fins elongate and falcate, anterior rays thickened. Anal fin in adults small, generally straight-edged, sometimes falcate. Caudal fin in adults large, widely forked, lobe tips slightly rounded to pointed, inner margins straight; both lobes about equal in length. Upper lobe more pointed and longer in young, juveniles, and some adults.

Meristic Features. Lateral line complete, nearly straight, scales 52–60, usually 53–58 (Table 3); body-circumferential scale rows 41–53, usually 41–49 (Table 2); predorsal scale rows 19–26, usually 20–24, scales number 19 (12), 20 (27), 21 (68), 22 (57), 23 (37), 24 (24), 25 (11), 26 (2); caudal-peduncle scale rows 18–21, modally 20 (Table 1); dorsal rays 24–35, usually 28–34 (Table 5); anal rays 7–8, modally 7, rays number 7 (159), 8 (31); pectoral rays 15–18, usually 16–17, rays number 15 (8), 16 (76), 17 (62), 18 (10); pelvic rays number 9 (13), 10 (122), or 11 (22); principal caudal rays number 17 (2), 18 (139), 19 (4); gill rakers on first arch 19–25 in adults, as few as 12 in small juveniles; pharyngeal teeth per arch 40–45 (Eastman 1977). Total vertebrae 48–50 (Cross, 1967; Sublette et al., 1990). Chromosomes 2n = 96–100 (Uyeno and Smith, 1972).

Internal Anatomy. Swim bladder two-chambered, anterior chamber short and rounded, posterior chamber rounded

Table 1. Frequency distribution in number of caudal-peduncle scale rows in drainage samples of *Cycleptus* from throughout its range. Value for holotype of *Cycleptus meridionalis* is in bold. Numbers in parentheses are numbers of specimens examined.

Species & Drainage	Number of Scales						\bar{x}	SD	
	15	16	17	18	19	20			21
<i>Cycleptus elongatus</i>									
Mississippi R. (45)					5	40		19.9	0.32
Missouri R. (24)					2	22		19.9	0.28
Ohio R. (38)					3	35		19.9	0.27
Arkansas R. (38)					1	35	2	20.0	0.28
Red R. (20)					1	18	1	20.0	0.32
Sabine-Neches R. (37)				1	3	33		19.9	0.42
Colorado R. (4)					4			19.0	0.00
Rios Grande-Conchos (47)				4	12	31		19.6	0.65
<i>Cycleptus meridionalis</i>									
Mobile Basin (47)	1	43	3					16.0	0.29
Pearl-Pascagoula R. (56)		40	13	3				16.3	0.58

Table 2. Frequency distribution in number of body-circumferential scale rows in drainage samples of *Cycleptus* from throughout its range. Value for holotype of *Cycleptus meridionalis* is in bold. Numbers in parentheses are numbers of specimens examined.

Species & Drainage	Number of Scales														\bar{x}	SD				
	36	37	38	39	40	41	42	43	44	45	46	47	48	49			50	51	52	53
<i>Cycleptus elongatus</i>																				
Mississippi R. (41)							1	6	6	9	6	7	2	2		2			45.6	2.12
Missouri R. (21)							3	1	2	3	1		6	2		2		1	46.6	3.17
Ohio R. (39)							9	6	5	8	4	3	2	2					44.5	2.09
Arkansas R. (35)								1	5	5	3	5	6	3	3	2	1	1	47.2	2.55
Red R. (20)							2	3	1	4	3	3	4						45.4	2.04
Sabine-Neches R. (38)						13	12	8	3	1	1								42.2	1.23
Colorado R. (4)						4													41.0	0.00
Rios Grande-Conchos (46)						2	13	8	6	6	7	3	1						43.9	1.85
<i>Cycleptus meridionalis</i>																				
Mobile Basin (47)	1	8	13	17	6	2													38.5	1.12
Pearl-Pascagoula R. (56)	2	8	11	15	15	5													38.9	1.31

Table 3. Frequency distribution in number of lateral-line scales in drainage samples of *Cycleptus* from throughout its range. Value for holotype of *Cycleptus meridionalis* is in bold. Numbers in parentheses are numbers of specimens examined.

Species & Drainage	Number of Scales												\bar{x}	SD		
	48	49	50	51	52	53	54	55	56	57	58	59			60	
<i>Cycleptus elongatus</i>																
Mississippi R. (44)						2	11	10	15	5	1				55.3	1.17
Missouri R. (24)						4	5	4	5	3	1	1	1		55.4	1.91
Ohio R. (38)						1	7	12	11	4	3				55.5	1.23
Arkansas R. (41)					1	10	9	11	2	4	4				54.8	1.66
Red R. (20)							3	7	5	4	1				55.7	1.14
Sabine-Neches R. (39)							21	9	4	4			1		54.9	1.31
Colorado R. (4)						2	1	1							53.8	0.96
Rios Grande-Conchos (47)						3	8	10	16	5	4	1			55.6	1.41
<i>Cycleptus meridionalis</i>																
Mobile Basin (47)	4	7	16	9	7	4									50.4	1.38
Pearl-Pascagoula R. (56)		3	10	16	16	11									51.4	1.16

Table 4. Frequency distribution in number of lateral-line scales + body-circumferential scale rows in drainage samples of *Cycleptus* from throughout its range. Value for holotype of *Cycleptus meridionalis* is in bold. Numbers in parentheses are numbers of specimens examined.

Species & Drainage	Number of Scales											
	86	87	88	89	90	91	92	93	94	95	96	97
<i>Cycleptus elongatus</i>												
Mississippi R. (41)											2	1
Missouri R. (21)										2		
Ohio R. (38)											2	5
Arkansas R. (35)												4
Red R. (20)												3
Sabine-Neches R. (37)										7	10	4
Colorado R. (4)									2	1	1	
Rios Grande-Conchos (46)									2		6	3
<i>Cycleptus meridionalis</i>												
Mobile Basin (47)	7	9	6	3	9	8	4	1				
Pearl-Pascagoula R. (56)	2	3	4	10	11	7	12	5	2			

anteriorly and tapering to a point posteriorly. Peritoneum silvery. Gut coiling patterns are shown in Jenkins (1970: fig. 11); young have a pattern similar to species of *Moxostoma*, adults have relatively long left and medial loops with a larger coil mass. Pharyngeal teeth in two skeletonized individuals (UMMZ 176973 [Red River, Texas], SIUC 26826 [Mississippi River, Illinois]) are 45 (right), 43 (left) and 41 (right), 43 (left), respectively (Fig. 8).

Coloration. In life, males: Olive blue or slate olive on dorsum and sides of body with brassy reflections; venter bluish-white; lips white; all fins dark blue-gray, dusky, or black. "Spring males almost black" (Forbes and Richardson, 1908). Our observations of living adults from various locations in the Mississippi River basin indicate that fall males are also blue-black. Late spring adults in the Rio Grande basin are generally more golden or brassy in color than those in the Mississippi River basin, although continuously turbid water conditions may effect color. An adult male, taken in July, from the Missouri River is shown in Figure 3 (above). In life, females: adult females, exclusive of the spring spawning season, indistinguishable from males in overall color pattern. Breeding females may be tan to light blue. Young (62–80 mm SL) described in detail by Cross (1967).

Tuberculation. Male: See Branson (1962b) for tubercle

description of male from Neosho River, Kansas. All males taken during the spring spawning runs are covered with thousands of white tubercles ranging in diameter from 0.2 to 1.0 mm. Tubercles cover most of head, nearly every scale, and all rays of all fins; none occur on fin membranes. Branchiostegals and gular region with small tubercles sparsely scattered. Breast and belly scales with few scattered tubercles, 1–5 along scale edge, 1–2 in center of scale. Scales on posterior two-thirds of body have twice as many tubercles as those on anterior one-third of body. The number of tubercles per scale ranges from 6–25, on fin rays from 20–100. Tubercles on snout, around eyes, and on opercle prominent. Females: Tubercles occur principally around the eyes in spawning females, but are smaller and less numerous than those on males.

Sexual Dimorphism. As with many North American fishes, females heavy with eggs have deeper and wider bodies during the spring spawning season when compared to males. In fact, females are heavier than males for their length (Beal, 1967) and can be sexed externally using size and shape characters. Measurements of body depth and body width were thus deleted from the PCA comparing species. Two other proportions, eye diameter and a modified measurement of head length were significantly ($\mu = 0.005$) different between males and females and were removed from the final PCA where we compared species.

98	99	100	101	102	103	104	105	106	107	108	109	\bar{x}	SD
3	8	5	7	5	6	2	1			1	100.8	2.57	
1	6		2	3	1	2	2		2			101.2	3.42
7	5	3	4	7	1	2	1	1				99.9	2.57
2	5	2	4	5	4	3	1	2	1	1	1	101.7	3.22
1	1	1	2	4	3	3	1	1				101.5	2.72
9	2	4			1							97.2	1.87
												94.8	0.96
4	11	4	8	2	4	1	1					99.3	2.56
												88.9	2.07
												90.3	1.96

Table 5. Frequency distribution in number of dorsal fin rays in drainage samples of *Cycleptus* from throughout its range. Value for holotype of *Cycleptus meridionalis* is in bold. Numbers in parentheses are numbers of specimens examined.

Species & Drainage	Number of Rays													\bar{x}	SD	
	23	24	25	26	27	28	29	30	31	32	33	34	35			
<i>Cycleptus elongatus</i>																
Mississippi R. (43)							2	11	13	8	7	2			31.3	1.28
Missouri R. (24)							3	2	6	6	2	3	2		31.8	1.77
Ohio R. (38)						1	3	7	10	9	7		1		31.3	1.45
Arkansas R. (37)					1	7	8	7	5	5		2	2		30.2	2.04
Red R. (20)					1	1	3	4	4	3	2	2			30.8	1.91
Sabine-Neches R. (37)		1	1		7	17	7	3	1						28.1	1.29
Colorado R. (4)							1	1		2					30.8	1.50
Rios Grande-Conchos (46)							3	12	15	8	5	1	2		31.2	1.42
<i>Cycleptus meridionalis</i>																
Mobile Basin (44)		1	4	8	16	6	5	2	2						27.3	1.57
Pearl-Pascagoula R. (56)	1	2	13	22	12	5	1								26.1	1.14

There are no significant color differences between males and females despite some statements to the contrary by authors having only limited experience with the species.

ETYMOLOGY.—*elongatus*, elongate, in reference to the general body shape. The common name, blue sucker, refers to populations in which adults are known to have blue (often black) on body and fins.

GEOGRAPHIC VARIATION.—The most substantial phenotypic variation occurs among samples from Gulf Coast streams from the Sabine River, Louisiana and Texas, to the Rio Grande basin, Texas, New Mexico, and Mexico. In this region the two most divergent populations are from the mainstems of the Sabine River and the Rio Grande. Characters or character complexes that vary substantially include: 1) aspects of body shape in the Sabine River samples, 2) elongation of lip papillae in the Rio Grande samples, 3) a scale pigmentation pattern producing vague body stripes in adults from the Rio Grande, and 4) perhaps general body color differences in the Rio Grande population when compared to other samples of *C. elongatus*.

