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Introduction

The fish fauna of Missouri is perhaps more diverse than that of any other inland area of comparable dimensions in North America. But, unlike many states that have a rich history of ichthyological investigations going back nearly to the time when the country was settled, systematic fish collections were not made in Missouri until the second quarter of the present century, and to date no general summary and synthesis of distributional information has been attempted. The objectives of this report are to summarize current knowledge concerning the distribution of Missouri fishes, and to interpret the distribution patterns in terms of the environmental conditions and historical events that have determined their development. Because the natural areas of the state extend beyond the political boundaries, and the character of the fish fauna has been determined in part by events that occurred far from Missouri, an attempt will be made to relate the distribution of fishes in Missouri to distribution in the Mississippi Valley as a whole. The unresolved biogeographic and taxonomic problems relating to the fishes of this region are many, and the conclusions reached will probably be altered by future investigations. If I succeed in casting some light on the subject, and pointing out areas where further research will prove fruitful, this report will have fulfilled its major objectives.

So that the report will be most useful to the general reader, I have departed from common practice by using vernacular names rather than scientific names wherever possible in the sections preceding the species accounts. If questions arise about the scientific name of the species being referred to, the scientific and vernacular names are associated on the pages indicated by bold face type in the index.

This report is written as a companion volume for a handbook to Missouri fishes still in preparation. Publication of a separate report on fish distribution permits more thorough treatment of the subject and inclusion of much material too technical for a popularized handbook. Emphasis in the handbook will be on identification, life history, and importance to man. Keys for identification of Mis-

Table Rock Reservoir; it has not been collected since impoundment. The taillight shiner, cypress minnow and golden topminnow originally occurred in the Southeastern Lowlands, but they have not been collected there since the 1940's. Recent efforts to take the redfin darter, known only from North Fork of Spring River in Jasper County, have been unsuccessful. The pallid shiner was widespread in eastern and southeastern Missouri in the early 1940's but has not been collected since 1954. The harelip sucker (*Lagochila lacera* Jordan and Brayton) formerly occurred in the White River near Eureka Springs, Arkansas, and must have occurred also in that stream system in Missouri. This species probably is extinct, because it has not been collected since about 1900.

Reductions in the abundance and distribution of many Missouri fishes are well documented. The lake sturgeon was an important commercial fish before 1900, but it is now so rare that the taking of one is worthy of note in newspapers. The blacknose shiner is exceedingly rare over most of its former Missouri range. Other species that are less abundant and widely distributed than formerly are: paddlefish, skipjack herring, Alabama shad, pugnose minnow, hornyhead chub, bigeye chub, striped shiner, common shiner, Ozark shiner, central silvery minnow, slim minnow, blue sucker, blue catfish, American eel, bluestripe darter, blackside darter, bluntnose darter, and harlequin darter.

Not all species have been adversely affected by habitat modifications. The bigmouth shiner has extended its Missouri range considerably within the last 25 or 30 years. The construction of large impoundments has favored several species; notable among these are: longnose gar, channel catfish, white bass, largemouth bass, spotted bass, bluegill, white crappie, black crappie, and walleye. A few range extensions that have occurred cannot be attributed definitely to man's activities. The threadfin shad and Mississippi silverside were not collected in Missouri until 1963. If they were formerly as abundant in the lower Mississippi River as they are now, it is unlikely that they would have been overlooked by early collectors. Possibly the same is true for occurrence of the Sabine shiner in the Black River, but it is so restricted in distribution that it may have been overlooked. Recent range extensions of the mosquitofish and the studfish are partly the result of introductions, but cannot be accounted for entirely in this manner. The mosquitofish has long had access to the Neosho River system, and its absence there until recent years indicates changes in environmental conditions favorable to it. Recent establishment of the studfish in streams

along the western and northern periphery of its Missouri range probably results from natural extensions, as well as from introduction.

ACCOUNTS OF SPECIES

Explanation of Accounts and Maps

The material in the accounts follows a uniform arrangement, and includes for each species a discussion of distribution and habitat in Missouri, comments on zoogeography, and references. If the taxonomic treatment adopted here is not in accord with that of other workers, the reasons are given under the heading "taxonomic considerations." The sequence in which the families of fishes are arranged follows that proposed by Greenwood *et al.* (1966). With few exceptions, the common and scientific names used are those in *"A list of common and scientific names of fishes from the United States and Canada"* (Amer. Fish. Soc., Spec. Publ. 2, 3rd ed., 1970).

In order to provide a nearly complete index to the literature on Missouri fishes, I have cited in the references many papers that are not strictly distributional or taxonomic in nature. Only papers that make reference to fishes in Missouri are cited; original descriptions are cited only if they are based on specimens from Missouri. If I did not examine specimens, allocation of names and name combinations was based on: (1) a knowledge of the name-changes that various species have undergone, (2) an evaluation of descriptions accompanying the name or name combinations, and (3) the known distribution of species to which the name could refer. Using these three criteria, most records could be allocated with a high degree of confidence; in the few cases where doubt remained about the allocation, the name or citation is preceded by a question mark. The distributions of all species are shown on maps that conclude this report.

Specimens of all species were examined at least superficially in an attempt to discern variational trends, but changes are proposed only in silvery minnows (*Hybognathus*) and stonerollers (*Campostoma*). In the accounts of some additional species I have described known variation, giving results of my preliminary investigations. Unless otherwise indicated, counts and measurements were made according to the methods outlined by Hubbs and Lagler (1947:8-15).

Petromyzontidae

Ichthyomyzon unicuspis Hubbs and Trautman—silver lamprey

(?) *Ichthyomyzon concolor:* Fowler, 1921:398 (Fox Cr., trib. of Meramec R.). Luce, 1933:87,95 (Mississippi R. and Kaskaskia R. near their confluence, Ill.).

Ichthyomyzon unicuspis: Hubbs and Trautman, 1937:47,60 (Mississippi R., Chester Ill.; Mississippi R., St. Louis). Starrett, Harth and Smith, 1960 (char.; abund.; Mississippi R. local. mapped).

Distribution and habitat.—The silver lamprey is known in Missouri only from the Mississippi River (Map 3). The specimen reported by Fowler (1921:398) from "Fox Creek, a tributary of the Meramec River, at a point about 26 miles from St. Louis" may have comes from the Mississippi River, or at least from a large river. The collection on which this record is based includes an unusual assemblage of big-river and small-creek fishes (paddlefish, shovelnose sturgeon, redbelly dace, and mottled sculpin), strongly suggesting a mixture of collections from two localities. At Fox Creek I have collected most of the small-creek species reported by Fowler but none of the big-river species.

In the Missouri section of the Mississippi River the silver lamprey is far less common than the chestnut lamprey. Starrett *et al.* (1960:table 1) recorded four silver lampreys from the Missouri section of the river, only one of which was taken below the mouth of the Missouri River. Since 1961 I have examined numerous lampreys from the Mississippi River between the mouth of the Missouri River and the mouth of the Ohio River, and all except one were chestnut lampreys. The reports by Bailey (1959:163) of a silver lamprey from the Missouri River in South Dakota, and by Cross and Metcalf (1963:187) of another presumably taken in the Missouri River at Omaha, Nebraska, suggest that this species occurs in the Missouri section of the Missouri River.

Adults of the silver lamprey are found only in large rivers and lakes, except when spawning. Spawning and larval development take place in streams of moderate size (Trautman, 1957:133). Spawning may occur but has not been observed in some direct tributaries of the Mississippi River in Missouri.

Zoogeography.—Although their original ranges probably have been altered by glaciation, the silver lamprey and its nonparasitic derivative (*I. fossor*) are clearly northern in their affinities. Possibly they were confined preglacially to the Hudson Bay or Laurentian systems and gained access to the Mississippi Valley through connectives that developed as the ice sheets moved southward. The occurrence of related kinds (*I. castaneus* and *I. gagei*) that seem to be autochthonous to the Mississippi Valley adds credence to this explanation.

Ichthyomyzon fossor Reighard and Cummins—northern brook lamprey

(?) *Ammocoetes branchialis:* Meek, 1891:116 (Meramec R. near Meramec Spring).

Distribution and habitat.—The northern brook lamprey is widely distributed on the northern slope of the Ozark Uplands from the Niangua River eastward to the Meramec system (Map 4). In this area it is by far the most common brook lamprey.

Both larvae and adults of the northern brook lamprey occur in medium-sized streams, avoiding both the smallest headwater creeks and the larger rivers. As is the case with other brook lampreys, this species requires clear, permanent-flowing streams having clean, gravelly riffles for spawning, and stable beds of silt, sand, and organic debris for larval development.

Zoogeography.—Populations of this species in the Ozark Uplands are broadly disjunct from the main range, which lies within the area covered by the Wisconsin ice sheet. The record nearest to Missouri is from the Kankakee River in Illinois (Smith, 1965b:5). Probably the Missouri populations are a glacial relict. The Ozark Uplands may have served as an important refugium (perhaps the only refugium) for this species during the Wisconsin ice advance, and perhaps also during earlier ice advances.

Ichthyomyzon castaneus Girard—chestnut lamprey

Ichthyomyzon castaneus: Hubbs and Trautman, 1937:44,76 (Mississippi R., Chester, Ill.; Mississippi R., St. Louis). Martin and Campbell, 1953:46 (abund.; Black R.). Bailey, 1959:163 (Missouri R. at Hermann, Gasconade Co.). Starrett, Harth and Smith, 1960 (char.; abund.; Mississippi R. local. mapped). Fisher, 1962:426-427 (Missouri R. local.). Cross and Metcalf, 1963:187 (Missouri R. near St. Joseph). Hanson and Campbell, 1963 (linear distr.; Perche Cr., Boone Co.). Cross, 1967:30 (Missouri R. local. mapped).

Distribution and habitat.—The chestnut lamprey is the most abundant and widely distributed lamprey in Missouri (Map 5). According to reports of commercial fishermen, parasitic lampreys (presumably all of this species) are common in the lower Missouri River. Abundance of parasitic lampreys decreases upstream, and above St. Joseph they are rarely encountered. In the Mississippi River the chestnut lamprey is common between the mouths of the Ohio and Missouri rivers but is uncommon above the town of Rockport, Illinois (Starrett *et al.*, 1960:table 1). Northward in the

Mississippi River, *I. castaneus* is replaced by the silver lamprey. Adults of the chestnut lamprey are rather common in large streams and reservoirs of the Ozarks, and larvae tentatively identified as this species have been collected at many localities in that region.

In its parasitic phase, the chestnut lamprey inhabits large streams and reservoirs, where there is an abundance of the large fishes on which it feeds. Spawning adults and larvae are found in medium-sized creeks to moderately large rivers. The larvae require clear, permanent-flowing streams having stable bars of silt, sand, and organic debris in which to complete their development. In Missouri, streams suitable for larval development are found only in the Ozark Uplands, accounting for the progressive decrease in abundance of the chestnut lamprey in the large rivers of Missouri away from that region.

Zoogeography.—The present distribution of *I. castaneus* and its non-parasitic derivative (*I. gagei*) suggests that they may have inhabited the Mississippi Valley continuously since before the earliest ice advance of the Pleistocene. Possibly they were not present in the preglacial Teays, since they are now represented eastward in the Ohio Valley by the related *I. bdellium* (Jordan), and *I. greeleyi* Hubbs and Trautman.

Ichthyomyzon gagei Hubbs and Trautman—southern brook lamprey

Distribution and habitat.—The only specimens of the southern brook lamprey known from Missouri are a larva tentatively identified as this species and two adults. One adult and the larva (UMMZ 173427) were collected in the Gasconade River east of Hartville in April 1952; the other adult was taken in the Elk River at Pineville in May 1965 (Map 6). The habitat requirements of this species are much like those of the northern brook lamprey.

Zoogeography.—The Gasconade River specimens are the only ones known from north of the Arkansas River system in northeastern Oklahoma and southwestern Missouri. Perhaps the Gasconade River population owes its present isolated position to a stream capture across the divide between the Gasconade and White rivers (physiographic evidence for such a capture was given by Bretz, 1965:46). Alternatively, *I. gagei* may have had a more widespread preglacial or interglacial distribution northward in the Mississippi Valley, and was replaced over parts of this range by its northern counterpart (*I. fossor*) during the Wisconsin or an earlier ice advance of the Pleistocene.