The Sabine River samples, consisting of 38 adults from the middle reach of the river only, have snout shapes most similar to *C. elongatus* samples, but dorsal fin base length is more like that in *C. meridionalis*. The shorter dorsal fin base length is reflected in the number of ray elements that compose that fin. Counts of dorsal fin rays from the Sabine River show that over half the sample have counts more in the general range of those for *C. meridionalis* (Table 5). This character is thus discordant primarily in Sabine River samples, all of which come from the same geographic location and were collected temporally close together. Samples from other reaches of the drainage might provide a less biased sample. Other than these features, the Sabine River samples are most similar to *C. elongatus* in other meristic features, pigmentation, and general lip morphology. We allocate the Sabine River samples to *C. elongatus*.

The most striking morphological distinction of the Rio Grande samples is the elongation of their lip papillae. This feature occurs in adults, not juveniles, on both the upper and lower lips, and results in almost barbel-like protrusions (Fig. 7F). Most other samples of both species of *Cycleptus* have round, blunt papillae (Fig. 7A-E), including adults from the Colorado River, Texas, a population geographically intermediate between the Sabine River and Rio Grande. Some individuals from the Sabine, Red, and Arkansas rivers also have somewhat elongated lip papillae, a feature that may have been influenced by the historically turbid water conditions known for these river drainages. Some adults and larger juveniles from the Rio Grande samples (Fig. 9) and those from the Colorado River, Texas, have stripes on their side produced by dark pigment at the bases (scale pockets) of lateral scales.

There may be as many as 12 vague stripes on the side of large adults. This feature, however, is variable and not consistent in the material studied, and could be due to the physiological state of specimens prior to preservation. One other character presumed to be distinctive is the general body color of adults from the Rio Grande, excluding the spawning season. Hundreds of live individuals taken from consistently turbid water appear brassy or golden in overall color of body and fins. Live individuals from other locations in the Mississippi River basin may have a color pattern similar to those from the Rio Grande, especially after the spring spawning season. Adults from the Colorado River, Texas, darken to blue-black in the spring and we suspect this would be the case for adults from the Rio Grande, although melanophores may be generally constricted in response to continuously turbid water conditions. Detailed information is needed on colors of spawning adults from the Rio Grande basin. There is no set of trenchant phenotypic characters that consistently allow for diagnosing the Rio Grande samples as a new taxon; we allocate these samples to *C. elongatus* but urge further study of tubercle patterns, spawning colors, lip morphology, and genetic data sets.

Literature references to pharyngeal tooth number and morphology of the arches of *C. elongatus* report, in some cases, non-overlapping counts in number of teeth. For example, Forbes and Richardson (1908) recorded 25–35 teeth per arch, and Eastman (1977) recorded 40–45 teeth per arch. The number and SL or TL of individuals examined by Forbes and Richardson are not indicated, but Eastman (1977) examined three adults. Our counts of two adults agree with the range in counts given in Eastman (1977). We note that many teeth are broken off and small teeth near the dorsal surface may be difficult to count; examination under a dissecting microscope is essential for accurate counts. We do not accept here the aberrant counts of teeth reported by Forbes and Richardson (1908) and Branson (1962a), but recommend further study of the problem. It appears that other authors (e.g., Becker, 1983; Sublette et al., 1990) have simply accepted the presumed original counts of Forbes and Richardson (1920) and Branson (1962a).

DISTRIBUTION.—All substantiated records are from large rivers (i.e., mainstems of Mississippi, Missouri, and Ohio rivers; Rio Grande), their lower reaches or their major tributaries (e.g., Wabash, Cumberland, Tennessee, Arkansas, Red, Sabine, and Pecos rivers). The historical range (Fig. 10) is the Mississippi River basin from western Pennsylvania to central Montana and from northern Wisconsin south to Louisiana; also in Gulf Slope drainages from the Sabine River to the Rio Grande basin of Texas, Mexico, and New Mexico. The species is extirpated from Pennsylvania (Cooper, 1983; Gilbert in Cooper, 1985), with the only substantiated specimens being those collected by E. D. Cope from the Kiskiminetas River and dating to the

Table 6. Sheared principal component loadings for 33 mensural variables taken from 82 *Cycleptus elongatus* and 28 *C. meridionalis*. Individuals of both species are from throughout their respective ranges. Four characters (i.e., body depth and width, modified snout length, and eye diameter) were deleted from this analysis because of significant differences between the sexes. Numbers in parentheses refer to measurements as illustrated in Figures 1 and 2, except gape width which is not shown.

Measurement	Sheared PC 2	Sheared PC 3
Standard Length (1)	-0.01433	0.13061
Predorsal Length (6)	-0.06246	0.01945
Head Length (3)	0.07549	-0.09263
Head Width (5)	0.03212	-0.05838
Snout Length (2)	0.21954	-0.15362
Gape Width	0.20244	-0.30347
Caudal Peduncle Depth (10)	-0.07821	0.09852
Dorsal Fin Length (8)	-0.21851	-0.11947
Anal Fin Length (11)	-0.10693	0.00431
Pectoral Fin Length (13)	0.00272	-0.16845
Snout to Head Occiput (14)	-0.06185	-0.20306
Head Occiput to Dorsal Fin Origin (15)	-0.14331	0.12123
Dorsal Fin Base Length (16)	0.01714	0.34339
Back of Dorsal Fin to Hypural Plate (17)	-0.06352	-0.07465
Tip of Snout to Pectoral Fin Origin (18)	0.06781	-0.15986
Pectoral Fin Origin to Pelvic Fin Origin (19)	-0.07197	0.23484
Pelvic Fin Origin to Anal Fin Origin (20)	-0.01609	0.20275
Anal Fin Origin to Hypural Plate (21)	-0.05272	0.10376
Head Occiput to Pectoral Fin Origin (22)	-0.13300	-0.13531
Head Occiput to Pelvic Fin Origin (23)	-0.08691	0.15480
Dorsal Fin Origin to Pectoral Fin Origin (24)	-0.14368	0.06599
Dorsal Fin Origin to Pelvic Fin Origin (25)	-0.13090	0.13094
Dorsal Fin Origin to Anal Fin Origin (26)	-0.00859	0.22768
Pelvic Fin Origin to Back of Dorsal Fin (27)	-0.02650	0.28578
Back of Dorsal Fin to Anal Fin Origin (28)	-0.15279	0.12601
Interorbital Length (29)	-0.07789	-0.15871
Top of Eye to Posterior Naris (34)	-0.20830	-0.43901
Tip of Snout to Posterior Naris (31)	0.26337	-0.08708
Top of Eye to Head Occiput (32)	-0.07235	-0.18590
Top of Eye to Lip Crease (33)	-0.07181	-0.08713
Posterior Naris to Lip Crease (35)	0.03672	-0.00548
Tip of Snout to Lip Crease (angled) (37)	0.57672	0.09389
Tip of Snout to Lip Crease (horizontal) (36)	0.49267	0.03439

Table 7. Measurements in thousandths of standard length for 82 *Cycleptus elongatus* from throughout the species range. Numbers in parentheses refer to measurements as illustrated in Figures 1 and 2, except gape width which is not shown.

Measurement	Minimum	Maximum	Mean	SD
Standard Length (1)	157.000	578.000	377.829	110.619
Predorsal Length (6)	0.380	0.481	0.424	0.023
Head Length (3)	0.151	0.207	0.183	0.011
Head Width (5)	0.105	0.141	0.122	0.008
Body Depth (9)	0.185	0.313	0.237	0.025
Body Width (7)	0.109	0.184	0.148	0.017
Snout Length (2)	0.053	0.107	0.089	0.009
Eye Diameter (4)	0.023	0.033	0.028	0.005
Gape Width	0.019	0.036	0.026	0.004
Caudal Peduncle Depth (10)	0.085	0.126	0.101	0.009
Dorsal Fin Length (8)	0.159	0.256	0.202	0.020
Anal Fin Length (11)	0.098	0.159	0.133	0.011
Pectoral Fin Length (13)	0.155	0.237	0.192	0.016
Pelvic Fin Length (12)	0.136	0.194	0.166	0.013
Snout to Head Occiput (14)	0.136	0.194	0.165	0.012
Head Occiput to Dorsal Fin Origin (15)	0.209	0.324	0.266	0.020
Dorsal Fin Base Length (16)	0.320	0.420	0.376	0.022
Back of Dorsal Fin to Hypural Plate (17)	0.182	0.268	0.231	0.019
Tip of Snout to Pectoral Fin Origin (18)	0.155	0.287	0.189	0.016
Pectoral Fin Origin to Pelvic Fin Origin (19)	0.257	0.336	0.296	0.017
Pelvic Fin Origin to Anal Fin Origin (20)	0.239	0.308	0.273	0.013
Anal Fin Origin to Hypural Plate (21)	0.227	0.315	0.256	0.014
Head Occiput to Pectoral Fin Origin (22)	0.114	0.148	0.128	0.009
Head Occiput to Pelvic Fin Origin (23)	0.320	0.422	0.370	0.020
Dorsal Fin Origin to Pectoral Fin Origin (24)	0.251	0.325	0.282	0.018
Dorsal Fin Origin to Pelvic Fin Origin (25)	0.188	0.299	0.234	0.022
Dorsal Fin Origin to Anal Fin Origin (26)	0.363	0.479	0.410	0.023
Pelvic Fin Origin to Back of Dorsal Fin (27)	0.283	0.369	0.326	0.017
Back of Dorsal Fin to Anal Fin Origin (28)	0.110	0.170	0.138	0.015
Interorbital Length (29)	0.076	0.105	0.088	0.006
Top of Eye to Posterior Naris (34)	0.021	0.035	0.028	0.003
Tip of Snout to Posterior Naris (31)	0.058	0.094	0.077	0.008
Top of Eye to Head Occiput (32)	0.064	0.099	0.078	0.007
Top of Eye to Lip Crease (33)	0.064	0.104	0.076	0.007
Posterior Naris to Lip Crease (35)	0.040	0.077	0.054	0.006
Tip of Snout to Lip Crease (angled) (37)	0.029	0.062	0.044	0.006
Tip of Snout to Lip Crease (horizontal) (36)	0.028	0.080	0.050	0.007

Table 8. Measurements in thousandths of standard length for 28 *Cycleptus meridionalis* from throughout the species range. Numbers in parentheses refer to measurements as illustrated in Figures 1 and 2, except gape width which is not shown.