Lampetra lamottei (Lesueur)—American brook lamprey

Petromyzon Lamottenii: Lesueur, 1827:9-11, pl. 6 (orig. descr.; types coll. at Wilkinson Cave, presumably near Mine La Motte, Madison Co.).

Entosphenus lamottenii: Hubbs and Trautman, 1937:22-24 (reprod. of orig. descr.; type local. erroneously listed in Jackson Co.).

Taxonomic considerations.—The troubled nomenclatorial history of the two eastern North American species now included in the genus *Lampetra* was reviewed and brought to its present state by Hubbs and Trautman (1937:22-24); they shifted *Petromyzon Lamottenii* Lesueur from the species now known as *L. aepyptera* to the species formerly known as *L. wilderi* or *L. appendix.* Although the basis for this change has been weakened by the discovery of *L. aepyptera* in the St. Francis River system, from which Lesueur presumably obtained his type specimens, there is no justification for further nomenclatural changes without additional evidence. I have tried without success to locate Wilkinson Cave, and I have been unable to collect any brook lampreys in the vicinity of Mine La Motte. The only brook lampreys known to me from the St. Francis River system are five ammocoetes collected in a tributary of Big Creek, six miles southeast of Ironton in Iron County. I have identified these as *L. aepyptera* on the basis of myomere count.

Distribution and habitat.—The only recent records for the American brook lamprey in Missouri are from the Current River system (two larvae and one adult) and a series of three larvae and 17 newly transformed adults from Castor River, Bollinger County (Map 7).

In Missouri the American brook lamprey inhabits medium-sized to moderately large streams, leaving the smaller creeks to the least brook lamprey. The two have not been taken in the same collections, although they occur in close proximity in the Current River system.

Zoogeography.—The main body of the range of *L. lamottei* is in the upper Mississippi, Ohio, and Great Lakes drainages. Northwestward into Alaska it is replaced by other species of *Lampetra.* Perhaps *L. lamottei* was confined preglacially to the Laurentian system or other northern drainages and entered the Mississippi Valley by way of glacial connectives that developed during the Pleistocene.

Lampetra aepyptera (Abbott)—least brook lamprey

Distribution and habitat.—The least brook lamprey is common in the upper Current and Eleven Point systems and is known from

a few localities in the White, St. Francis and Meramec systems (Map 8). It probably has a more widespread distribution in the Ozarks than these records indicate. The least brook lamprey is decidedly a small-stream fish, occurring most abundantly, both as adults and as larvae, in clear, permanent-flowing headwater creeks and spring branches.

Zoogeography.—*Lampetra aepyptera* is probably autochthonous to the preglacial Teays-Mississippi system. Ozarkian populations are broadly disjunct from the main body of the range east of the Mississippi River. Perhaps Ozarkian populations owe their isolated position to fragmentation of a more widespread preglacial range in the central Mississippi Valley. Alternatively, this species may have invaded the Ozark Uplands during one of the Pleistocene ice advances, when conditions in the Mississippi Embayment were more favorable to the east-west dispersal of upland fishes.

Acipenseridae

Acipenser fulvescens Rafinesque—lake sturgeon

Acipenser rauchi: Duméril, 1870:105,118 (orig. descr.; type local. Osage R.).
Acipenser anasimos: Duméril, 1870:105,122 (orig. descr.; type local. Missouri R. near St. Louis).
Acipenser rubicundus: Forbes and Richardson, 1920:25 (decline in abund.; Mississippi R. at Alton, Ill.). Coker, 1930:150-152 (Mississippi R. below mouth Des Moines R.; Mississippi R., Canton).
Acipenser fulvescens: Barnickol and Starrett, 1951:288-290 (utiliz.; decline in abund. in Mississippi R.). Fisher, 1962:426 (Missouri R. near Lisbon, Howard Co.). Cross, 1967:33-34 (Missouri R., Rulo, Nebr.; Osage R., Mo.).

Distribution and habitat.—Before 1900 the lake sturgeon was common in Missouri. The commercial fishing report of the U.S. Commissioner of Fish and Fisheries for 1894 shows that Missouri fishermen harvested 50,000 pounds of lake sturgeon in that year. By 1908, Forbes and Richardson (1920:25) reported that this species was steadily decreasing in abundance and was only rarely taken in the Illinois section of the Mississippi River. At present the lake sturgeon is extremely rare in Missouri waters, and apparently exists primarily as occasional stray individuals from farther north (Map 9). A farmer along the lower Osage River informed me that large sturgeons were taken from that stream until Bagnell Dam was constructed. If these were *A. fulvescens*, reproducing populations may have persisted in Missouri at least until 1930. I have examined the head of a specimen taken from the Missouri River near Easley, Boone County, in a hoop net on 25 July 1967. It reportedly was 5 feet in length and weighed approximately 65 pounds.

Also, I have seen a recognizable photograph of a specimen, reported to have weighed 97 pounds, taken in the Missouri River near Lupus, Moniteau County, in 1938. Another recent report is of a 32-pound specimen taken in the Mississippi River near Ellsbery, Lincoln County, in August 1966. Elsewhere in its range this fish inhabits lakes as well as streams, but in Missouri it is known only from large rivers. The marked decline in abundance which it has undergone could have resulted from overfishing, increased siltation, and/or the construction of dams which block its movements and destroy its habitat.

Zoogeography.—This ancient species is northern in its affinities, and may have long occupied the preglacial Hudson Bay, Laurentian, and/or Teays-Mississippi drainages. It undoubtedly survived the Wisconsin, and probably also earlier ice advances of the Pleistocene, in the Mississippi Valley.

Scaphirhynchus platorynchus (Rafinesque)—shovelnose sturgeon

Scaphirhynchus platorynchus: Fowler, 1921:398 (young example; Fox Cr., trib. Meramec R.). Barnickol and Starrett, 1951:288-290 (utiliz.; hab.; abund.; Mississippi R. local.). Bailey and Cross, 1954:169-199 (char.; compar.; hab.; Missouri local. compiled and mapped). Fisher, 1962:427 (Missouri R. local.). Cross, 1967:34 (Missouri R. local. mapped).

Distribution and habitat.—The shovelnose sturgeon is the most abundant sturgeon in the Missouri and Mississippi mainstreams but is rare elsewhere in the state (Map 10). The record by Fowler (1921:398) is doubted for reasons given in the account of *I. unicuspis*. In the Michigan collections there are five specimens (UMMZ 177858) with a label indicating that they were taken in the Niangua River drainage by L. C. Salyer on August 27-29, 1931. Bailey and Cross (1954) made no mention of these specimens and did not include this locality on their distribution map. This record, if authentic, indicates that the shovelnose sturgeon was present in the Osage River and its major tributaries before construction of Bagnell Dam. I have reliable reports of shovelnose sturgeon taken by fishermen in the lower Current River in recent years.

The shovelnose sturgeon inhabits the open channels of large rivers, and is usually found in a strong current over a firm sand or gravel bottom.

Zoogeography.—Metcalf (1966:94-95) suggested that the shovelnose sturgeon may be autochthonous to the preglacial Teays-Mississippi system, perhaps occupying that system at a time when ancestral stocks of the closely related *S. albus* were localized in the Hudson Bay system.

Scaphirhynchus albus (Forbes and Richardson)—pallid sturgeon

Parascaphirhynchus albus: Forbes and Richardson, 1905:37-44 (orig. descr.; type local. Mississippi R. at Grafton, Ill.; also in lower Missouri R.). Forbes and Richardson, 1920:29 (Mississippi R. at Grafton and Alton, Ill.). Barnickol and Starrett, 1951:290 (abund.; Mississippi R. above mouth Missouri R.).

Scaphirhynchus album: Bailey and Cross, 1954:169-190,199-202 (char.; compar.; hab.; Missouri R. at Rocheport, and just above confl. with Mississippi R.).

Scaphirhynchus albus: Fisher, 1962:427 (Missouri R. at Easley. Rocheport, Lexington, and St. Joseph). Cross, 1967:37 (Missouri R. local. mapped).

Distribution and habitat.—The pallid sturgeon occurs in the Missouri and lower Mississippi rivers, and ascends the Mississippi River upstream from the mouth of the Missouri for only a few miles (Map 11). It seems to be extremely rare in Missouri. The habitat of the pallid sturgeon seems to be much like that of the shovelnose sturgeon.

Zoogeography.—If the pallid sturgeon evolved in the preglacial Hudson Bay system as suggested by Metcalf (1966:95), its presence in the Mississippi Valley dates from the time of the southward deflection of the upper Missouri River during the Pleistocene.

Polyodontidae

Polyodon spathula (Walbaum)—paddlefish

Procerus maculatus: Rafinesque, 1820:87 (orig. descr.; type local. Ste. Genevieve, Mo.).

Polyodon spathula: Garman, 1890:148 (Mississippi R. near Quincy, Ill.). Ellis, 1916:93-94 (Dry Wood Cr. near Nevada, Vernon Co.). Forbes and Richardson, 1920:17 (abund.; bayous Mississippi R. about Alton). Fowler, 1921:398 (young; Fox Cr., trib. Meramec R.). Borges, 1950:16-33 (Niangua Arm, Lake Ozark). Barnickol and Starrett, 1951:290-291 (utiliz.; abund.; hab.; Mississippi R. local.). Wilson, 1956 (parasites; Missouri R. near St. Joseph). Purkett, 1961 (reprod. and early develop.; Osage R.). Fisher, 1962:427 (Missouri R. local.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.). Purkett, 1963 (artif. prop.; Osage R.). Needham, 1965 (artif. induct. spawning; Osage R.). Ballard and Needham, 1964 (embryol.; Osage R.). Cross, 1967:38 (Missouri R. local. mapped).

Paddlefish: Fry, 1962 (harv.; Black R. below Clearwater Res.).

Distribution and habitat.—The paddlefish probably occurs in all the major rivers of the state where its movements are not blocked by dams (Map 12). It now seems less abundant in the Mississippi River than formerly (Barnickol and Starrett, 1951:291). Destruction of spawning grounds and blocking of movements by dams, along with overfishing, are probably the major factors responsible for this decline. A similar decline has occurred in the Missouri River, perhaps as a result of channelization and the consequent elimination of backwaters. Construction of Kaysinger Bluff Dam on the Osage River near Warsaw will probably destroy the principal spawning grounds for the large population of paddlefish presently found in Lake of the Ozarks. Since no suitable spawning areas are present above the reservoir to be created by this dam, a marked decline in abundance of the paddlefish in the Osage River can be expected. This fish inhabits quiet pools and backwaters of large rivers. It thrives in large man-made impoundments if they have large tributaries that are suitable for spawning. Construction of Lake of the Ozarks has provided these conditions.

Zoogeography.—This ancient fish probably has long inhabited the Mississippi Valley.

Lepisosteidae

Lepisosteus spatula Lacépède—alligator gar

Lepisosteus spatula: Barnickol and Starrett, 1951:320-321 (utiliz.; abund.; Mississippi R. local.).

Distribution and Habitat.—The alligator gar is known in Missouri only from the Mississippi River, where it is rare (Map 13). Forbes and Richardson (1920:35) reported that this species ascends the Mississippi River above St. Louis, but they listed no specific localities, and gave no indication of abundance. Barnickol and Starrett (1951:320) reported the alligator gar from five stations in the Missouri section of the Mississippi River; 80 of their 85 specimens were taken at Cairo. The only recent reports known to me from the Mississippi River where it bounds Missouri are of two specimens taken by fishermen in 1965. One specimen, weighing 110 pounds, was taken near Chester, Illinois; the other, weighing 130 pounds, was taken near Cairo. These records, along with photographs of the specimens, were furnished by Philip W. Smith.

The alligator gar inhabits the sluggish pools and overflow waters of large rivers.

Zoogeography.—*Lepisosteus spatula* reaches the northern limit of its range in the Mississippi River near the mouth of the Missouri. It probably has long inhabited the Mississippi Valley.

Lepisosteus platostomus Rafinesque—shortnose gar

Cylindrosteus agassizii: Duméril, 1870:351 (orig. descr.; St. Louis).