Measurement	Minimum	Maximum	Mean	SD
Standard Length (1)	197.000	525.000	419.071	85.217
Predorsal Length (6)	0.404	0.482	0.443	0.020
Head Length (3)	0.169	0.206	0.185	0.008
Head Width (5)	0.113	0.149	0.126	0.007
Body Depth (9)	0.212	0.297	0.249	0.021
Body Width (7)	0.134	0.171	0.149	0.010
Snout Length (2)	0.080	0.103	0.089	0.006
Eye Diameter (4)	0.026	0.032	0.029	0.005
Gape Width	0.021	0.033	0.025	0.003
Caudal Peduncle Depth (10)	0.093	0.112	0.104	0.005
Dorsal Fin Length (8)	0.193	0.255	0.223	0.018
Anal Fin Length (11)	0.123	0.159	0.138	0.009
Pectoral Fin Length (13)	0.182	0.225	0.202	0.012
Pelvic Fin Length (12)	0.161	0.205	0.182	0.012
Snout to Head Occiput (14)	0.156	0.205	0.182	0.013
Head Occiput to Dorsal Fin Origin (15)	0.242	0.317	0.280	0.020
Dorsal Fin Base Length (16)	0.324	0.379	0.351	0.015
Back of Dorsal Fin to Hypural Plate (17)	0.199	0.280	0.248	0.017
Tip of Snout to Pectoral Fin Origin (18)	0.180	0.210	0.194	0.008
Pectoral Fin Origin to Pelvic Fin Origin (19)	0.257	0.332	0.301	0.019
Pelvic Fin Origin to Anal Fin Origin (20)	0.244	0.307	0.269	0.015
Anal Fin Origin to Hypural Plate (21)	0.215	0.304	0.260	0.018
Head Occiput to Pectoral Fin Origin (22)	0.129	0.159	0.143	0.007
Head Occiput to Pelvic Fin Origin (23)	0.344	0.418	0.384	0.018
Dorsal Fin Origin to Pectoral Fin Origin (24)	0.269	0.327	0.304	0.017
Dorsal Fin Origin to Pelvic Fin Origin (25)	0.216	0.270	0.247	0.014
Dorsal Fin Origin to Anal Fin Origin (26)	0.367	0.436	0.403	0.017
Pelvic Fin Origin to Back of Dorsal Fin (27)	0.277	0.335	0.316	0.013
Back of Dorsal Fin to Anal Fin Origin (28)	0.127	0.178	0.148	0.010
Interorbital Length (29)	0.084	0.109	0.096	0.006
Top of Eye to Posterior Naris (34)	0.030	0.038	0.033	0.002
Tip of Snout to Posterior Naris (31)	0.064	0.090	0.074	0.006
Top of Eye to Head Occiput (32)	0.068	0.096	0.084	0.006
Top of Eye to Lip Crease (33)	0.072	0.090	0.082	0.005
Posterior Naris to Lip Crease (35)	0.046	0.068	0.055	0.005
Tip of Snout to Lip Crease (angled) (37)	0.027	0.043	0.036	0.004
Tip of Snout to Lip Crease (horizontal) (36)	0.037	0.053	0.044	0.004

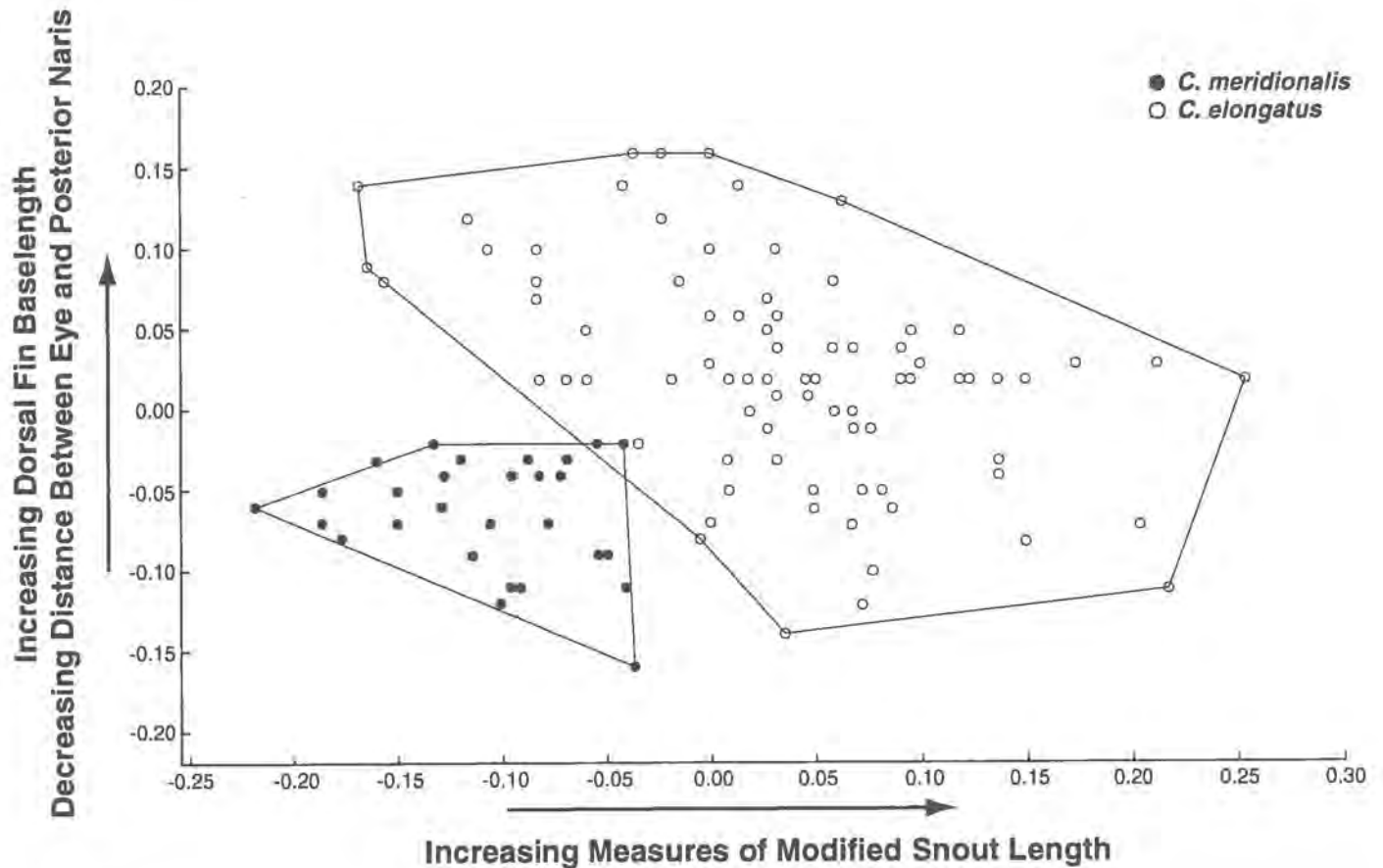


Figure 5. Scores of *Cycleptus elongatus* (open circles) and *C. meridionalis* (solid circles) on sheared principal component axes II and III for 33 morphometric variables.

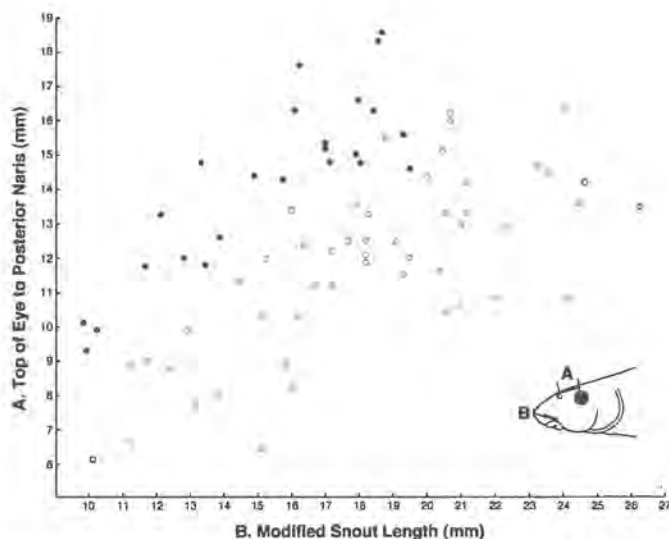


Figure 6. Relationship between length of snout and top of eye to posterior nares in *Cycleptus elongatus* (open circles) and *C. meridionalis* (solid circles).

1860s (Fowler, 1919; 1948). It apparently once occurred upstream in the Ohio River drainage at least to Pittsburgh (Rafinesque, 1820). It is present in adjacent West Virginia, in the mainstem Ohio River. The one record from a small headwater stream in the Monongahela River drainage (Stauffer et al., 1995) is not plotted in Figure 10; almost certainly it is erroneous. One adult (UMMZ Accession No. 1941-IV:19) was captured in the Tennessee River near Decatur, Alabama, in 1939 (Etnier et al., 1979) prior to impoundment of that reach of the river; a recent (1997) record from below Wilson Dam is now available (C. Saylor, pers. comm.).

The largest and most significant gap in the range is that of central Texas. In a canvass of museum collections, we have been unable to document a vouchered record in any Gulf Coast stream between the Colorado River and the Rio Grande or between the Neches River and Colorado River. Observational records for Texas include those for the San Marcos (ca. 1965), Frio (ca. 1958), and Colorado rivers (ca. 1965) (J. Van Conner, pers. comm.) and a thesis with two records for the Colorado River at Austin (one in 1953, the other undated) (Tilton, 1961). These records were plotted and included in the range map in the "Atlas

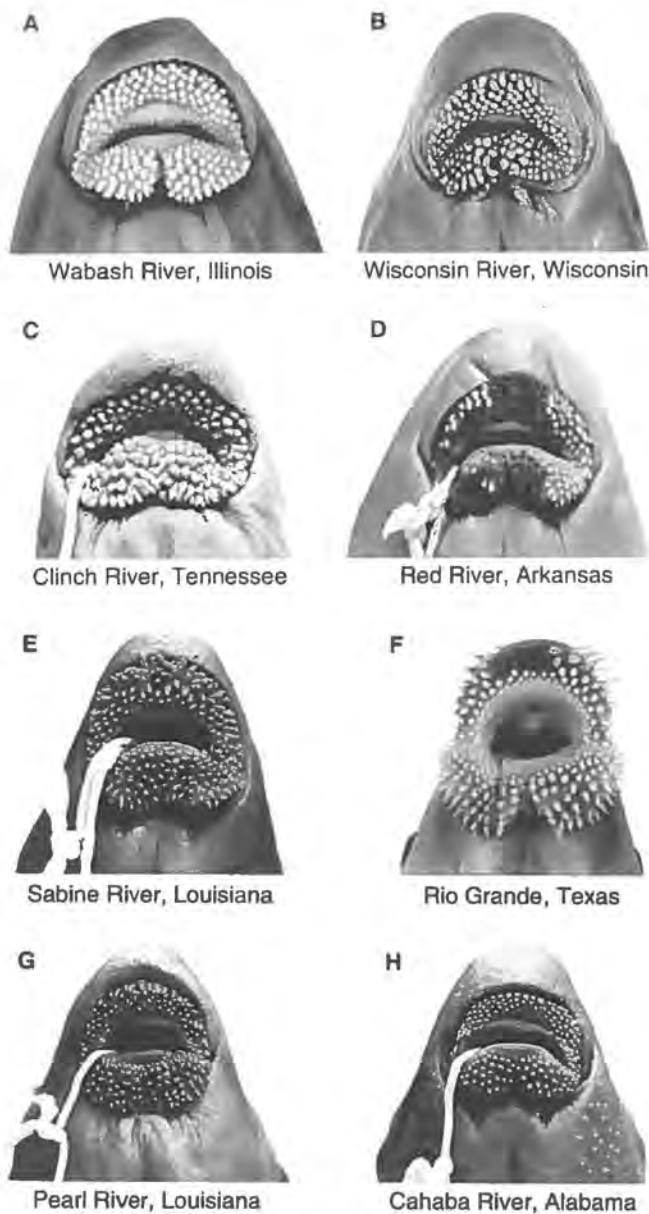


Figure 7. Lip morphology of individuals of *Cycleptus* from selected river systems: *C. elongatus*—A) Wabash River (SIUC 25857), B) Wisconsin River (MPM 17851), C) Clinch River (TU 36996), D) Red River (TU 47600), E) Sabine River (TU 36979), F) Rio Grande (MSB 10010); *C. meridionalis*—G) Pearl River (TU 27850), H) Cahaba River (TU 40351).

of North American Freshwater Fishes” account by Gilbert (1980). Recent (1996, 1997) vouchered records for the Colorado River, Texas, lend considerable credibility to the sight records reported for other central Texas drainages.

Its status in the Rio Grande would appear in the literature to be almost conjectural. For example, Williams et al. (1985:23) stated that this species has been greatly reduced in the Río Grande basin. This is erroneous. Recent (1990s) electrofishing and seining data along the entire

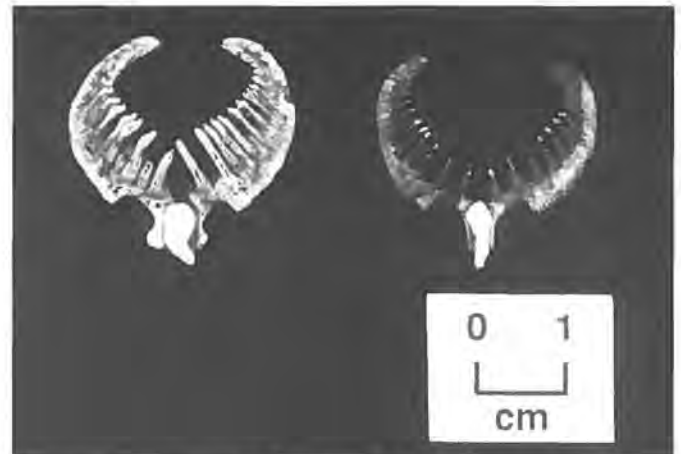


Figure 8. Pharyngeal arches of *Cycleptus elongatus* (left, SIUC 26826, ca. 500 mm SL) and *C. meridionalis* (right, UAIC 11927.01, ca. 410 mm SL).

Big Bend National Park region of Texas clearly shows *C. elongatus* to be the most abundant fish species in that reach of the river, with larvae collected every few river miles and adults numerous at all stations. It is said to be extirpated in the Rio Grande in New Mexico (Sublette et al., 1990), although individuals have been captured there since the “Fishes of New Mexico” was published (S. P. Platania, pers. comm.). It is perhaps gone from the lower Rio Grande (Edwards and Contreras-Balderas, 1991) although a specimen is available from Laredo taken in 1939.

Its status in the Mexican portion of the Rio Grande basin is more difficult to determine, although Contreras-B. and Rivera-T. (1972) reported a subadult from the Rio Grande (or Río Bravo) near Ciudad Acuña. One of us (BMB) has observed large numbers of this species on the Mexican side of the river in the Big Bend National Park region, but elsewhere its status is poorly known. Meek (1908) reported a specimen from the Río Salado; very few



Figure 9. Lateral view of *Cycleptus elongatus* (MSB 10010, 528 mm SL) from Rio Grande, Texas, showing darkened scale pockets that create horizontal “striping” in adults.

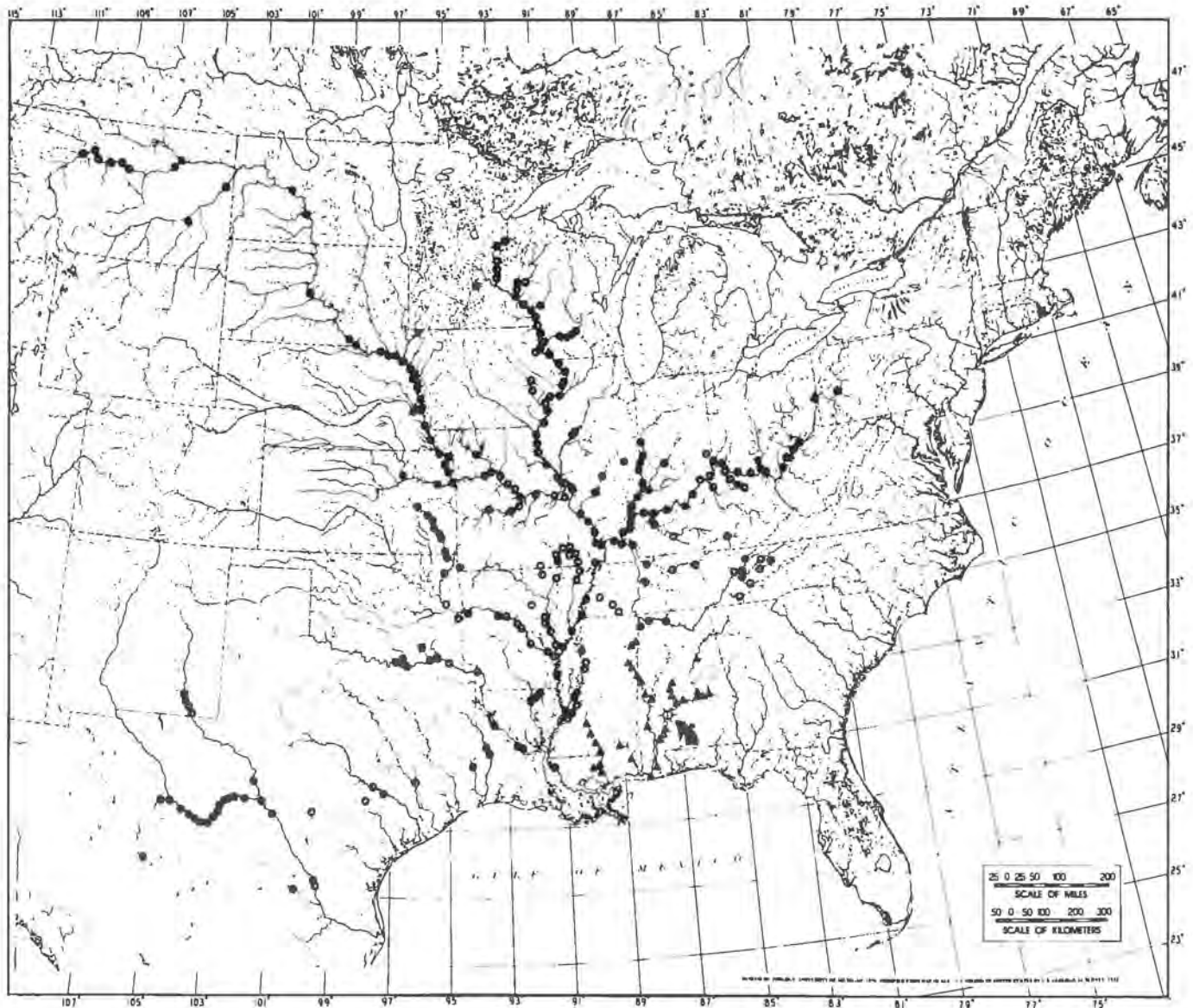


Figure 10. Distribution of *Cycleptus* in the United States and Mexico. Closed circles are record stations (i.e., vouchered specimens) for *C. elongatus*. Closed triangles are record stations for *C. meridionalis*. Open circles are literature records of *C. elongatus* accepted as valid. Open triangles are literature records of *C. meridionalis* accepted as valid. The type locality for *C. meridionalis* is indicated by a star.

collections are available from the Río Conchos. Curiously, Espinosa Pérez et al. (1993) reported that this species enters the Río Panuco on the Atlantic Slope of Mexico; this is the first report from that basin. There are no other records of *C. elongatus* from that basin (Darnell, 1962), and no voucher specimens are available; the report needs substantiation. Other than these exceptions, records in the various state ichthyofaunal treatments as cited in the synonymy, and plotted in Figure 10, help fill in small distributional gaps throughout the range.

Archaeological evidence from Bandelier National Monument and dating to the thirteenth century docu-

ments the occurrence of this species in the Río Grande of New Mexico (Gehlbach and Miller, 1961). Remains from prior to 1800 also have been recovered at the Cochiti Dam site far upriver in the Río Grande (Sublette et al., 1990).

HABITAT.—*Cycleptus elongatus* inhabits strong currents in the main channels of medium to large-size rivers over sand, cobble, gravel, or bedrock bottoms. Juveniles may occupy shallower (<1 m) riffles than adults (1.0–2.5 m). According to Cross and Collins (1975), in summer the young are found along gravel bars in slightly shallower and less swift currents than adults. The species is often

now associated with human-made structures that help constrict the channel including the ends of wing dykes, the bases of dams, deep zones of reservoirs, and bridge abutments. In the highly modified Missouri River along the Iowa-Nebraska border, *C. elongatus* was common in dike fields and near revetted banks (Sandheinrich and Atchison, 1986). It also was found to be associated with revetted banks in the lower Mississippi River, Mississippi (Pennington et al., 1983). Riggs and Bonn (1959) recorded adults as deep as 15 feet (4.57 m) in Lake Texoma, Oklahoma. The species tolerates some turbidity if the water is swift enough to prevent deposition of silt (Pflieger, 1997).

According to Moss et al. (1983) "the presence of adequate areas of swift, deep water over firm substrates with sufficient spring flows over spawning riffles is probably the most important factor in maintaining populations of blue suckers."

LIFE HISTORY.—To gain a better understanding of the conservation issues that are perceived as vital to the continued existence of *C. elongatus* and how they relate to potential for management of a species deemed in need of protection, we have summarized below what is known of the details of the biology of this species. Information is taken largely from Beal (1967), Elrod and Hassler (1971), Walburg et al. (1971), Christenson (1974), Rupprecht and Jahn (1980), and Moss et al. (1983).

Age and Growth. The blue sucker lives at least 12 years (Elrod and Hassler, 1971; Walburg et al., 1971) and three studies of populations in the Mississippi (Rupprecht and Jahn, 1980), Missouri (Beal 1967), and Neosho (Moss et al., 1983) rivers found the fish to live 9–10 years. In the Mississippi River near Keokuk, scale analysis of 140 blue suckers revealed that age II fish averaged 413 mm TL, age III fish 473 mm, age IV fish 510 mm, age V fish 557 mm, age VI fish 605 mm, age VII fish 655 mm, age VIII fish 679 mm, age IX fish 726 mm, and age X fish 817 mm (Rupprecht and Jahn, 1980). Males were slightly longer than females at each annulus, and both sexes lived to about the same age. In the lower Chippewa and Red Cedar rivers, Wisconsin, the lengths of 181 specimens ranged from 457 to 759 mm TL; the modal length interval was 610 to 632 mm (Christenson, 1974). Weights in the same rivers ranged from 2.8 (1.3 kg) to 8.8 pounds (4.0 kg), with an average of 4.8 pounds (2.2 kg). In Lake Sharpe, South Dakota, the mean TL of both sexes was similar for most ages; annual survival rate was 52 % from ages VI to XII (Elrod and Hassler, 1971). Trautman (1957, 1981) gives a maximum size of 40 inches TL (102 cm) and 12–15 pounds (5.4–6.8 kg).