Lepisosteus platostomus: Forbes and Richardson, 1920:map VI (Mississippi R. local.). Fowler, 1921:398 (young; Fox Cr., trib. Meramec R.). Barnickol and Starrett, 1951:320-321 (utiliz.; abund.; Mississippi R. local.). Patriarche, 1953 (abund.; import.; Lake Wappapello). Fisher, 1962:427 (Missouri R. local.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.). Cross, 1967:41 (Missouri R. local. mapped).

Distribution and habitat.—The shortnose gar is the most abundant gar over all of Missouri except the Ozark Uplands (Map 14). It is most often found along major rivers, in quiet pools, backwaters,

and oxbow lakes. It seems to be more tolerant of high turbidity than the longnose and spotted gars.

Zoogeography.—The preference by *L. platostomus* for large turbid rivers and its distributional relationships with the related *L. oculatus* suggest that *L. platostomus* may have occurred preglacially in the Hudson Bay system and entered the Mississippi Valley when the upper Missouri River was deflected southward during the Pleistocene.

Lepisosteus oculatus (Winchell)—spotted gar

Lepisosteus productus: Funk and Campbell, 1953:79 (abund.; Black R.). Patriarche, 1953 (abund.; import.; Lake Wappapello).

Distribution and habitat.—The spotted gar is rather common in the ditches of the lowlands (Map 15). It was not reported by Barnickol and Starrett (1951) from the Mississippi River, but the records of George V. Harry indicate that Barnickol and Shoemaker took a specimen near Grafton in 1944. The spotted gar is known from the Neosho River in southeastern Kansas (Branson and Hartmann, 1963:591), and therefore is to be expected in southwestern Missouri. In most Missouri collections, the spotted gar has been outnumbered by the shortnose or longnose gars. It seems less tolerant of turbidity, and shows a greater affinity for aquatic vegetation than the other gars; it attains its greatest abundance in quiet, clear waters having considerable aquatic vegetation or standing timber.

Zoogeography.—The widespread distribution of *L. oculatus* in Gulf coastal drainages, and presence of the closely related *L. platyrhincus* DeKay in Florida, suggest that this species may have long occupied the Mississippi Valley.

Lepisosteus osseus (Linnaeus)—longnose gar

Lepidosteus osseus: Jordan and Meek, 1885:13,16 (Missouri R. at St. Joseph; Grand R. at Clinton and/or Tebo Cr. at Calhoun).

Lepisosteus osseus: Forbes and Richardson, 1920:map V (Mississippi R. local.). Borges, 1950 (Niangua Arm, Lake Ozark). Cleary, 1956:map 5 (Des Moines R. local.). Fisher, 1962:427 (Missouri R. local.). Netsch and Witt, 1962 (life history; Osage and Pomme de Terre rivers, Benton Co.; Perche Cr., Boone Co.; Loose Cr., Osage Co.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.). Cross, 1967:43 (Missouri R. local. mapped).

Lepisosteus osseus oxyurus: Barnickol and Starrett, 1951:320-321 (utiliz.; abund.; Mississippi R. local.). Martin and Campbell, 1953:46 (abund.; Black R.).

Distribution and habitat.—The longnose gar is nearly statewide in distribution and occurs in all the major stream systems (Map 16). It is the only gar in the clear, high-gradient streams of the Ozarks and reaches its greatest abundance in large reservoirs of that region. Elsewhere it is less abundant at most localities than the shortnose gar.

The longnose gar typically inhabits the sluggish pools, backwaters, and oxbows along large, moderately clear streams. Adults usually are found in large, deep pools; young occur in shallow backwaters, often in thick beds of aquatic vegetation. Spawning is preceded by upstream migrations into smaller streams than those inhabited at other times, and the young usually remain in these smaller streams during the first summer of life.

Zoogeography.—Lepisosteus osseus was likely an inhabitant of the Teays-Mississippi system but may have occupied other preglacial drainages as well.

Amiidae

Amia calva Linnaeus—bowfin

Amia calva: Forbes and Richardson, 1920:map VII (Mississippi R. local.). Barnickol and Starrett, 1951:321-322 (utiliz.; abund.; Mississippi R. local.). Funk and Campbell, 1953:72-81 (abund.; Black R. local.). Patriarche, 1953 (abund.; import.; Lake Wappapello). Fisher, 1962:427 (Missouri R. at St. Charles).

Amiatus calvus: Fowler, 1921:398 (Fox Cr., trib. Meramec R.).

Bowfin: Fry, 1962 (harv.; Black R. below Clearwater Res.).

Distribution and habitat.—The bowfin occurs in the lowlands and northward along the Mississippi River (Map 17). Barnickol and Starrett (1951:321) found this fish to be more common in the Mississippi above the mouth of the Missouri River than below. It shows an affinity for clear, quiet water; this may account for the decrease in abundance in the swifter, more turbid water below the mouth of the Missouri River. Fisher (1962:427) took only a single specimen near St. Charles in his extensive survey of the Missouri River. The only other record known to me from the Missouri River system in Missouri is of a 4½ pound specimen taken from Fishing River in Clay County in June, 1966. Cross (1967:46-47) examined a specimen caught by a fisherman in Independence Creek, Atchison County, Kansas, in 1965, and heard reports of others caught in oxbows and backwaters of the Missouri River where it borders Kansas. Except for the specimen reported by Fisher from near St. Charles not far above the mouth of the Missouri, all recent records for the Missouri system in Missouri may be attributable to introductions. Bailey and Allum (1962:30) reported that they knew of no firm evidence for the native occurrence of the bowfin in the Missouri River system of South Dakota.

In the lowlands the bowfin is found in a variety of habitats, including swamps, sloughs, borrow pits, ditches, abandoned stream channels, and the sluggish lower reaches of Ozark streams that enter from the north. In the ditches it is most abundant in sections having thick beds of aquatic vegetation or other cover. Along the Mississippi River the bowfin is more often found in backwaters and oxbows than in the main channel.

Zoogeography.—This ancient species probably has long inhabited the Mississippi Valley. It was reported from Pliocene fossil deposits in Nebraska by C. L. Smith (1962:506).

Anguillidae

Anguilla rostrata (Lesueur)—American eel

Anguilla rostrata: Coker, 1930:171-173 (abund.; nat. hist.; Mississippi R. at Canton and Alexandria). Funk and Campbell, 1953 (abund.; Black R. local.).

Anguilla bostoniensis: Barnickol and Starrett, 1951:291-292 (abund.; Mississippi R. local.). Berner, 1951:table 5 (commer. catch; Missouri and Mississippi rivers).

Distribution and habitat.—The eel probably occurs occasionally in every large stream in the state where its movements are not impeded by dams (Map 18). Its exact distribution and abundance are difficult to assess, because it is not readily captured by the kind of gear ordinarily used in fish surveys. It seems to be more abundant in the southern Ozarks and the lowlands than elsewere. Coker (1930:173) noted that the eel was declining in abundance in the Mississippi River by the early 1900's. A decline has also occurred in the Ozark Uplands, where high dams deny the eel access to large areas. This fish is still present in the upper Mississippi River, in spite of several navigation dams (Barnickol and Starrett, 1951: 291-292). The eel occurs in a variety of stream types but is most abundant in medium-sized or large streams with continuous flow and moderately clear water. It is most often found in the deeper pools near logs, boulders, or other cover.

Zoogeography.—This catadromous species has probably long occupied the Mississippi Valley.

Clupeidae

Alosa chrysochloris (Rafinesque)—skipjack herring

Pomolobus chrysochloris: Forbes and Richardson, 1920:49 (Mississippi R. at Alton). Coker, 1930:165-169 (Mississippi R. below Warsaw, Ill.; Mississippi R. at Canton, Mo.). Barnickol and Starrett, 1951:323 (abund.; utiliz.; Mississippi R. local.).

Distribution and habitat.—The highly vagile skipjack herring must occur at least occasionally in most large rivers of Missouri (Map 19). In the Mississippi it was formerly abundant above the mouth of the Missouri River but has undergone a marked decline since that section of the river was impounded (Coker, 1930:169; Barnickol and Starrett, 1951:323). It is rare between the mouths of the Missouri and Ohio rivers but is abundant in the Mississippi River below the mouth of the Ohio. Elsewhere only occasional individuals have been found. The skipjack herring inhabits the open waters of large rivers. It seems intolerant of extreme turbidity, as indicated by the paucity of records for the Missouri River and the Mississippi River downstream from the mouth of the Missouri.

Zoogeography.—Alosa chrysochloris probably was derived from marine stocks that became adapted to life in the larger inland streams of the Mississippi River system and other Gulf coastal drainages.

Alosa alabamae Jordan and Evermann—Alabama shad

Distribution and habitat.—The Alabama shad was not collected in Missouri until 1940. Since that time it has been taken at least eight times, from the Meramec, Gasconade, and Osage rivers (Map 20). Previously it had been reported in the Mississippi River system (as *Alosa ohiensis* Evermann) only from the Ohio River at Louisville (Evermann, 1902), from the Mississippi River near Keokuk, Iowa (Coker, 1930:169-171), and from the Poteau River, Oklahoma (Hutchins and Hall, 1951:83-84). Evidently it has declined in abundance in the Mississippi River system since the early 1900's, because both Evermann and Coker judged it to be common enough to support a limited commercial fishery.

That the Alabama shad is anadromous in the Mississippi River system, as elsewhere in its range, was suggested by Coker (1930: 171), who noted that it was present near Keokuk only from early May to the middle or latter part of July, and that all fish were in a spawning condition. From this he concluded that its appearance at Keokuk coincided with a spawning migration. Data from the Missouri collections support this conclusion. The only adult specimen was collected in July; all of the remaining 90-plus specimens are young-of-the-year collected between late July and early October. The scarcity of adults suggests that they are present only briefly, and the occurrence of young only in late summer and early fall suggests a movement into other waters before the second summer of life.

Zoogeography.—The distribution of *A. alabamae* suggests an

origin in the eastern part of the Gulf of Mexico. It seems to be most closely allied to the American shad, *Alosa sapidissima* (Wilson), and may have been derived from a common ancestral stock that invaded the Gulf of Mexico at a later time than the skipjack herring.

Dorosoma cepedianum (Lesueur)—gizzard shad

Dorosoma cepedianum: Jordan and Meek, 1885:14,17 (Missouri R. at St. Joseph; Grand R. at Clinton and/or Tebo Cr. at Calhoun). Meek, 1891: 122 (Little Piney Cr. near Arlington). Forbes and Richardson, 1920:map VIII (Mississippi R. local.). Borges, 1950 (Niangua Arm, Lake Ozark). Barnickol and Starrett, 1951:323 (abund.; Mississippi R. local.). Patriarche, 1953 (abund.; import.; growth; Lake Wappapello). Martin and Campbell, 1953:46-64 (abund.; hab.; Black R.). Funk and Campbell, 1953:72-81 (abund.; Black R. local.). Cleary, 1956:map 10 (Des Moines R. local.). Purkett, 1958a:125-126 (growth; import.; Salt R.). Patriarche and Campbell, 1958:251-252 (Clearwater Lake; abund.; growth; import.). Fisher, 1962:427 (Missouri R. local.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.).

Gizzard shad: Purkett, 1958b:4,21,43 (growth; length-weight relationship; Missouri streams). Fry, 1962 (harv.; Black R. below Clearwater Res.). Hanson, 1962 (abund.; utiliz. by largemouth bass; Table Rock Res.).

Distribution and habitat.—The gizzard shad is one of the most widely distributed of the larger fishes in Missouri and occurs at least occasionally in every principal stream in the state (Map 21). It is most abundant along the Missouri and Mississippi rivers and in large reservoirs. This fish inhabits lowland lakes and ponds, man-made impoundments, and the pools and backwaters of streams. It occurs in both extremely clear and very turbid waters, and exhibits no obvious preference for a particular bottom type. *D. cepedianum* avoids streams with extremely high gradients and those which lack large, permanent pools.

Zoogeography.—This wide-ranging species was probably present in the Teays-Mississippi system, as well as other preglacial drainages of eastern North America. It is essentially southern in distribution and perhaps was not present preglacially in the Hudson Bay or Laurentian systems.