In the Neosho River, Kansas, young were 100 mm TL by midsummer and over 200 mm in the autumn of the first year (Moss et al., 1983). One-year-old suckers averaged 266 mm and 2-year-olds, 323 mm. In the Neosho river,

females were consistently larger than males at all ages. Average sizes of 70 adults for each year of life were: age III females 554 mm TL, males 525 mm; age IV females 563 mm, males 566 mm; age V females 633 mm, males 601 mm; age VI females 655 mm, males 622 mm; age VII females 681 mm, males 653 mm; age VIII females 655 mm, males 647; and age IX females 763 mm, males 666 mm. Some older fish (e.g., age VIII) had mean TL less than younger fish probably because of small sample sizes. Females attain a greater maximum age, weight, and length (9 years, 4.1 kg, 763 mm TL) than males (7 years, 3.7 kg, 749 mm TL) in Kansas (Moss et al., 1983).

Individuals from the lower Wisconsin River, 545, 555, and 737 mm TL were 5, 5, and 7 years old; twelve from the Red Cedar River, were 4–11 years old and ranged in TL from 582–750 mm (Becker, 1983).

In Lake Texoma, Oklahoma, two-year-old fish were between 365 and 387 mm SL (Moore and Cross, 1950).

Because scale-aging is known to underestimate the ages of large fish we presume that *C. elongatus* reaches much older ages, probably 30+ years as indicated by examination of annuli on the opercular bone of specimens of *C. meridionalis* from Alabama and Mississippi (M. Peterson and R. E. Jenkins, pers. comm.).

Reproductive Biology. Adults in breeding condition from the Current River, Missouri, have appeared as early as February and March (Pflieger, 1975). Most spawning, however, usually occurs from late April through May at water temperatures ranging from 10 to 20 C (Cross, 1967; Walburg et al., 1971; Rupprecht and Jahn, 1980; Moss et al., 1983); peak spawning temperature in the Missouri River was 15 C (Beal, 1967). In the Rio Grande, Texas, the appearance of young in April and May suggests egg deposition in March or April (Hubbs and Wauer, 1973). There is a massive upstream migration of adults to large riffles with strong current. In the Neosho River, one spawning riffle was 2 km in length with substantial deep riffle habitat downstream that was uninterrupted by dams. When spawning adults were captured the flow velocity was 1.8 m/sec in water 1.4 m deep. The spawning act has not been observed. Territoriality has not been observed and apparently does not occur (Page and Johnston, 1990). In large rivers such as the Mississippi, this species probably participates in the "flood-pulse" strategy of reproduction. Many young-of-the-year were observed for the first time on both sides of the river in Illinois and Missouri in June (Anonymous, 1993; Burr et al., 1996) after the major floods of 1993 and 1994. As water levels decline subsequent to spawning, eggs and larvae may be carried downstream.

The sex ratio of spawning adults in the Neosho River is about 1:1 (Moss et al., 1983) and both sexes have tubercles. In Lake Sharpe, 65% of fish captured in April and May were sexually mature, and the sex ratio was two males to one female; in the first week of June, 50% were spent and females outnumbered males (Walburg et al., 1971).

In the Missouri and James rivers, South Dakota, the sex ratio was 2 males:1 female (Beal 1967). In Kansas, the smallest mature specimen was age III and 507 mm TL, while in the Mississippi River males were mature at age IV and 503 mm TL and females at age VI and 573 mm (Rupprecht and Jahn, 1980). The relationship of number of eggs produced to TL was $Y = -375,000 + 771.5L$, where Y = number of eggs and L = TL (Rupprecht and Jahn, 1980). In South Dakota, mature females averaged 61,008 eggs \pm 2008. Ovaries of ripe females averaged 9.7% of body weight and the testes of spawning males averaged 5.4% (Beal, 1967).

In Kentucky, weakly to moderately tuberculate males have been taken from the Green and Ohio rivers in June. The large numbers of tuberculate males from the Ohio River near the Falls during spring indicates that some spawning probably still occurs there or in nearby tributaries. Eggs are deposited in May or June in Illinois (Forbes and Richardson, 1908). Elsewhere in the midwestern states, tuberculation in males reaches its peak in April and May, with most individuals examined from June and July having no or weak tubercle development. Preserved females with ripe ova are rare in research collections.

Eggs and Development. Two size classes of eggs occur in gravid females, opaque white eggs averaging 1.0 mm in diameter and transparent eggs averaging 0.4 mm in diameter (Rupprecht and Jahn, 1980). The yellow adhesive eggs of mature South Dakota females had a mean diameter of 1.7 mm (Beal, 1967). Eggs released from ripe females in Kansas were opaque, slightly yellow, adhesive, and averaged 2.2 mm in diameter (Moss et al., 1983). Illustrations of blue sucker larvae from 9.7 to 27.2 mm TL are shown in Hogue et al. (1981). Yolk is absorbed by 13 mm, the mesolarval stage is attained at about 12 mm, and the metalarval stage at about 15 mm. Lip papillae occur on specimens as small as 17 mm and by 20 mm lips are covered with papillae. By 15 mm, specimens are nearly black from stellate melanophores. A summary of development with detailed descriptions and illustrations is provided by Kay et al. (1994).

Diet. According to Eastman (1977) the pharyngeal apparatus of *C. elongatus* is adapted to permit moderate mastication, and he noted that the diet consisted principally of aquatic insect larvae, small thin-shelled mollusks, and individuals of Entomostraca. Aspects of brain and lip morphology indicate a highly developed sense of taste (Miller and Evans, 1965). When observed over smooth substrates, this species "glides" over the bottom and makes feeding movements (Moss et al., 1983). Food of 46 specimens from the Mississippi River was dominated by caddisflies, dipteran larvae and pupae, mayfly larvae, and amphipods (Rupprecht and Jahn, 1980). Debris and detritus made up 51% of the volume in the 46 digestive tracts examined. In Lewis and Clarke tailwaters, the diet of 93

adults taken from throughout the year consisted primarily of zooplankton, algae, bryozoans, and aquatic insects (Walburg et al., 1971). In the fall, however, when water temperatures ranged 9–17 C, the important food item was algae, coinciding with the high biomass of aufwuchs algae at that time. In New Mexico, midge and caddisfly larvae are eaten as well as some algae and other plant material (Cowley and Sublette, 1987a). Similar foods were eaten in Kansas, although hellgrammites, fingernail clams, and filamentous algae were important diet items. Young-of-the-year fed on smaller insect larvae (dipterans and caddisflies) than adults (Moss et al., 1983); several adults contained large numbers of ingested nematodes in their digestive tracts.

Predation and Parasitism. Predators are not known, but probably include various fishes and invertebrates that eat freshly-laid eggs and perhaps birds that prey on newly hatched young. The species grows so rapidly that it soon becomes too large for most predators.

A new helminth, *Anonchohaptor olseni*, was described by Leiby et al. (1973) from the gills of *C. elongatus* taken in the Missouri River, North Dakota; these authors also reported *Myzotrema cyclepti* present in the gills. Robinson and Jahn (1980) found 2 of 4 specimens infected with 18 individuals of the trematode *Myzotrema cyclepti* in pool 20 of the upper Mississippi River.

CONSERVATION STATUS.—Similar to large redhorse suckers (e.g., *Moxostoma carinatum*, *M. valenciennesi*), *C. elongatus* is infrequently captured using conventional seining techniques. Use of electrofishing gear and sometimes gill netting enhances capturing this species and other catostomids, provided that suitable habitat and conditions are available. The perception that *C. elongatus* is declining in abundance and has been decimated throughout much of its range is perhaps biased by sampling techniques, seasonality, and a misunderstanding of its critical habitat. For example, Moss et al. (1983) point out that in the Neosho River, Kansas, an historically well-sampled stream (Cross, 1967), their records of *C. elongatus* from Labette County were new locality records. Electrofishing in high velocity waters difficult to sample by conventional methods produced the previously unrecorded specimens. Using gill nets, Walburg et al. (1971) reported *C. elongatus* to be the most common species in Lewis and Clarke tailwaters with 1,097 adults captured during seasonal sampling from February 1968 to April 1969. In the twenty or so years since the first edition of the "Fishes of Missouri" (Pflieger, 1975), there are many new records for this species from the Missouri lowlands, the lower Mississippi River, and the mainstem Missouri River (Pflieger, 1997; Fig. 10)

As early as 1930, Robert E. Coker, then Director of the Fairport Biological Station, noted a marked decline in abundance of the species in the upper Mississippi River, in

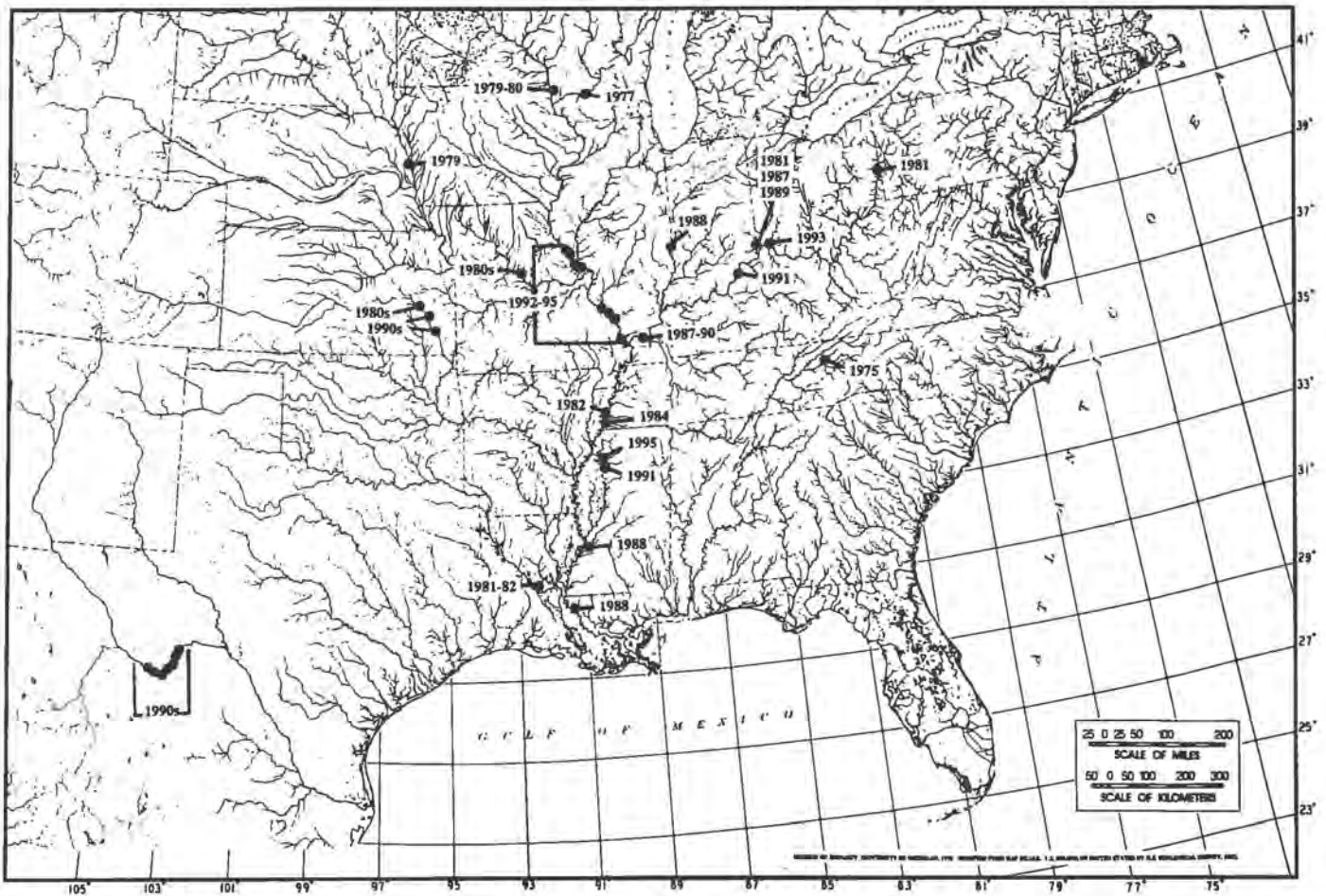


Figure 11. Distribution of sites where production of larvae or recruitment of juveniles of *Cycleptus elongatus* is known to have occurred during the decades of the 1970s, 1980s, and 1990s. As of spring 1998, there are no known sites of larval production for *C. meridionalis*.

part because of the construction of dams which blocked this highly migratory fish. However, he (Coker, 1930) also pointed out that commercial catches of suckers in general already had declined considerably by the late 1800s and early 1900s prior to the construction of the dam in 1913. Pearson and Froedge (1989) found 556 adults stranded below the McAlpine Dam on the Ohio River in 1984–1985, and this is clearly a significant source of mortality for pre-spawning adults. Walburg et al. (1971) reported significant numbers of *C. elongatus* in tailwaters below dams but virtually none in the reservoir above. This suggests that upstream migration of this species has been interrupted by dam construction contributing to the decline of this species. *Cycleptus* apparently participates in the “flood pulse” reproductive strategy and during periods of excessive high water (e.g., 1993 Mississippi River flood) could bypass dams and other obstructions. Dams may be a limiting factor to successful reproduction in years of low water levels, but are perhaps superfluous during excessive spring flooding in other years. Nevertheless, apparent and perhaps real declines prompted the

placement of this species as threatened in Indiana, Montana, North and South Dakota, West Virginia, and Wisconsin in one of the earliest comprehensive lists of threatened freshwater fishes in the United States (Miller, 1972:243). The species is now considered jeopardized throughout much or all of its range (Johnson, 1987; Williams et al., 1989) and is a recent candidate for listing as a federally endangered species by the U. S. Fish and Wildlife Service (Elstad and Werdon, 1993).

As with many organisms, *C. elongatus* is uncommon or disappearing at the edges of its range. Consequently, it is among the rarest of Minnesota’s suckers (Phillips and Underhill, 1971) and has been extirpated from Pennsylvania (Cooper, 1983), the known northeastern limit of its range. In the midwestern agricultural states, declines in abundance have been attributed to the construction of dams on navigable rivers, the deterioration of water quality, excessive catches of adults in spawning runs, and the gradually decreasing depths of river channels through sand and silt choking (Smith, 1979). In Alabama, the status of the species in the Tennessee River drainage is

somewhat enigmatic. It was known in the Tennessee River from a 1939 collection, but C. Saylor (pers. comm.) found an adult in 1993 downstream of the Wilson Dam, and there is a very recent record (1997) from the Bear Creek system, Alabama (GSA 3122). In Kansas, Cross (1967) suggested that decimation of populations in the Kansas River was likely a result of physical changes in the lower mainstem. The main channel was apparently deeper and narrower, whereas now it is a uniform, sand-choked channel. Recent, post-1993 flood data on the upper Mississippi River indicates that spawning occurred at several locations in the mainstem from near Thebes in southern Illinois to at least the Cincinnati Landing, Pike County, Illinois (Burr et al. 1996).

In the Southwest, the depletion of surface water combined with cold winter temperatures and poor water quality stemming from sewage effluent and toxic agricultural runoff have been the major causes of the decline of this species in New Mexico (Sublette et al., 1990). According to Sublette et al. (1990), enforcement of water quality standards and maintenance of perennial flows of approximately 0.7 m³/second or greater in the Pecos River between Sumner Dam and Red Bluff Reservoir would greatly enhance the prospects of survival in New Mexico. Numerous individuals are stranded in the Avalon irrigation canal, Eddy County, New Mexico, each year at the conclusion of the irrigation season when the canals are dewatered.

In the 1970s, 1980s and 1990s, records of larvae and juveniles in samples from various localities (Fig. 11) demonstrate that *C. elongatus* is showing evidence of spawning and recruitment in the lower Wisconsin River and upper Mississippi River, Wisconsin; the upper and middle Mississippi River mainstem between Pike County, Illinois, and Tipton County, Tennessee; the lower Mississippi and lower Red rivers, Louisiana; in the Big Black and Yazoo rivers, Mississippi; in the Wabash River, Clarke County, Indiana; at several sites on the Ohio River; the upper Tennessee River (Nolichucky River), Tennessee; in the middle Missouri River between Nebraska and central Missouri; and in the Neosho River, Kansas. As judged from preserved material in museums, the species has spawned and recruited continuously in the middle Rio Grande since at least the 1940s. Collections made by one of us (BMB), Steve Platania of the University of New Mexico, and others, demonstrate spawning and recruitment of *C. elongatus* at every seining and electrofishing station (i.e., every few river miles) along the Big Bend National Park region and just beyond its borders in 1991. In fact, *C. elongatus* was the most abundant species and made up the greatest biomass of the other large species (e.g., *Ictalurus*, *Ictiobus*, *Lepisosteus*) that occur in that reach of the river. In summary, recent records unequivocally demonstrate that reproduction, and in some cases recruitment, have occurred throughout large reaches of the range of *C. elongatus*. While it is difficult to show in any quantitative

manner that the species is more abundant now than previously thought, it is clearly not jeopardized throughout all or a significant portion of its range. If water quality standards are maintained and construction of dams and other habitat modification kept to a minimum, the species should be able to reproduce and maintain itself into the reasonable future.

Cycleptus meridionalis, new species

Southeastern Blue Sucker

Figure 3, bottom

Cycleptus elongatus: Scott 1951:38 (Coosa River, Alabama). Cook 1959:77–78 (Pearl River, Mississippi). Moore 1968:91 (Pearl River). Smith-Vaniz 1968:61, figure 102 (Coosa, Cahaba, and Tombigbee rivers, Alabama; 245 mm SL specimen figured from Tombigbee River). Swingle 1971:19 (distressed specimen from Dauphin Island Bay, salinity 5.7 ppt). Miller and Robison 1973:121 (Pearl River). Douglas 1974:190–191 (records from Pearl River drainage [Bogue Chitto River], Louisiana). Guillory et al. 1978:706 (conservation status in southeastern states, in part). Mettee 1978:88–89 (Coosa River, Alabama). Eddy and Underhill 1978:111 (range includes Mobile basin). Gilbert 1980:396 (records from Mobile basin and Pearl River drainage; photograph of specimen from Tombigbee River, Alabama). Boschung et al. 1983:460, plate 100 (range, in part; color figure of male from Tallapoosa River, Alabama). Pierson and Schultz 1984:2–3 (Bull Mountain Creek, Mississippi). Ramsey et al. 1984:7, figure 11 (Mobile basin drainages, Alabama; color photograph of adult male). Semmens 1985:119–120 (induced spawning; Alabama River fish). Swift et al. 1986:260–261 (Coosa, Cahaba, Tombigbee, and Pearl rivers). Yeager and Semmens 1987:312–315 (larval description from Alabama River). Boschung 1989:63 (11 Sites on upper Tombigbee River, Mississippi-Alabama). Mettee et al. 1989:82 (7 sites on Tombigbee River, Alabama and Mississippi). Pierson et al. 1989:110 (5 sites in Cahaba River, Alabama; males running milt in early April in lower Tallapoosa River). Williams et al. 1989:6 (in part, special concern status). Tomelleri and Eberle 1990:97 (Mobile Bay, Alabama). Ross and Brenneman 1991:211–212 (Pearl, Pascagoula and Tombigbee river drainages, Mississippi). Page and Burr 1991:167, plate 23 (range includes Gulf Slope drainages; color figure of male from Tallapoosa River, Alabama). Boschung 1992:60 (Tombigbee, Cahaba, Tallapoosa, and Tensaw rivers, Alabama; specimens from Mobile basin may represent undescribed species). Smith 1992:800 (Gulf Coastal drainages). Etnier and Starnes 1993:268–270, plate 111a (color photograph of adult from Tallapoosa River, Alabama). Kay et al. 1994:114–121 (principal

account on these pages, many comparisons throughout volume, in part; in key; description of eggs and larvae; illustrations). Stauffer et al. 1995:182 (Gulf Slope tributaries, Alabama and westward). Mettee et al. 1996:321, 334–335 (in key; description, in part; Alabama distribution, in part; biology, in part; color plate and map). Gilbert 1998:181 (possible undescribed species in Mobile basin).

HOLOTYPE.—UAIC 11431.03, male, 500 mm SL. Alabama, Wilcox Co., Alabama River below turbines at power plant at Millers Ferry Lock and Dam, 2 mi WSW of Millers Ferry. T13N, R7E, Sec. 20 NW 1/4. 9 April 1996. Water turbid, depth: 20–35 ft. Captured with gill nets. Collectors: R. L. Mayden, B. R. Kuhajda, P. L. Kilpatrick, M. F. Mettee, T. E. Shepard. Field numbers: RLM 96-29, BRK 96-24.

PARATYPES.—**ALABAMA:** UAIC 11431.01, male, 495 mm SL. Same data as holotype. UAIC 11430.01, female, 420 mm SL. Same data as holotype, 2 April 1996. SIUC 30615 (formerly UAIC 11431.01), male, 460 mm SL. Same data as holotype. UF 107750 (formerly UAIC 11431.01), male, 440 mm SL. Same data as holotype. INHS 44769 (formerly UAIC 11431.01), male, 480 mm SL. Same data as holotype. NLU 74976 (formerly UAIC 11431.01), male, 470 mm SL. Same data as holotype. UT 45.1505 (formerly UAIC 11431.01), male, 440 mm SL. Same data as holotype. KU 26885 (formerly UAIC 11431.01), male, 435 mm SL. Same data as holotype. TU 184867 (formerly UAIC 11431.01), male, 415 mm SL. Same data as holotype. AUM 27700 (2, 490–495 mm SL), Alabama River, below Jones Bluff Dam, Lowndes Co., 1 March 1981, K. Semmens. UMMZ 234192 (1, 409 mm SL), Alabama River, in tailwaters below Millers Ferry Lock & Dam, T13N, R7E, Sec. 17, Wilcox Co., 27 March 1993. USNM 348714 (1, 410 mm SL), Alabama River, in tailwaters below Millers Ferry Lock & Dam, T13N, R7E, Sec. 17, Wilcox Co., 27 March 1993. UAIC 11973.01 (formerly AUM 27697) (1, 485 mm SL), Tallapoosa River, ca. 1 mi. below Tallassee, Elmore Co., 5 May 1980.