Dorosoma petenense (Günther)—threadfin shad

Distribution and habitat.—The threadfin shad seems to be more common than the gizzard shad in the Mississippi River downstream from the mouth of the Ohio River (Map 22). There it outnumbered the gizzard shad 2:1 in a series of collections made in 1963. It is rare above the mouth of the Ohio, and apparently reaches the upstream limit of its range in southern Perry County. I have collected this species from only one locality in the ditches of the lowlands. The threadfin has been stocked in Bull Shoals and Table Rock reservoirs, and is now well established there. It has also

been introduced into Montrose Lake in Henry County, and spawned successfully in 1965; survival there is presumably dependent on continuous warm-water discharge by a power plant. Efforts are being made to establish the threadfin shad in Thomas Hill Reservoir, where there is similar warm-water discharge; the status of this stock is not yet known. The habitat of *D. petenense* is similar to that of the gizzard shad, except that the threadfin is more often found in strong current.

Zoogeography.—*Dorosoma petenense* probably inhabited the preglacial Teays-Mississippi system. It is probably native to the lower Mississipi and Ohio rivers but seems to have increased in abundance there over the last few decades. Recent changes in the distribution of this species were discussed by Minckley and Krumholz, 1960:176-178.

Hiodontidae

Hiodon alosoides (Rafinesque)—goldeye

Hyodon tergisus: Girard, 1858:333, plate LXXV, figs. 1-4 (St. Louis, Mo.).

Hiodon alosoides: Jordan and Meek, 1885:14 (Missouri R. at St. Joseph; Tabo Cr. 6 mi. E Lexington). Fisher, 1962:427 (Missouri R. local.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.). Cross, 1967:56 (Missouri R. local. mapped).

Amphiodon alosoides: Borges, 1950 (Niangua Arm, Lake Ozark). Barnickol and Starrett, 1951:322 (abund.; Mississippi R. local.).

Distribution and habitat.—The goldeye inhabits the Missouri and Mississippi rivers and the larger prairie streams of the Missouri system (Map 23). In the Mississippi River it is much more common below the mouth of the Missouri River than above. This fish is found most often in the open waters of large rivers, where it frequents areas with strong current as well as quieter waters. It occasionally occurs in deep pools of small rivers and creeks, where these are adjacent to large rivers. The goldeye is more tolerant of continuous high turbidity than the related mooneye.

Zoogeography.—The habitat preferences of *H. alosoides,* and its distributional relationships with the related *H. tergisus,* suggest an origin for *H. alosoides* in the preglacial Hudson Bay system (Metcalf, 1966:97).

Hiodon tergisus Lesueur—mooneye

Hiodon tergisus: Borges, 1950 (Niangua Arm, Lake Ozark). Barnickol and Starrett, 1951:322 (abund.; Mississippi R. local.). Martin and Campbell, 1953:46 (abund.; Black R.). Funk and Campbell, 1953 (abund.; Black R. local.). Fisher, 1962:427 (Missouri R. local.).

Distribution and habitat.—The mooneye is nowhere abundant in Missouri, but it occurs frequently in the Mississippi River and

in the larger streams and reservoirs of the Ozarks (Map 24). It is rare in the Missouri River and the larger prairie streams, where it is largely replaced by the goldeye. The habitat of the mooneye is much like that of the goldeye, except that it generally occurs in clearer and quieter waters.

Zoogeography.—The distributional relationships of this fish and the closely related *H. alosoides* suggest an origin for *H. tergisus* in the preglacial Teays-Mississippi River system (Metcalf, 1966:97).

Salmonidae

Salmo gairdneri Richardson—rainbow trout

Rainbow trout: Maynard, 1889:55-56 (growth and reprod. after stocking; spring at head of Spring R., Lawrence Co.). Fry, 1962 (harv.; tailwaters of Table Rock and Taneycomo reservoirs).

Salmo irideus: Meek, 1891:118 (Meramec Spring).

Distribution and habitat.—The rainbow trout is not native to Missouri; it has had only limited success in maintaining wild populations. Small, self-sustaining populations occur in a few cold-water streams and spring branches in the Ozarks, but the populations at most localities (Map 25) are maintained by continuous stocking.

In recent years, experimental stockings have been made in Missouri of two other salmonids. The brown trout, *Salmo trutta* Linnaeus, was stocked in some Ozark streams, and the Kokanee, *Oncorhynchus nerka* (Walbaum), was stocked in Lake Taneycomo. There is no evidence as yet of natural reproduction of either of these species.

Esocidae

Esox americanus Gmelin—grass pickerel

Esox vermiculatus: Call, 1887:77 (in part (?), Sinking Cr., Spring Valley Cr., and Jacks Fork, Shannon Co.). Barnickol and Starrett, 1951:314 (Mississippi R. at Grafton, Ill.). Martin and Campbell, 1953 (abund.; hab.; Black R.). Funk and Campbell, 1953 (abund.; Black R. local.).

Lucius vermiculatus: Meek, 1891:119,130 (char.; abund.; Meramec Spring and Meramec R. near St. James; North Fork White R., S Cabool).

Esox americanus vermiculatus: Crossman, 1966 (char.; syn.; Missouri local. mapped).

Distribution and habitat.—The grass pickerel is the most abundant and widely distributed pike in Missouri (Map 26). It is common in the lowlands, and occurs sparingly in overflow waters of the Mississippi River northward at least as far as St. Charles County. It is locally abundant in streams draining the eastern and southern slopes of the Ozark Uplands but is absent from the Missouri and Neosho systems. In the Black and St. Francis systems its distribution largely complements that of *E. niger* with one or the other predominating at any locality. In the lowlands the grass pickerel frequents natural lakes, sloughs, borrow pits, and the sluggish sections of ditches, often around thick beds of submergent aquatic vegetation. In the Ozarks it inhabits pools of small creeks draining undissected uplands, as well as spring pools, protected inlets, and overflow waters along major streams.

Zoogeography.—Crossman (1966:fig. 1) reported the grass pickerel from the Missouri River at St. Joseph. This record is based on a collection at the U.S. National Museum (USNM 6833) having a label stating only "St. Joseph's, Bridger." Cross (1967:63-64) discussed this record and suggested that the "St. Joseph's" intended is elsewhere than in Missouri, perhaps the St. Joseph's River in Indiana.

At present the grass pickerel occurs in the Missouri Basin only in eastern Nebraska. Crossman (1966:18) suggested that this population is a remnant of a more widespread distribution that was reduced by a recent drying trend or changes in flow patterns. It is also possible that the Nebraska records are the result of introductions (Cross, 1967:64). If the populations are natural, it is likely that they date from pre-Pleistocene or Pleistocene times, when the drainage of this area was eastward through central Iowa to the Mississippi River. If the grass pickerel formerly had a continuous distribution downstream to the mouth of the Missouri, it should now be present in the Osage and Gasconade systems of central Missouri, where there appears to be an abundance of suitable habitat, and where conditions for long-term survival would seem as favorable as those in Nebraska.

Occurrence of a well defined subspecies (*E. a. vermiculatus* Lesueur) in the Mississippi Valley suggests that the grass pickerel has long inhabited this region. Probably the grass pickerel has been present in the Mississippi Valley since preglacial time.

Esox niger Lesueur—chain pickerel

Esox vermiculatus: Call, 1887:77 (at least in part; Sinking Cr., Spring Valley Cr., and Jacks Fork, Shannon Co.).

Lucius reticulatus: Meek, 1889:140 (reident. of a spec. recorded by Call, 1887:77 as *E. vermiculatus;* Spring Valley Cr., Shannon Co.).

Distribution and habitat.—The chain pickerel occurs in streams on the southeastern slope of the Ozarks from Eleven Point River east to the St. Francis River (Map 27). In the Eleven Point and Current rivers it is far more common than the grass pickerel. The

complementary distribution patterns of the chain pickerel and grass pickerel are perhaps the result of competition. *Esox niger* is found along the major streams of the Ozarks in spring pools and marginal waters having thick growths of submergent aquatic vegetation and no perceptible current. Unlike the grass pickerel, it does not penetrate into small headwater creeks, and avoids the warmer lowland rivers and ditches.

Zoogeography.—Esox niger has only a limited distribution in the Mississippi Valley and may be a recent invader from the east. Possibly it was localized preglacially on the Atlantic Slope and dispersed westward along the Gulf Coast into the lower Mississippi Valley, when the lowering of sea levels accompanying Pleistocene glaciation created stream connectives that facilitated such dispersal.

Esox lucius Linnaeus—northern pike

Esox lucius: Cross, 1967:63 (Fishing R., Ray Co.).

Distribution and habitat.—At present there seem to be no established populations of northern pike in Missouri. All localities plotted for this species (Map 28) are based on one or a few specimens taken by fishermen. Most reports are from the lower Osage River, where a few northern pike are taken every year. Possibly there is a self-sustaining population in the Osage River, but most specimens taken in Missouri are probably strays that enter Missouri from farther north along the Missouri and Mississippi rivers. The northern pike has been stocked in a few reservoirs by the Missouri Department of Conservation in recent years, but there is little evidence as yet of natural reproduction.

The muskellunge (*Esox masquinongy* Mitchill), a pike not native to Missouri, is also being stocked on an experimental basis.

Zoogeography.—The widespread northern distribution of *E. lucius* and its distributional relationships with other *Esox* suggest that it may have been localized preglacially in drainages north of the Mississippi Valley, and dispersed southward through glacial connectives that developed during the Pleistocene.

Cyprinidae

Cyprinus carpio Linnaeus—carp

Cyprinus carpio: Steedman, 1884:64 (introd. into Missouri). Borges, 1950 (Niangua Arm, Lake Ozark). Berner, 1951:9,10 (food; Missouri R.). Barnickol and Starrett, 1951:298-303 (utiliz.; abund.; Mississippi R. local.). Patriarche, 1953:242-254 (abund.; import.; growth; Lake Wappapello). Martin and Campbell, 1953 (abund.; hab.; Black R.). Funk and Campbell, 1953 (abund.; Black R. local.). Funk, 1957:39-57 (movements; Missouri streams). Purkett, 1958a:122-123 (growth; import.; Salt R.). Patriarche and Campbell, 1958:253-254 (abund.; import.; Clearwater Lake). Fisher, 1962:427 (Missouri R. local.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.). Cross, 1967:72 (Missouri R. local. mapped).

Carp: Purkett, 1958b:10,30,43 (growth; length-weight relationship; Missouri streams). Fry, 1962 (harv.; tailwaters of Table Rock, Taneycomo, and Clearwater res.).

Distribution and habitat.—A summary of early introductions of carp into Missouri is given by Steedman (1884:64), and information on subsequent stocking can be gleaned from biennial reports of the Missouri State Fish Commission. The first carp were brought into Missouri in the autumn of 1879, when the U.S. Fish Commission supplied several persons with consignments of 20 carp each for stocking in private ponds. At the same time, the Missouri Fish Commission received 240 young carp, most of which were lost, and the following spring they received another consignment of 500. Between 1880 and 1885, the Missouri Fish Commission reared over 80,000 carp in their hatcheries at Forest Park, St. Louis, and St. Joseph, and these were stocked in private and public waters throughout the state. The program was discontinued in 1895, largely because the carp had lost its early popularity, but by that time it was well established in Missouri waters.

The carp is one of the most abundant and widespread large fishes in the state (Map 29). In the Missouri and Mississippi rivers the total poundage taken by commercial fishermen consistently exceeds that of any other species. Carp are likewise abundant in the prairie streams of north and west Missouri, the drainage ditches of the lowlands, and in man-made impoundments and natural lowland lakes throughout the state. *C. carpio* has been least successful in the clear, high-gradient streams of the Ozarks, but even there it is abundant locally in warm backwaters and in streams polluted by domestic wastes.

The invasion of the Current and Eleven Point rivers, two of the clearest and least polluted Ozark streams, by carp in 1957 demonstrates the adaptability of this species In previous years carp had made up only a very minor part of the fish population, but in 1957 they appeared in large numbers. These carp were of uniform age, and their sudden appearance seems to have been the result of population pressure caused by production of an unusually large year-class in the lowland sections of these streams in Arkansas. Carp have remained an important element in the fish populations of Current and Eleven Point rivers since that time, but their numbers have progressively diminished. A few smaller carp were found

in 1965 and 1966, indicating limited spawning success or additional recruitment from downstream.

The carp is most abundant in large streams, natural lakes, and impoundments that are highly productive as a result of natural fertility or organic pollutants. It is often found in rather small creeks if these have large, permanent pools. The carp is tolerant of a wide range of turbidities, bottom types, and temperatures. When not feeding, adult carp are usually found in the deeper parts of pools, often associated with piles of drift, logs, or other submerged cover.