NONTYPE MATERIALS USED FOR COUNTS AND MEASUREMENTS.—

Numbers in parentheses are numbers of specimens examined followed by range in length mm SL. **Mobile Basin.** *Tombigbee River Drainage.* **ALABAMA:** AUM 9224 (3, 300–470 mm SL), Tombigbee River, near Epes, Sumter Co., 31 July 1953. AUM 21119 (1, 445 mm SL), Tombigbee River, ca. 3 airmi. NE of Warsaw, Sumter Co., 24 July 1980. CU 50708 (1, 250 mm SL), CU 53303 (3, 468–475 mm SL), UAIC 1789.01 (1, 530 mm SL), all from Tombigbee River, 1 mi. below mouth of Sipsey River, Green/Sumter Co. line, 5 August 1965. AUM 20844 (1, 525 mm SL), Aliceville Lake, 1 mi. NNW of Pickensville, Pickens Co., 18 May 1981. GSA 4025.03 (1, 465 mm SL), Lower Tombigbee River below Coffeetown Lock and Dam, T9N, R1W, Sec. 7, Clarke-Choctaw Co., 11 September 1991.

MISSISSIPPI: AUM 20557 (3, 305–330 mm SL), Tombigbee River, ca. 2.2 mi. WNW of Smithville, Monroe Co., 4 September 1980. MSU 1859 (1, 480 mm SL), Tombigbee River, W of Smithville, Monroe Co., March 1970. AUM 21484 (1, 500 mm SL), Aliceville Lake, ca. 9 airmi. SSE of Columbus, Lowndes Co., 29 June 1981. UAIC 7185.01 (1, 195 mm SL), Tombigbee River, ca. 0.8 mi. upstream from old U.S. Hwy. 82 bridge, in Columbus, Lowndes Co., 21 December 1979. UAIC 4339 (1, 460 mm SL), Tombigbee River, below Hairston Bend for about 1.5 mi. of river, T17N, R18W, Sec. 10, Lowndes Co., no date. *Alabama River Drainage. Tallapoosa River System.* **ALABAMA:** UAIC 10451 (1, 548 mm SL), Tallapoosa River, ca. 5 mi. S of Wetumpka and 3.0 mi. NNW of Bingham (above Hwy. 231), T17N, R19E, Sec. 20, Elmore Co., 20 May 1992. UAIC 10029.01 (2, 490–520 mm SL), Tallapoosa River, 3.4 mi. S of Ware, below Line Creek confluence, T17 N, R20E, Sec. 34, Elmore Co., 13 October 1990. *Coosa River System.* AUM 24062 (1, 495 mm SL), Coosa River, 1 mi. below Jordan Dam, Elmore Co., 18 October 1983. UAIC 6800 (1, 540 mm SL), Coosa River, ca. 2.8 mi. below Jordan Dam, Elmore Co., 6 May 1983. *Cahaba River System.* AUM 5115 (2, 353–363 mm SL), Cahaba River, ca. 2 mi. W of Suttle, Perry Co., 18 July 1968. TU 40351 (2, 465–475 mm SL), Cahaba River, 2 mi. S of Centreville, Bibb Co., 20–21 April 1966. AUM 8084 (1, 530 mm SL), Cahaba River, at Harrisburg Bridge, below Centreville (2.1 airmi. SE Harrisburg), Bibb Co., 12 July 1954. UAIC 2167.03 (1, 490 mm SL), Cahaba River, from bridge 1 mi. W of Sprott to large bar behind Marion Fish Hatchery, T20N, R8E, Sec. 13, Perry Co., 12 July 1966. UAIC 3634 (1, 380 mm SL), at jct. of Cahaba and Alabama rivers, T16N, R10E, Sec. 32, Dallas Co., 21 March 1969. *Alabama River System.* AUM uncat. (1, 375 mm SL), Alabama River, Claiborne Lock & Dam, Lock No. 71.8, Monroe Co., 14 August 1991. AUM 9217 (1, 383 mm SL), Alabama River, 1951. UAIC 10765.01 (3, 383–425 mm SL), Alabama River, in tailwaters below Millers Ferry Lock & Dam, T13N, R7E, Sec. 17, Wilcox Co., 27 March 1993. *Pearl River Drainage.* **MISSISSIPPI:** TU 26354 (1, 100 mm SL), Pearl River, at mouth of Brushy Creek, ca. 1 mi. SE of Hopewell, Copiah Co., 12 July 1962. TU 23109 (1, 430 mm SL), Pearl River, 3.5 mi. E of Sandy Hook, Marion Co., 20–21 April 1960. TU 27189 (1, 182 mm SL), Pearl River, about 1.5 mi. SE Monticello, Lawrence Co., 28 August 1962. SIUC 27064 (1, 528 mm SL), Pearl River, 12 mi. upstream from Columbia, Marion Co., 11 April 1996. GCRL 28376 (1, 479 mm SL), Pearl River, 16 mi. downstream from Columbia, Marion Co., 11 April 1996. GCRL 28375 (1, 510 mm SL), Pearl River, 14 mi. downstream from Columbia, Marion Co., 11 April 1996. **LOUISIANA:** TU 27850 (20, 385–485 mm SL), Pearl River, at Pools Bluff Sill, 4 mi. S of Bogalusa, Washington Par., 12 February 1965. TU 41030 (1, 64 mm SL), Pearl River, just below Pools Bluff Sill, 4 mi. S of Bogalusa, Washington Par., 3 July 1966. NLU 6044 (6, 335–470 mm SL), 15198 (4, 420–470 mm SL), 7437 (3,

345–400 mm SL), all from Bogue Chitto River, at Isabel Landing, Washington Par., 7 & 9 March 1967, 7 August 1967. NLU 6533 (4, 410–470 mm SL), 6532 (2, 355–400 mm SL), both from Bogue Chitto River, 0.5 mi. above Isabel Landing, Washington Par., 8 June 1967. NLU 6859 (8, 350–450 mm SL), Bogue Chitto River, 4 mi. N of Talisheek, T5S, R13E, Sec. 45, St. Tammany Par., 27 June 1967. NLU 60837 (1, 475 mm SL), Bogue Chitto River, 0.5 mi. N of Pearl River Canal, T5S, R13E, Sec. 53, St. Tammany Par., 19 August 1987. TU 62183 (1, 153 mm SL), West Pearl River, ca. 2 mi. below jct. of West Pearl and Wilson Slough, St. Tammany Par., 26 November 1969.

Pascagoula River Drainage. MISSISSIPPI: USM 10699 (1, 390 mm SL), Black Creek, ca. 2 mi. below Hwy. 57, George Co., 25 September 1990. USM 8255 (1, 438 mm SL), Leaf River, ca. 6.5 km upstream of Hwy. 29 bridge, Perry Co., 27 October 1989.

SKELETONS EXAMINED.—UAIC 11927.01 (2), Alabama River near RM 68, N of U.S. Hwy. 84 on W side, ca. 1.5 mi. N of Claiborne, T7N, R5E/6E, Secs. 19 and 24), 18 April 1997.

VOUCHERED SPECIMENS USED FOR RANGE MAP, NOT FOR COUNTS OR MEASUREMENTS (DUPLICATIONS EXCLUDED).—**Mobile Basin. Alabama River Drainage. Coosa River System ALABAMA:** UGAMNH 139 (1), Coosa River, Willingham's fish trap [about 17 river mi. N Childersburg], Talladega Co., 3 August 1949.

DIAGNOSIS.—A species of *Cycleptus* as diagnosed above and distinguished from its congener by having fewer scales, usually 16 caudal-peduncle scale rows (Table 1), usually 37–40 body-circumferential scale rows (Table 2), usually 49–53 lateral-line scales (Table 3), and usually 86–92 lateral-line scales plus body-circumferential scale rows (Table 4); fewer dorsal fin rays, usually 25–29 (Table 5); a shorter snout and a shorter dorsal fin base (Table 6, Figs. 5–6).

DESCRIPTION.—**Morphometry.** Body usually elongate, oval in cross section, body depth 21 to 30% SL; body width 13 to 17% SL; head width 11 to 15% SL. Caudal peduncle elongate, its length averaging 25% SL. Head moderately long, averaging 19% SL in adults over 197 mm SL; snout lateral profile declivous to slightly bulbous, projecting anterior to upper lip; snout length averaging 48% of head length (Table 8). Orbit small, its diameter averaging 14 to 17% of head length in specimens 197–525 mm SL. The largest specimen measured to date is 710 mm TL (Mettee et al., 1995) or about 573 mm SL. The largest specimen examined from the Mobile basin is 550 mm SL (from the Pearl River, 530 mm SL).

Lips. Mouth relatively small. Posterior margin of lips ranging from a rounded or slightly emarginate edge to deeply indented and nearly dividing the lower lip into halves.

Surfaces papillose, with short, blunt, and rounded papillae only (Fig. 7G–H).

Fins. Dorsal fin margin falcate, 1st and 2nd principal rays long, rapidly shortening to about 7th or 8th ray, remaining rays all short. Pectoral and pelvic fins elongate and falcate, anterior rays thickened. Anal fin in adults small, generally straight edged on posterior margin, sometimes falcate. Caudal fin in adults large, widely forked, lobe tips slightly rounded to pointed, inner margins straight; both lobes about equal in length. Upper lobe somewhat more pointed and longer in juveniles.

Meristic Features. Values for holotype are in bold type. Lateral line complete, nearly straight, scales 48–53, usually 49–53 (Table 3); body-circumferential scale rows 36–41, usually 37–40 (Table 2); predorsal scale rows 17–22, usually 18–21, scales number 17 (3), 18 (17), **19** (21), 20 (27), 21 (16), 22 (7); caudal-peduncle scale rows 15–18, modally 16 (Table 1); dorsal rays 23–31, usually 25–29 (Table 5); anal rays **7** (81); pectoral rays 14–17, usually 15–16, rays number 14 (6), **15** (38), 16 (31), 17 (2); pelvic rays number 9 (5), **10** (67), or 11 (11); principal caudal rays 17 (3), **18** (74), 19 (2); gill rakers on first arch 23 (3), 25 (3), 26 (3), 27 (1), 28 (1), 29 (2) in adults; pharyngeal teeth per arch 32–36. Numbers of vertebrae not investigated.

Internal Anatomy. Swim bladder two-chambered, anterior chamber short and rounded, posterior chamber rounded anteriorly and tapering to a point posteriorly. Pharyngeal teeth in two skeletonized individuals (UAIC 11927.01 [Alabama River, Alabama], are 32 (right), 32 (left) and 36 (right), 36 (left), respectively (Fig. 8). From the limited data presented here there may be a consistent difference in pharyngeal tooth number between *C. elongatus* and *C. meridionalis*. Accurate counts are best made from skeletonized material, of which only two specimens are presently available.

Coloration. In life, males: All observations, color transparencies, and field notes of *C. meridionalis* indicate that males do not differ appreciably in coloration from males of *C. elongatus* during any season. Color of pre-spawning male is shown in Figure 3 (bottom). Adult male color changes from olive, blue-green, gray-green, sometimes brassy-green reflective hues to deep blue, almost black hues during the spring spawning runs. In life, females: color of adult females is similar to males, somewhat more subdued.

Tuberculation. Male tuberculation similar to that of *C. elongatus* and shown in Figure 3 (bottom). Prominent white tubercles ranging from 0.2–1.0 mm in diameter occur on opercle, subopercle, cheek, snout, top of head, and nearly every scale; branchiostegals and belly mostly

naked, a few scattered tubercles. Breast with enlarged padded scales, a few small tubercles. From 1 to 4 tubercles on each scale on anterior one-third of body; 3–7 tubercles on each scale on posterior two-thirds of body. Peripheral edges of scales with row of small erect tubercles. More minute tubercles on every branch of every ray of all fins, those on leading rays somewhat larger than those on remaining rays, crowded scales at bases of dorsal and anal fins with 1 tubercle per scale. There is much variability in the number of tubercles per scale and fin ray. We initially considered that there was a taxonomic difference in tubercle pattern between the two species, but individual variability appears to exceed population variability. Tubercle patterns in females have not been studied but are probably similar to those described for *C. elongatus*.

Sexual Dimorphism. As with many North American fishes, females heavy with eggs have deeper and wider bodies during the spring spawning season when compared to males. These measurements were deleted from the PCA. Two other proportions, eye diameter and a modified measurement of head length, were significantly ($\mu = 0.005$) different between males and females and were eliminated from the final PCA. We are not aware of any color differences between mature adults, although females may appear "lighter" than the darkened males.

ETYMOLOGY.—The specific epithet, *meridionalis*, Latin for "southern" (Brown, 1956), refers to the geographic range restriction of the species. The common name, Southeastern Blue Sucker, refers to the species geographic range restriction to freshwater rivers of the central Gulf Slope.

DISTRIBUTION.—The range of *C. meridionalis* is restricted when compared to its congener, and as presently known is limited to the Mobile basin, Alabama and Mississippi, and the Pascagoula and Pearl River drainages of Mississippi and Louisiana (Fig. 10). Although *C. elongatus* has been known since the early 1800s, *C. meridionalis* was not reported (as *C. elongatus*) until 1949 (Scott, 1949; 1951) from the upper Coosa River, and ironically, where it has not been reported since. Nearly all records are from mainstem reaches. In the Mobile basin, vouchered records are available from the Coosa, Tallapoosa, Cahaba, upper Tombigbee, and Alabama rivers. We have not seen vouchered records for the Black Warrior River, a possible artifact, although neither Boschung (1992) nor Mettee et al. (1996) reported records from the Black Warrior River. The most unusual record is that of Swingle (1971) who reported a 575-mm adult taken by cast net from the boat slip at the Alabama Marine Resources Laboratory on Dauphin Island on 24 February 1969. Surface and bottom salinity were 5.7 ppt and water temperature was just over 12 C. According to Swingle the fish was distressed when caught and probably moved down the Bay with a freshet

and became stranded in the boat slip. Boschung (1992) indicated that *C. meridionalis* also is known to inhabit the Tensaw River, Alabama, based on a vouchered record at the Alabama Marine Resources Laboratory; we have not seen this specimen, but accept the record as valid.

Two other species, *Noturus munitus* and *Percina lenticula*, show a pattern of drainage distribution (Rohde, 1980; Douglas, 1980) nearly identical to that of *C. meridionalis*. These patterns and others in this region have been discussed in detail by Swift et al. (1986).

HABITAT.—Stream sizes, substrate conditions, and water velocities observed or recorded for *C. meridionalis* in the Pearl and Pascagoula rivers and the Mobile basin indicate clearly that this species occupies habitats nearly identical to those of *C. elongatus*. Adults occupy deep channels and pools in the mainstem of large to medium-sized rivers. They reportedly move into fast current over gravel and cobble runs in early spring (Pierson et al., 1989). In Mississippi, the species is frequently collected in swift, shallow water in areas of woody debris or cut-banks. Of 108 tagged individuals from the Pearl and Pascagoula rivers, Mississippi, only two were recaptured; distance moved was between 1.6 and 3.2 km upstream (Peterson and Nicholson, 1997).

LIFE HISTORY.—Because there has been concern for the conservation of *C. meridionalis*, we summarize here the information on biology that we have gleaned from museum specimens, unpublished reports (Mettee et al., 1995; Peterson and Nicholson, 1997), and peer-reviewed publications (i.e., Semmens, 1985; Yeager and Semmens, 1987; Peterson et al., 1999).

Age and Growth. R. E. Jenkins (pers. comm.) used annuli on an opercle to age a single adult, 460 mm, from the Cahaba River, collected in 1968. These data indicate the specimen is age 22 and serve to point out that both *C. meridionalis* and *C. elongatus* probably live considerably longer than previous scale-aging suggests (see below). In samples from the Alabama River, males were smaller than females and weighed less (Mettee et al., 1995). The 52 males ranged from 481 to 593 mm TL and weighed from 0.9 to 2.2 kg; the 62 females ranged from 504 to 710 mm TL and weighed from 1.2 to 5.3 kg. Similar results are available for populations in the Pearl and Pascagoula rivers, Mississippi, where females are heavier than males per given length (Peterson and Nicholson, 1997; Peterson et al. 1999), although growth patterns are not significantly different between the sexes. Using marginal increment analysis of opercle bones in Mississippi-captured *C. meridionalis*, the smallest female was 452 mm TL (age 6) and the largest was 702 mm TL (age 31); the smallest male was 327 mm TL (age 4) and the largest was 593 mm TL (age 33). Young grow about 1 mm day in fish below 37.5 mm TL (Semmens 1985)

Reproductive Biology. Semmens (1985) captured two gravid females from the Alabama River on 1 March at a water temperature of 12 C; two males were captured on 8 March. From these adults, eggs were stripped, fertilized, and hatched under laboratory conditions. Tuberculation in males across the range of *C. meridionalis* peaks in March and April, with strongly tuberculate males available as early as February and weakly tuberculate males appearing in June and July. In the Alabama River, Mettee et al. (1995) found spawning to occur on or near 4–5 April and continuing through 18–19 April, as evidenced by the collection of 88 adults, many of which were tuberculate and “running either eggs or sperm with little or no pressure.” Females slightly outnumbered males during spawning and most vacated the area shortly after the spawning ended. Their sampling revealed a total of 52 males and 62 females, and another 20 individuals that could not be sexed reliably. In Mississippi, the sex ratio did not differ significantly from 1:1. Mean GSI peaked in females (up to 17%) between October–March, and in males (up to 7%) between November and March. Spawning begins in February to early March in Mississippi when water temperatures approach 13–14 C (Peterson and Nicholson, 1997; Peterson et al., 1999).

Eggs and Development. Fertilized eggs are adhesive and average 2.8 mm in diameter. With agitation and under laboratory conditions, eggs increased from 2.8 to 4.0 mm (Semmens 1985). About 20% of fertilized eggs developed normally, with most eggs hatching 6 days following fertilization with water temperatures reaching as high as 20 C during incubation. Hatchlings averaged 8.7 mm TL and were 13.2 mm four days later (Semmens 1985). Yolk absorption was apparently complete 10-days post induced spawning. Young averaged 23.2 mm and 37.5 mm at 25 and 39 days post-spawning, respectively. Yeager and Semmens (1987) provided a description and illustrations of larvae from 7.1 to 46.5 mm TL, based on artificially spawned eggs taken from brood stock from the Alabama River. Kay et al. (1994) provided a detailed description of meristic features and morphometry, although there is some confusion of specimens and illustrations with *C. elongatus*.

Diet. Examination of “stomachs” (i.e., the first descending section of the intestine) of 206 adults (sexes pooled), and expressed as frequency of occurrence, showed that *C. meridionalis* consumes trichopteran larvae (83.0% of specimens examined) and pupae (21.3%), coleopteran larvae (32.5%), chironomid larvae (76.2%) and pupae (9.2%), and nematodes (17.5%) (Peterson and Nicholson, 1997; Peterson et al., 1999). These prey items are similar to those reported for *C. elongatus*.

Predation and Parasitism. At least one adult (431 mm SL) from the Alabama River had a possible lamprey (almost

certainly *Ichthyomyzon castaneus*) scar on the right side of the head (Mettee et al., 1995). There seems little doubt that the large size of adults precludes most predation and that larval stages and young are the most vulnerable to predation. Rogers (1967) described a new genus and species of trematode (*Myzotrema cyclepti*) from the gills of this species (as *C. elongatus*) from the Tombigbee River, Pickens County, Alabama.

CONSERVATION STATUS.—Between 29 March and 31 May 1995, Mettee et al. (1995) captured 135 adults from the Alabama River below Millers Ferry Lock and Dam. They noted that the reach from near the junction of the Alabama and lower Tombigbee rivers upstream to the tailwaters of Millers Ferry Lock and Dam may harbor the largest population of this species in Alabama. Further, this species has been collected at 18 of 36 known stations in Alabama since 1985. In 1996–1997, a total of 559 *C. meridionalis* was observed or captured in the Pearl and Pascagoula rivers, Mississippi, where the species is considered abundant (Peterson and Nicholson, 1997). Use of two boats with electrofishing gear allowed a “chase” boat to capture or observe *C. meridionalis* in greater numbers than if only one boat had been used. Earlier reports (Guillory et al., 1978; Williams et al., 1989) of the “rarity” of *C. meridionalis* are based largely on insufficient data and would appear now to be misleading. Specific information on young-of-the-year habitat and evidence of recruitment of juveniles into the adult population are lacking. But, even a conservative estimate of the abundance and ubiquity of this fish in the mainstems of large rivers would indicate that most populations are stable and reproducing regularly.

Discussion

Since its description in the early 1800s, *Cycleptus* has received limited systematic attention, and most of it has been directed toward an understanding of its relationships with other catostomids. The accumulated museum material has never been critically reviewed. Indeed, with few exceptions, most descriptions in state fish-books repeat a few details on general morphology of Mississippi basin samples from early accounts of the species by David Starr Jordan and others. *Cycleptus* was not even known from southern coastal drainages until 1949, and it was many years later before a number of specimens became available for study. Analysis of the over 390 museum specimens reveals some patterns in morphological characters that are geographically concordant and permit allocation of samples to taxonomic units, including one new species, *Cycleptus meridionalis*, from Gulf slope rivers of Alabama, Mississippi, and Louisiana.

Other patterns of geographic variation in phenotypic characters of *Cycleptus elongatus*, as shown herein, reflect the rather long isolation from active gene exchange of fishes in coastal drainages, particularly those streams on

the Texas Coastal Plain and including the Rio Grande basin. Divergence occurs here in a few features, but is not concordant geographically, and some of the characters are not consistently expressed to allow for diagnosing other taxonomic units. Preliminary studies of enzyme products by Donald G. Buth, University of California at Los Angeles and one of us (RLM), reveal fixed differences in isozymes and allozymes in samples of *Cycleptus* from the Rio Grande mainstem when compared to samples from other parts of the range. Samples from Texas coastal rivers have not yet been examined. Perhaps with thorough geographic sampling, including material from the Sabine and Colorado rivers, a unique set of allozyme patterns will allow for diagnosis of the Rio Grande form of *Cycleptus* as a new taxon.

We strongly urge continued systematic study of North American catostomids and other large fishes in general. In addition to this report, new catostomid taxa recently have been discovered in Atlantic Slope streams and the Little Tennessee River (Robert E. Jenkins, pers. comm.), and some of these are large species. The *Myxocyprinus* complex of China and the complex of western North American *Catostomus* (sensu stricto) warrant critical systematic review before we can arrive at a reasonable assessment of species-level diversity in the Catostomidae.

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Materials Examined

Appendices

References

Figures

Figure Captions [BULLETIN does not use designation "Plates"]

Tables

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