Carassius auratus (Linnaeus)—goldfish

Goldfish: Fry, 1962 (harv.; Clearwater Res. tailwater).

Distribution and habitat.—The goldfish has proved to be far less adaptable and successful in Missouri waters than the carp (Map 30). No intensive efforts have been made to establish *C. auratus*, but the innumerable goldfish that are released annually from hatcheries, bait buckets, home aquaria and artificial lakes have afforded ample opportunity for its establishment. In spite of this, there seem to be no self-sustaining populations of goldfish in natural waters of the state. Goldfish are sometimes common in streams below hatcheries, where their numbers are maintained by continuous escape, and in large impoundments, where they are used for bait. Otherwise there is no pattern to the distribution of this species, and individuals may be encountered anywhere in the state.

Notemigonus crysoleucas (Mitchill)—golden shiner

Notemigonus americanus crysoleucas: Jordan and Meek, 1885:15 (Blackwater R. at Brownsville).

Notemigonus crysoleucas: Meek, 1891:118,125 (Little Dry Fork near Rolla; Maries R. near Dixon). Patriarche and Campbell, 1958:255-256 (abund.; Clearwater Lake). Fisher, 1962:427 (Missouri R. trib., Rocheport). Hanson and Campbell, 1963 (linear distr.; Perche Cr.).

Notemigonus crysoleucas auratus: Barnickol and Starrett, 1951:322 (Mississippi R. at Grafton, Ill.). Martin and Campbell, 1953 (abund.; hab.; Black R.).

Distribution and habitat.—The golden shiner is most abundant in the prairie and Ozark border streams of west-central and northeastern Missouri, and in the drainage ditches, sloughs and borrow pits of the lowlands (Map 31). Distribution in Ozark streams is sporadic, but *N. crysoleucas* is locally abundant in backwaters of large Ozark reservoirs. The sandy, highly turbid streams of northwestern Missouri do not provide suitable habitat for this species; there the golden shiner occurs only as strays or highly localized

populations. In Missouri, the golden shiner seldom attains the extreme abundance that has been attributed to it elsewhere in its range, and many distributional records are based on one or a few specimens.

The golden shiner is characteristic of standing-water habitats. It is most often found in sloughs, ponds, lakes, impoundments, the quiet pools of low-gradient streams and ditches, and the permanent pools of small, intermittent upland creeks. It occurs only as strays in the swifter sections of streams. The golden shiner is tolerant of moderate amounts of turbidity, but thrives best in clear, heavily vegetated habitats.

Zoogeography.—The golden shiner is widespread in the eastern United States and southern Canada. Some workers recognize three subspecies, but Bailey, Winn and Smith (1954:123-124) indicated that this is unwise, because the characters used are in part clinal and discordant in distribution. Perhaps this pattern of variation has resulted from mixing of stocks that were localized in different preglacial drainages. If so, *N. crysoleucas* may have been as widespread then as it is today.

Semotilus atromaculatus (Mitchill)—creek chub

Semotilus atromaculatus: Jordan and Meek, 1885:12,14,16,17 (Hundred and Two R. at Maryville; Tabo Cr. 6 miles E Lexington; Flat Cr. near Sedalia and/or Blackwater R. at Brownsville; Grand R. at Clinton and/or Tebo Cr. at Calhoun). Call, 1887:77,80 (West Fork Black R., Tom's Cr., and Barren Fork, Reynolds Co.; Spring Valley Cr., Shannon Co.; Big Cr., Texas Co.; Meramec R., Dent Co.; Bear Cr., Boone Co.). Meek, 1891: 118,122,125,126,130 (Meramec Spring, 5 mi. SE St. James; Big Dry Fork near Meramec Spring; Little Dry Fork near Rolla; scarce in all collections, Gasconade system; Niangua R. near Marshfield; Sac R. near Springfield; Maries R. near Dixon; one spec. from Neosho system; Bryants Cr. near Mansfield). Martin and Campbell, 1953:46 (abund.; Black R.). Fisher, 1962: 427 (Missouri R. local.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.). Metcalf, 1966:tables 7 and 8 (meristics; Moniteau Cr., Moniteau Co.; Richland Cr., Morgan Co.; trib. Eleven Point R., Ripley Co.). Cross, 1967: 79 (Missouri R. local. mapped).

Distribution and habitat.—The creek chub is one of the most widely distributed Missouri minnows (Map 32). Its main area of abundance is in the smaller prairie creeks of central and east-central Missouri. Westward, it becomes increasingly spotty in distribution, but where it does occur it is often abundant. It is present in virtually all small creeks and spring branches of the Ozarks but is seldom abundant. In the lowlands it is known only from a few small creeks in Crowley's Ridge.

The creek chub is well named, for it is most abundant in small headwater creeks where few other fishes are present. These small creeks often cease to flow in dry weather, and the creek chub

survives in isolated pools, or repopulates from below when the creeks again begin to flow. The creek chub requires flowing water for spawning, but does not thrive in streams with a continuous strong flow. Such streams usually harbor numerous fish species, and in this situation the rather generalized creek chub seems unable to compete successfully. In many Ozark streams its niche seems to be largely filled by the hornyhead chub, and competition with that species may be an important factor in limiting the abundance of the creek chub in these streams. *Semotilus atromaculatus* can tolerate moderately high turbidity, as long as the stream gradient is sufficient to create stretches of coarse gravel for spawning. The scarcity of this bottom type in many small streams of northern and western Missouri and in the ditches of the lowlands may be the most important factor limiting the distribution and abundance of the creek chub in those regions.

Zoogeography.—The creek chub occurs widely in the eastern United States and may have been present preglacially in all the principal stream systems. Occurrence of a disjunct population in the upper Canadian and Pecos stream systems indicates a more extensive southwestern distribution in the past. Perhaps this disjunction dates from one of the ice advances of the Pleistocene, when the climate in the southern plains was more favorable for the creek chub than it is today. *Semotilus atromaculatus* is known from Illinoian fossil deposits of southwestern Kansas and the Oklahoma panhandle (Smith, C. L., 1958:177; Smith, G. R., 1963:279).

Opsopoeodus emiliae Hay—pugnose minnow

Distribution and habitat.—The pugnose minnow is largely confined in Missouri to the lowlands, where it is rare (Map 33). It was formerly more abundant there, as indicated by its greater frequency in collections made before 1945. It formerly occurred along the upper Mississippi River, and in the Neosho system of southwestern Missouri, but there are no recent records from these areas. In the Neosho system of Kansas it is known only from a single collection made in 1931 (Cross, 1967:83-84). A single specimen (MU 5190) was taken from the Gasconade River east of Rich Fountain by an ichthyology class from the University of Missouri in 1961. Dr. Arthur Witt informed me that annual seining at that locality since 1961 has yielded no more specimens. Trautman (1957:335-337) noted a drastic reduction in abundance of the pugnose minnow in Ohio, attributing the decline to increased turbidity and siltation, and to the disappearance of aquatic vegetation.

Similar changes may have caused a decline of this species in Missouri, but habitats with clear water and an abundance of aquatic vegetation are still common in southeastern Missouri.

The pugnose minnow thrives only in clear waters where there is an abundance of aquatic vegetation and no noticeable current. Usually it is found in lentic environments or the quiet pools and backwaters of low-gradient streams.

Zoogeography.—*Opsopoeodus emiliae* probably inhabited the preglacial Teays-Mississippi system. Redispersal into glaciated regions undoubtedly took place solely from a refugium in the lower Mississippi Valley.

Phoxinus erythrogaster (Rafinesque)—southern redbelly dace

Chrosomus erythrogaster: Agassiz, 1854:359 (Osage R.). Call, 1887:75 (West Fork Black R. and Toms Cr., Reynolds Co.; Sinking Cr., Spring Valley Cr., and Jacks Fork, Shannon Co.). Meek, 1891:117,121,124 (Meramec Spring and Big Dry Fork near St. James; Osage Fork SE of Marshfield; Big Piney R. near Cabool; Jones Cr. and Maries R. near Dixon; Niangua R. near Marshfield; Sac R. near Springfield; Bryants Cr. near Mansfield). Evermann and Kendall, 1895:470 (spring branch at Neosho). Fowler, 1921:398 (Fox Cr., trib. Meramec R.). Hubbs and Ortenburger, 1929:89 (two mi. S DeSoto). Martin and Campbell, 1953:46 (abund.; Black R.).

Distribution and habitat.—The southern redbelly dace is virtually restricted to the Ozarks, occurring elsewhere only in a few spring-fed creeks in Lincoln County (Map 34). Populations of the redbelly dace are found mainly in small streams where springs maintain permanent flow. Along the larger creeks and rivers of the Ozarks it occurs only as strays, or as highly localized populations in spring pools away from the main channel.

Zoogeography.—Isolated populations of *P. erythrogaster* in the Flint Hills of Kansas (Metcalf, 1966:102-103; Cross, 1967:82) may date from Pleistocene time, when cooler and moister conditions permitted westward dispersal from the Ozark Uplands. Disjunct populations in the upper Canadian River of northeastern New Mexico (Koster, 1957:59) may likewise be Pleistocene relicts. Perhaps *P. erythrogaster* has occupied the Ozark Uplands continuously since late-Tertiary times.

Nocomis biguttatus (Kirtland)—hornyhead chub

Hybopsis biguttatus: Jordan and Meek, 1885:12,16 (Hundred and Two R. at Maryville; Flat Cr. near Sedalia and/or Blackwater R. at Brownsville). Martin and Campbell, 1953:46 (abund.; Black R.). Patriarche and Campbell, 1958:255-256 (abund.; Clearwater Res.).

Hybopsis kentuckiensis: Meek, 1891:118,122,125,126,130 (Meramec R. and Big Dry Fork near St. James; Little Dry Fork near Rolla; "abundant in all streams examined," Gasconade and Osage systems; "common in all streams examined," Neosho system; James R. near Springfield; North Fork

White R. S Cabool). Evermann and Kendall, 1895:471 (Indian Cr. near Neosho).

Distribution and habitat.—The hornyhead chub occurs throughout the Ozarks, where it is one of the common and characteristic stream fishes (Map 35). However, it never attains the abundance of some of the other common minnows of the region. Scattered early records document a former rather widespread distribution for *N. biguttatus* in the Till Plains. These populations are now largely or entirely extirpated. Listing of the hornyhead chub from the Hundred and Two River in northwest Missouri by Jordan and Meek (1885:12) is far removed from any recent records, and this species has not been collected in northeastern Missouri since the early 1940's. Even in the Ozarks *N. biguttatus* seems to be less abundant and widespread. There are no recent records for the Bourbeuse system, for example, although that area has been quite thoroughly sampled. Similar but more dramatic changes in the distribution of the hornyhead chub have been noted in Ohio by Trautman (1957:294) and in Kansas by Metcalf (1966:105-106) and Cross (1967:87). Increased siltation and intermittent flow resulting from destruction of vegetative cover and intensive cultivation may be major factors in elimination of this chub from parts of Missouri.

The hornyhead chub inhabits clear streams with permanent flow and a predominance of clean gravel or rubble bottoms. Adults are most often found near riffles, but not in the swifter currents. The young frequently occur where there is no current, among growths of algae or higher aquatic plants.

Zoogeography.—The range of *N. biguttatus* is principally north and west of other *Nocomis*. Perhaps the ancestral stock of *N. biguttatus* occupied most of the preglacial upper Mississippi or Laurentian systems, with ancestral stocks of other *Nocomis* occupying the preglacial Ohio and Teays stream systems. Occurrence of the closely related *N. effusus* Lachner and Jenkins in the Cumberland, Greene, and lower Tennessee drainages indicate that *N. biguttatus* was not present in the preglacial Ohio River system. That *N. biguttatus* may have long occupied the Ozark Uplands is indicated by the occurrence there of an undescribed form (Lachner and Jenkins, 1967:558). Disjunct populations of *N. biguttatus* in Colorado and Wyoming may be glacial relicts.

Hybopsis storeriana (Kirtland)—silver chub

Hybopsis storerianus: Jordan and Meek, 1885:17 (Grand R. at Clinton and/or Tebo Cr. at Calhoun). Forbes and Richardson, 1920:map L (Missouri R. local.).

Hybopsis storeriana: Fisher, 1962:427 (Missouri R. local.). Cross, 1967:92 (Missouri R. local. mapped).

Distribution and habitat.—The silver chub is one of the common minnows in the Missouri and Mississippi rivers (Map 36). It also occurs in other large streams of the state but is seldom abundant. The paucity of recent records from the Grand and upper Osage rivers is probably due to inadequate sampling rather than to a recent restriction in distribution. *Hybopsis storeriana* is an inhabitant of large streams and occurs most abundantly in quiet pools and backwaters.

Zoogeography.—The present distribution of *H. storeriana* suggests that it was an inhabitant of the preglacial Teays-Mississippi system.

Hybopsis amblops (Rafinesque)—bigeye chub

Hybopsis amblops: Meek, 1891 (Big Dry Fork near St. James; Shoal Cr. and Hickory Cr. near Neosho; James R. near Springfield; North Fork White R. S Cabool). Evermann and Kendall, 1895:471 (Indian Cr. near Neosho). Hubbs and Ortenburger, 1929:66 (Sarcoxie). Martin and Campbell, 1953 (abund.; Black R.). Patriarche and Campbell, 1958:255-256 (abund.; Clearwater Res.).

Distribution and habitat.—The bigeye chub is confined to the Ozarks, where it occurs in all the principal stream systems except the Osage and Gasconade (Map 37). It is still common in the White, Current, and Black river systems, but seems to have declined in abundance in the Meramec and Neosho systems since the early 1940's. This suggests a pattern of extirpation like that reported by Trautman (1957:301-303) in Ohio. The bigeye chub is an inhabitant of clear streams having permanent flow and silt-free gravel or rubble bottoms. It often occurs near riffles, but not in the main current. Rather, it is found at the foot of the riffle, where the current slackens, or in quiet pools with no current.

Zoogeography.—Hybopsis amblops was probably an inhabitant of the preglacial Teays-Mississippi system. Its present distribution suggests that it may be a recent invader of the Ozark Uplands. The presence of closely related or conspecific forms in eastern Gulf coastal drainages suggests that this species and its ancestral stocks have long occupied uplands east of the Mississippi River.

Hybopsis dissimilis (Kirtland)—streamline chub

Hybopsis dissimilis: Martin and Campbell, 1953 (abund.; hab.; Black R.).
Hybopsis dissimilis harryi: Hubbs and Crowe, 1956:2-4,6 (orig. descr.; type local. White R., 3 mi. SE of Mano, Barry Co.).
Erimystax dissimilis: Patriarche and Campbell, 1958:255-256 (abund.; Clearwater Res.).

Distribution and habitat.—The streamline chub is confined to

the southern slope of the Ozark Uplands (Map 38). It is the most abundant chub in many of the larger streams of that region. This minnow inhabits moderately large, clear streams with continuous strong flow and clean gravelly or rocky bottoms. It is most often found just below riffles or in pools with a noticeable current. The distribution of this species complements that of the related gravel chub in Missouri; the two have been taken together only at a single locality on lower Current River. Trautman (1957:309) indicated that the two are competitive and tend to occupy different habitats where they occur together in Ohio. Possibly competition is responsible for the complementary distribution of the two species in Missouri.

Zoogeography.—Populations of the streamline chub in the Ozarks are broadly disjunct from those east of the Mississippi Embayment. Possibly disjunction resulted from fragmentation of a continuous preglacial distribution, but could also indicate a Pleistocene invasion of the Ozarks. The streamline chub may have had its origin south and east of the area occupied by ancestral stocks of the gravel chub. Perhaps stocks of *H. dissimilis* occupied the preglacial Teays and/or Ohio systems, at a time when *H. x-punctata* occupied the northern and western part of the Mississippi system, and stocks of the closely related *H. insignis* occupied the Tennessee system.

Hybopsis x-punctata Hubbs and Crowe—gravel chub

Hybopsis dissimilis: Meek, 1891:122 (Gasconade R. at Arlington; Little Piney Cr. at Newburg and/or Arlington).

Hybopsis x-punctata x-punctata: Hubbs and Crowe, 1956:2-4,7 (orig. descr.; type local. Gasconade R. at Starks Ford, 8 mi. S Richland, Pulaski Co.).

Distribution and habitat.—The gravel chub is rather common and generally distributed in the northern and western Ozarks (Map 39). It is otherwise known only from the Salt River system of northeastern Missouri, and from single localities on the lower Mississippi and lower Current rivers. Hubbs and Crowe (1956:7) recognized two subspecies of the gravel chub, and described the nominate subspecies from Missouri. They erronously listed the type locality as "Starks Fork of Gasconade River." Examination of field data sheets indicates that this should read "Gasconade River at Starks Ford."

The gravel chub inhabits clear to moderately turbid streams with permanent flow and well defined gravel riffles. In the Ozarks it tends to be most abundant in the downstream sections of the larger streams, where the gradient is less, and the water is warmer and less clear than in the headwaters. This minnow is most often found in slight to moderate current, over a silt-free gravel or rubble bottom.

Zoogeography.—The range of the gravel chub is primarily north and west of that of other members of the subgenus *Erimystax,* suggesting an origin in the pre-glacial lower Missouri, Iowa, or upper Mississippi systems. This species undoubtedly survived the Wisconsin ice advance in the Ozark Uplands, and perhaps also in the Driftless Area of Wisconsin.

Hybopsis aestivalis (Girard)—speckled chub

Hybopsis aestivalis: Fisher, 1962:427 (Missouri R. local.). Cleary, 1956: map 35 (Des Moines R. local.). Cross, 1967:96 (Missouri R. local. mapped).

Distribution and habitat.—The speckled chub is most abundant in the Missouri and Mississippi rivers, where it is one of the characteristic minnows (Map 40). It is also common in the main ditches of the lowlands and some of the larger prairie streams of the till plains. It seems to have only recently invaded the lowland ditches, since it did not occur in collections made there in the early 1940's.

Hybopsis aestivalis inhabits the main channels of large, low gradient streams. It is found over a sand or fine gravel bottom, often in a moderate to strong current.

Zoogeography.—Variation and zoogeography of the speckled chub were discussed at length by Metcalf (1966:108-110). The widespread distribution and strong regional differentiation of the speckled chub in the Mississippi River system and other Gulf coastal drainages indicate that it has long resided there. Several well marked forms are recognized, but until variation in this species has been thoroughly studied, it would be unwise to assign Missouri populations to one of these.

Hybopsis gracilis (Richardson)—flathead chub

Platygobio gracilis: Jordan and Meek, 1885:13 (Missouri R. at St. Joseph). Berner, 1951:9 (abund.; Missouri R.). Shoemaker, Pickering and Durham, 1951 (Mississippi R. at Cates, Lake Co., Tenn.).

Hybopsis gracilis gracilis: Olund and Cross, 1961 (char.; syn.; Missouri local. comp. and mapped). Cross, 1967:84 (Missouri R. local. mapped).

Hybopsis gracilis: Fisher, 1962:427 (Missouri R. local.).

Taxonomic considerations.—Olund and Cross (1961) found statistically significant differences in several meristic and proportional characters among populations of *H. gracilis.* They recognized a northern and eastern subspecies (*H. g. gracilis*) which characteristically inhabits large rivers, and a southern and western subspecies

(*H. g. gulonellus*) that characteristically inhabits small streams. Bailey and Allum (1962:44-45) suggested that the differences may be phenotypic, resulting from differing temperatures during development. They hypothesized that the big river form undergoes development at lower temperatures than the creek form, because the larger streams are fed by cooler water from mountain tributaries. This argument loses force when it is applied to the populations of *H. g. gracilis* in the lower Missouri and Mississippi rivers, which are not under the influence of cool mountain streams. I have recorded a temperature of 80°F in the lower Missouri River as early as mid-June. I therefore concur with Metcalf (1966:103-104) that the differences between the two forms have a genetic basis.

Distribution and habitat.—The flathead chub is one of the most abundant minnows in the Missouri and lower Mississippi rivers (Map 41). It does not ascend the Mississippi River above the mouth of the Missouri, and enters tributary streams only in the extreme northwestern part of the state. Possibly competition is an important factor limiting the distribution of the flathead chub, and its occurrence in the faunally depauperate streams of northwest Missouri reflects a release from competition. Olund and Cross (1961:341) noted the absence of this species from creeks in eastern Kansas and Missouri that appeared to have suitable habitat and suggested that the flathead chub was excluded from these creeks by competition from the creek chub. I subsequently found both species in Mill Creek and Rock Creek of northwestern Missouri, where they were taken in the same seine hauls.

This minnow is most abundant in the main channels of large silty rivers, where it lives in a strong current over a firm, sandy bottom. Where it enters tributary streams in Missouri it inhabits the pools of small creeks with little current and bottoms composed mostly of gravel or bedrock. These small creeks are turbid after heavy rains, but are clear during periods of little rainfall.

Variation and zoogeography.—To determine whether or not the flathead chubs from tributary streams of northwestern Missouri are the creek subspecies (*H. g. gulonellus*), counts of lateral line scales and pectoral rays were made on a sample from Mill Creek, Atchison County, and another from the Missouri River, Platte County (Table 4). Counts of lateral line scales did not differ in the two samples, but they were significantly lower than counts reported by Olund and Cross (1961:fig. 1) for *H. g. gracilis* from the Missouri River below the Platte River, Nebraska. Counts of

TABLE 4.—Frequency Distribution of Lateral Line Scale Counts and Pectoral Fin-ray Counts in Two Samples of *Hybopsis gracilis* from Missouri.

		Lateral line scales											
Locality	N	44	45	46	47	48	49	50	51	52	53	$\bar{X}$	S.D.
Mill Cr., Atchison Co.	30			6	5	7	3	4	4	1		48.3	1.79
Missouri R., Platte Co.	29	1	1	2	4	9	4	6	1		1	48.3	1.83

		Pectoral fin rays						
Locality	N	16	17	18	19	20	$\bar{X}$	S.D.
Mill Cr.. Atchison Co.	30	17	12	1			16.5	0.56
Missouri R., Platte Co.	29	4	17	7		1	17.2	0.82

pectoral rays differed slightly in the two samples from Missouri; the mean ray-count of Missouri River specimens was close to that reported by Olund and Cross (1961:fig. 1) for *H. g. gracilis* from the Missouri River below the Platte River, Nebraska, and the mean count for Mill Creek specimens was close to that reported by Olund and Cross for intergrades from the Republican River in Nebraska. The small size of the Mill Creek specimens (42.8-58.4 mm. standard length, mean 50.8 mm.) precluded a comparison of proportional measurements but the pectoral fins in the Mill Creek specimens are less falcate than those of specimens of comparable size from the Missouri River. Thus, specimens from Mill Creek are morphologically intermediate between the two subspecies. This is consistent with the report by Olund and Cross (1961:plate 21) of intergrades from other nearby tributary streams entering the Missouri River from Nebraska and Kansas. The low number of lateral line scales in specimens from the Missouri River in Missouri are suggestive of intergradation, but the ray count and shape of the pectoral fin indicate that the Missouri River population is closer to *H. g. gracilis* than is the Mill Creek population.

Metcalf (1966:104) suggested that *H. g. gracilis* had its origin in the ancestral north-flowing upper Missouri River, whereas *H. g. gulonellus* had its origin in the preglacial drainage of the central and southern plains. If this interpretation is correct, mixing of the two stocks and penetration of *H. g. gracilis* into Missouri resulted from drainage diversions during the Pleistocene. Partial segregation of the two forms evidently occurs in northwest Missouri, where the species inhabits creeks as well as the mainstream of the Missouri River.

Hybopsis gelida (Girard)—sturgeon chub

Hybopsis gelida: Fisher, 1962:427 (Missouri R. local.). Bailey and Allum, 1962:46 and fig. 4 (Missouri local. compiled and mapped). Cross, 1967:97 (Missouri R. local. mapped).

Distribution and habitat.—The sturgeon chub occurs only in the Missouri and lower Mississippi rivers (Map 42). Like several other fishes of the upper Missouri system, the sturgeon chub ascends neither the Ohio River nor the Mississippi River above the mouth of the Missouri. This chub inhabits the main channels of large silty rivers and occurs in swift current over a bottom of sand or fine gravel. According to Bailey and Allum (1962:46), the sturgeon chub is most often found over gravel, and this may account for its rarity in the lower Missouri River, where sand is the principal bottom type.

Zoogeography.—Metcalf (1966:11) suggested that *H. gelida* evolved in the preglacial Hudson Bay system, perhaps from the same stock that gave rise to *H. aestivalis* in the preglacial Mississippi River system. If this is correct, the presence of *H. gelida* in the Mississippi Valley dates from diversion of the upper Missouri into its present course during the Pleistocene.

Hybopsis meeki Jordan and Evermann—sicklefin chub

Hybopsis gelidus: (misident.) Jordan and Meek, 1885:13 (Missouri R. at St. Joseph).

Hybopsis meeki: Jordan and Evermann, 1896:317 (orig. descr.; type local. Missouri R. at St. Joseph). Fisher, 1962:427 (Missouri R. local.). Bailey and Allum, 1962:48 and fig. 5 (Missouri local. compiled and mapped). Cross, 1967:95 (Missouri R. local. mapped).

Distribution and habitat.—The distribution of the sicklefin chub in Missouri is similar to that of the sturgeon chub, but the sicklefin chub is decidedly more abundant (Map 43). The sicklefin chub seems to increase in abundance in the Missouri River towards its mouth. Its habitat in Missouri is not notably different than that of the sturgeon chub.

Zoogeography.—Metcalf (1966:107-108) suggested that *H. meeki* originated in the preglacial upper Missouri River system, possibly from the same stock that gave rise to *H. storeriana* in the Mississippi River system.

Phenacobius mirabilis (Girard)—suckermouth minnow

Sarcidium scopiferum: Cope, 1871:440-441 (orig. descr.; type local. Missouri R. near St. Joseph).

Phenacobius mirabilis: Jordan and Meek, 1885:12,14,16,17 (Hundred and Two R. at Maryville; Tabo Cr. 6 mi. E Lexington; Flat Cr. near Sedalia and/or Blackwater R. at Brownsville; Grand R. at Clinton and/or Tebo Cr. at Calhoun). Fisher, 1962:427 (Missouri R. local.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.). Cross, 1967:100 (Missouri R. local. mapped).

Phenacobius mirabilis scopifer: Call, 1887:80 (Bear Cr. at Columbia).

Distribution and habitat.—The suckermouth minnow is abundant and widespread in the prairie region and occurs occasionally in lowland ditches of the southeast (Map 44). It is rather common in the warmer and more turbid streams of the Ozark border, but avoids the clear streams of the central Ozarks. This minnow is found in streams of all sizes, but avoids those with intermittent flow or cold, clear water. It is tolerant of turbidity and siltation, as long as there is enough current to keep the riffle areas free of silt. The suckermouth minnow is strictly a riffle fish, and reaches its greatest abundance on the sluggish riffles of warm, moderately turbid streams with low gradient.

Zoogeography.—Metcalf (1966:111) suggested that *P. mirabilis* originated in the central and southern plains and gained access to the central Mississippi Valley when part of the plains drainage was diverted eastward. Eastward dispersal of this species into Ohio within historic time was documented by Trautman (1957:323-324). This range expansion is presumably correlated with increased siltation and turbidity of the streams as a result of the removal of vegetative cover and intensive cultivation.

Notropis atherinoides Rafinesque—emerald shiner

Alburnellus percobromus: Cope, 1871:440 (orig. descr.; type local. St. Joseph, Mo.).

Notropis dilectus: Jordan and Meek, 1885:16 (Grand R. and/or Tebo Cr. at Clinton).

Notropis atherinoides: Garman, 1890:142 (Mississippi R. near Quincy, Ill.). Forbes and Richardson, 1920:map XLIII (Mississippi R. local.). Patriarche, 1953:247 (Lake Wappapello). Cleary, 1956:map 41 (Des Moines R. local.). Fisher, 1962:427 (Missouri R. local.). Cross, 1967:102 (Missouri R. local. mapped).

Notropis rubrifrons: Fowler, 1910:290, plate 21, fig. 50 (in part.; char.; type of *Alburnellus percobromus* figured).

Notropis percobromus: Hubbs, 1945:16-17 (not the southern representative of *N. rubellus;* compar. with *N. atherinoides atherinoides*). Cross and Minckley, 1958:104 (char.; Missouri R., Atchison Co., Kansas).

Distribution and habitat.—The emerald shiner is the most abundant fish in the Missouri and Mississippi rivers and is common in large streams elsewhere in the state (Map 45). It penetrates the Ozarks only along a few of the largest streams. In Missouri, the emerald shiner lives primarily in the open waters of large, permament-flowing streams with moderate or low gradients. It is tolerant of a wide range of turbidities, bottom types, and current velocities. Elsewhere in its range the emerald shiner is often abundant in large lakes and reservoirs, but it is not especially abundant in such habitats in Missouri.

Taxonomic considerations.—Since its original description by Cope (1871:440) from specimens collected at St. Joseph, Missouri,

Alburnellus percobromus has had a complicated nomenclatural history. At various times it has been treated as a distinct species (*e.g.*, Jordan and Gilbert, 1883:202; Hubbs, 1945:16-17; Hubbs and Bonham, 1951:93), as a synonym of *N. rubifrons* (=*N. rubellus*) (*e.g.*, Jordan and Evermann, 1896:295; Fowler, 1910:290), and as the southwestern representative of *N. rubellus* (Hubbs and Ortenburger, 1929:83-85). In the most recent treatment of this form, Bailey and Allum (1962:56-60) placed it in the synonymy of *N. atherinoides*. They indicated that the supposed differences between *N. percobromus* and *N. atherinoides* vary locally and are not geographically consistent, and suggested that such differences as do exist represent phenotypic responses to varying environmental conditions. I follow Bailey and Allum in considering the two forms to be conspecific, but I doubt that there is no genetic basis for the differences.

Variation and zoogeography.—The emerald shiner exhibits considerable variability in body proportions both within collections from one locality and between localities. In Missouri there seems to be a character gradient from northwest to southeast; populations in the Missouri River and its tributaries of northwestern Missouri are more chubby than those from the lower Mississippi River and the Southeastern Lowlands.

Notropis atherinoides probably occurred in the preglacial Teays-Mississippi system, as well as in other ancient drainages. If there is a genetic basis for the *percobromus* phenotype, this form may have occupied the preglacial drainage of the central and southern plains (Metcalf, 1966:113-114).

Notropis rubellus (Agassiz)—rosyface shiner

Notropis rubrifrons: Meek, 1891:118,122,125,126,129 (Meramec R. and Big Dry Fork near St. James; Little Dry Fork near Rolla; Osage Fork SE Marshfield; Lick Fork and Bryants Cr. near Mansfield; Little Piney Cr. at Newburg and Arlington; Sac R. and James R. near Springfield; Shoal Cr. and Hickory Cr. near Neosho). Jordan and Meek, 1885:15 (Flat Cr. near Sedalia and/or Blackwater R. at Brownsville). Evermann and Kendall, 1895:470 (Indian Cr. near Neosho). Fowler, 1910:290 (in part.; char.; Carthage, Mo.).

Notropis dilectus: Fowler, 1910:290 (Greenfield, Mo).

Notropis percobromus: Hubbs and Ortenburger, 1929:83 (Sac R.).

Notropis rubellus: Martin and Campbell, 1953 (abund.; hab.; Black R.). Metcalf, 1966:table 10 (char.; Richland Cr., Morgan Co.).

Distribution and habitat.—The rosyface shiner is confined to the Ozarks, where it is one of the most abundant and generally distributed minnows (Map 46). The rosyface shiner is intolerant of continuous high turbidity or siltation, and is most abundant in streams

of medium size having well defined gravel or rubble riffles. It is generally found in a moderate to swift current, either just below riffles or in rocky pools where riffles and pools alternate in rapid succession.

Zoogeography.—Ozark populations of *N. rubellus* are disjunct from the main body of the range, which is north and east of Missouri. The distributional hiatus between Missouri populations and those in Illinois and Iowa is at least 100 miles wide at its narrowest point. That this species has long resided in the Ozark Uplands is suggested by the presence of marked regional differentiation in body form, number of fin rays and pigmentation. Possibly *N. rubellus* invaded the Ozark Uplands during the Pleistocene Epoch, but more likely it has occurred there continously since preglacial time.

Notropis telescopus (Cope)—telescope shiner

(?) *Notropis micropteryx:* Call, 1887:76 (Spring Valley Cr., Shannon Co.). Meek, 1891:129 (James R.).

Notropis ariommus: Martin and Campbell, 1953 (abund.; hab.; Black R.). Patriarche and Campbell, 1958:255-256 (abund.; Clearwater Res.).

Notropis telescopus: Gilbert, 1969:474-492, fig. 4 (syn.; char.; compar.; Missouri local. mapped).

Distribution and habitat.—The telescope shiner is one of the must abundant minnows in streams draining the southern slope of the Ozark Uplands (Map 47). It is most often found in medium-sized to moderately large streams, occurring only rarely in headwater creeks. The telescope shiner is usually found near riffles, where there is a moderately swift current, and a bottom composed of gravel, rubble, or boulders.

Gilbert (1969:485) has called attention to two specimens (UMMZ 187280) of a related species, *Notropis ariommus* Cope, that were presumably collected by S. E. Meek in 1889 from Big and Little Dry Forks, Phelps County, Missouri. Since Meek (1891) did not mention *N. ariommus*, and this species has not been otherwise collected in Missouri or elsewhere west of the Mississippi River, Gilbert doubted the validity of the record.

Variation and Zoogeography.—*N. telescopus* from different stream systems of the Ozarks exhibit differences in counts of anal fin rays. Specimens from the St. Francis River and Headwater Diversion have 9 and 10 anal rays in about equal numbers; only a few specimens have 11. Those from the Black and White river systems have modally 10 anal rays and far more specimens have 11 rays than 9 rays.

Notropis telescopus is one of several species that occur dis-

junctly in the two main uplands of the southcentral United States east and west of the Mississippi Embayment. Possibly *N. telescopus* evolved in the Ozark Uplands from the common ancestral stock that gave rise to *N. ariommus* east of the Mississippi Embayment. At some time during the Pleistocene, *N. telescopus* may have moved across the embayment, replacing *N. ariommus* in part of its preglacial range.

Notropis umbratilis (Girard)—redfin shiner

Notropis umbratilis: Jordan and Meek, 1885:11,15,17 (Hundred and Two R. at Maryville; Flat Cr. near Sedalia and/or Blackwater R. at Brownsville; Grand R. at Clinton and/or Tebo Cr. at Calhoun). Call, 1887:76 (Spring Valley Cr.. Shannon Co.). Meek, 1891:125 (Maries R. near Dixon; Sac R. near Springfield). Fowler, 1910:291-292 (Marshfield and Sedalia). Martin and Campbell, 1953 (abund.; hab.; Black R.). Fisher, 1962:427 (Missouri R. tribs.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.).

Notropis umbratilis cyanocephalis: Meek, 1891:118,121 (Big Dry Fork near St. James; Little Dry Fork near Rolla; Osage Fork SE Marshfield; Lick Fork at Mansfield).

Distribution and habitat.—The redfin shiner is nearly statewide in distribution, but it is absent from the White River system of the southern Ozarks, and is scarce in the northwestern till plains (Map 48). It is most abundant in streams of the northern and western Ozark border. *Notropis umbratilis* is common in ditches of the lowlands and adjacent streams of the southeastern Ozarks.

The redfin shiner occurs in a variety of habitats. In the prairie region it occurs most abundantly in rocky or gravelly creeks with high gradient and low or intermittent flow. In the lowlands *N. umbratilis* occurs in quiet ditches with an abundance of submerged aquatic vegetation. Along the cool, spring-fed streams of the Ozarks it is almost invariably found in protected backwaters and overflow pools that are several degrees warmer than the main stream. The common denominators of all these habitats are relatively clear, warm water and the absence of strong current.

Variaton and zoogeography.—Notropis umbratilis, as currently recognized, is an extremely variable species, and probably consists of a complex of recognizable subspecies, or perhaps of two or more species. Some workers recognize two subspecies, referring populations from the Ohio, Great Lakes and Mississippi systems to *N. u. cyanocephalus* (Copeland), and referring populations from the lower Mississippi and western Gulf coastal drainages to *N. u. umbratilis* (Girard).

At least two well marked forms occur in Missouri. Populations in the Missouri River system have modally 10 anal rays and have

the dark spot at the anterior base of the dorsal fin weakly developed. Breeding males of this form have tubercles over the operculum and predominantly black fins. An isolated population of this form occurs in the Salt River drainage of northeastern Missouri, and a similar form but with modally 11 anal rays occurs in the Neosho River system of southwestern Missouri. In all direct tributaries of the Mississippi River, except for Salt River, in the Southeastern Lowlands, and in streams draining the southeastern slope of the Ozark Uplands, *N. umbratilis* is represented by a form having modally 11 anal rays and a prominent black spot at the anterior base of the dorsal fin. Breeding males in this form lack tubercles on the operculum and have predominantly red fins. All Missouri populations are assignable to one form or the other, but those from Salt River and adjacent tributaries of the upper Mississippi River show evidence of intergradation or introgression. The distributional relationship of the two suggests an origin for the red-finned form in the preglacial Teays-Mississippi system and an origin for the black-finned form in the preglacial drainage of the central and southern plains. Differences between populations of the black-finned form in the Missouri and Arkansas systems suggest a rather long separation.

Notropis fumeus Evermann—ribbon shiner

Distribution and habitat.—The ribbon shiner is common in the lowlands (Map 49), where it is confined primarily to open water of the larger, swifter, and more sparsely vegetated ditches. It generally occurs over a sandy bottom in a slight to moderate current.

Zoogeography.—The ribbon shiner is southern in its affinities, reaching the northern limit of its range in southeastern Missouri and southern Illinois. It may have occupied the lower Mississippi Valley continuously since preglacial times, or entered the Mississippi Valley from western Gulf coastal drainages at a more recent date.

Notropis shumardi (Girard)—silverband shiner

Notropis illecebrosus: Cross and Minckley, 1958:104-105 (descr.; ecol.; Missouri R., Atchison Co., Kans.). Fisher, 1962:427 (Missouri R. at St. Charles). Bailey and Allum, 1962:61 (Missouri local. compiled).

Notropis shumardi: Gilbert and Bailey, 1962 (char.; syn.; Missouri local. compiled and mapped). Cross, 1967:107 (Missouri R. local. mapped).

Distribution and habitat.—The silverband shiner is a characteristic element in the fauna of the Missouri and Mississippi rivers, penetrating only rarely into the lower sections of tributaries (Map 50). In the Mississippi it has never been collected above Pike

County. The silverband shiner is fairly common in the lower Mississippi River, but it is rare elsewhere in its Missouri range. *Notropis shumardi* inhabits the open channels of large rivers, where there is strong current and a firm sand or gravel bottom.

Zoogeography.—Probably *N. shumardi* had its origin in the Mississippi Valley (Gilbert and Bailey, 1962:817). These authors suggested that *N. shumardi* gained access to the Alabama River through stream connections created by lowering of sea levels during the Pleistocene, and may have reached western Gulf coastal drainages in the same manner or as a result of stream transfer between the upper Red and Brazos rivers.

Notropis zonatus (Agassiz)—bleeding shiner

Alburnus zonatus: Agassiz *in* Putnam, 1863:9 (orig. descr.; type local. Osage River).

Notropis zonatus: Call, 1887:76 (West Fork Black R., Reynolds Co.; Jacks Fork, Shannon Co.; Piney R., Texas Co.; Meramec R., Dent Co.). Meek, 1891:118,121,125 (Meramec R. and Meramec Spring near St. James; Big Piney R. at Cabool; Little Piney Cr. at Newburg and Arlington; Gasconade R. at Arlington; Lick Fork at Mansfield; Osage Fork SE Marshfield; Jones Cr. and Maries R. near Dixon; Niangua R. near Marshfield; Sac R. near Springfield). Fowler, 1921:399 (Fox Cr., trib. Meramec R.). Hubbs and Ortenburger, 1929:81 (Big R. trib. 4 mi. S Potosi). Patriarche and Campbell, 1958:255-256 (Clearwater Res.). Gilbert, 1964:95-121, 129-133, map 2 (char.; compar.; syn.; Missouri local. mapped).

Notropis zonatus zonatus: Hubbs and Moore, 1940 (char.; compar.; syn.; Missouri local. mapped). Martin and Campbell, 1953 (abund.; hab.; Black R.).

Distribution and habitat.—The bleeding shiner is endemic to the Ozark Uplands of Missouri and northeastern Arkansas (Map 51). In Missouri it occurs in all major drainages not occupied by the closely related duskystripe shiner. Within its area of occurrence *N. zonatus* is one of the most abundant minnows. The bleeding shiner inhabits clear, small to medium-sized streams with continuous strong flow and clean gravel or rubble bottoms. It avoids sections of the Ozarks that are underlain by shale bedrock, probably because of increased turbidity and intermittency of the streams. *Notropis zonatus* is most often found in a moderate to swift current near riffles, or in small pools where riffles and pools alternate in rapid succession. The young tend to occupy quieter water than the adults.

Zoogeography.—Gilbert (1964:104-105) suggested that the common *zonatus-pilsbryi* stock became isolated in the Ozark Uplands during the Pliocene. He further indicated that the present distribution of the two species suggests a long separation between the Missouri and White river systems and that the presence of *N. zonatus* in the Black River system indicates that this stream

was formerly a tributary of the Missouri. According to Gilbert, the Black River underwent a reversal of flow at a recent date, after *N. zonatus* and *N. pilsbryi* had differentiated. I doubt this explanation. There is no geological evidence to indicate that the Black River was ever a tributary of the Missouri River, and the distribution of *N. zonatus* can be accounted for without such a hypothesis. This species has a continuous distribution from the Missouri to the Black by way of the St. Francis and Little rivers and direct tributaries of the Mississippi River, and there is no reason to believe that this has not long been the case. All of the major streams of the southeastern Ozarks were direct tributaries of the Mississippi River at the time the latter stream flowed west of Crowley's Ridge; thus, there was ample opportunity for waif dispersal westward to the Black River through the Mississippi River. Before drainage of the northern and central plains was diverted to the lower Missouri River, it and the Mississippi River may have been less of a barrier to dispersal by upland species such as *N. zonatus* than now.

Notropis pilsbryi Fowler—duskystripe shiner

Notropis zonatus: Meek, 1891:126-129 (Shoal Cr. and Hickory Cr. near Neosho; James R. near Springfield; Bryants Cr. near Mansfield; North Fork White R. S Cabool). Evermann and Kendall, 1895:470 (Indian Cr. S Neosho; spring branch at Neosho). Fowler, 1910:285-286 (Marshfield?; Carthage; and James R.). Hubbs and Ortenburger, 1929:81 (Sarcoxie).

Notropis zonatus pilsbryi: Hubbs and Moore, 1940 (char.; compar.; syn.; Missouri local. mapped).

Notropis pilsbryi: Gilbert, 1964:95-121,133-136, map 2 (char.; compar.; syn.; Missouri local. mapped).

Distribution and habitat.—The duskystripe shiner replaces the closely related bleeding shiner in the Neosho and upper White river systems of the southwestern Ozarks (Map 52). In that region it is one of the most abundant fishes in small and medium-sized streams. Its habitat is like that of the bleeding shiner.

Zoogeography.—*N. pilsbryi* probably originated in clear upland streams of the Flint Hills and western slope of the Ozark-Ouachita uplands. It likely attained its present distribution in the White River system by stream capture between the upper White and Neosho systems (Hubbs and Moore, 1940:94). The argument for a western origin of this species is strengthened by the occurrence of disjunct populations in the Red River system, which presumably had connections with the preglacial upper Arkansas River. Hubbs and Moore (1940:94) suggested that presence of the duskystripe shiner in the Red River system was perhaps due to "an accidental

transfer, either by data or of the living fish" because of the isolated position of the records. However, occurrence at three localities suggests natural distribution (Gilbert, 1964:135).

Notropis cornutus (Mitchell)—common shiner

Notropis megalops: Jordan and Meek, 1885:12,15 (Hundred and Two R. at Maryville; Flat Cr. near Sedalia and/or Blackwater R. at Brownsville).

Notropis cornutus: Gilbert, 1961 (char.; compar.; Missouri local. mapped). Fisher, 1962:427 (Moniteau Cr. near Rocheport). Hanson and Campbell, 1963 (linear distr.; Perche Cr.). Gilbert, 1964:95-121,140-151 (char.; compar.; syn.; Missouri local. mapped). Cross, 1967:113 (Missouri R. local mapped).

Distribution and habitat.—The present center of abundance for the common shiner is in short, direct tributaries of the Missouri River in central and west-central Missouri with isolated populations in a few tributaries of the upper Chariton River (Map 53). An early report for the Hundred and Two River near Maryville (Jordan and Meek, 1885:12) suggests a former more widespread distribution in northwestern Missouri. The common shiner is one of the most abundant minnows in the creeks of central Missouri, and seems not to have suffered any further restriction in distribution since the early 1940's. It inhabits small, moderately clear streams having high gradients and a predominance of gravel, rubble and bedrock pools. These streams lack permanent strong flow and are frequently reduced to a series of isolated pools by late summer and early autumn.

Taxonomic considerations and zoogeography.—The taxonomic and distributional relationships of *N. cornutus* and *N. chrysocephalus* are complex. Over much of their extensive ranges they are allopatric, but they are broadly sympatric in the upper Ohio, Mississippi, and Great Lakes systems. There they exhibit all degrees of relationship. In places only one form occurs; in others they act as subspecies and at some localities they occur together and remain distinct. The two were long treated as subspecies, but Gilbert (1961) subjected them to a thorough analysis and considered them to be valid species. *Notropis cornutus* and *N. chrysocephalus* are allopatric in Missouri, although they occur in adjacent tributaries of the Missouri River in southern Warren County. Gilbert (1961: 189) suggested that the distributional relationship of these two species in Missouri indicates that they have come together at certain times since they invaded the area, and the present allopatric relationship is most likely due to competition. Missouri populations of *N. cornutus* and *N. chrysocephalus* exhibit no evidence of introgression or intergradation.

Gilbert (1964:106-107) favored an origin for *N. cornutus* in the pre-Pleistocene Laurentian system. If this hypothesis is correct, occurrence of *N. cornutus* in Missouri dates from one of the Pleistocene ice advances. This species, as well as many other northern species, may have invaded Missouri during more than one ice advance, only to be eliminated with the warming trend that occurred during the interglacial periods. The present populations of *N. cornutus* in Missouri may date no farther back than the Wisconsin glacial period.

Notropis chrysocephalus (Rafinesque)—striped shiner

Notropis megalops: Jordan and Meek, 1885:17 (Grand R. at Clinton and/or Tebo Cr. at Calhoun). Call, 1887:76 (West Fork Black R., Reynolds Co.; Jacks Fork, Shannon Co.; Piney R., Texas Co.; Meramec R., Dent Co.). Meek, 1891:117,121,126,129 (Big Piney R. at Cabool; Lick Fork at Mansfield; Shoal Cr. near Neosho; James R. near Springfield; Bryants Cr. near Mansfield; North Fork White R. S Cabool).

Notropis cornutus: Fowler, 1921:399 (Fox Cr., trib. Meramec R.). Patriarche and Campbell, 1958 (abund.; Clearwater Res.).

Notropis cornutus chrysocephalus: Martin and Campbell, 1953:46 (abund.; Black R.).

Notropis chrysocephalus chrysocephalus: Gilbert, 1961 (char.; compar.; Missouri local. mapped). Gilbert, 1964:95-121,157-166, map 5 (char.; compar.; syn.; Missouri local. mapped).

Distribution and habitat.—The striped shiner occurs over most of the Ozarks, and at scattered localities in the eastern till plains (Map 54). It is not uniformly abundant over its Missouri range, and in some streams it seems to have declined in the past 80 years. At present, it is one of the most abundant minnows in the eastern and southern Ozarks. It is now rare in the Gasconade system, although it was reported "common" by early collectors (Call, 1887: 76; Meek, 1891:121). No specimens have been taken in Big Piney River in spite of almost annual seining since 1950. In the Spring River drainage of southwestern Missouri it was reported as "very common" by Meek (1891:126), and it occurred in several collections made there in 1940 and 1941. However, only a single specimen occurred in numerous collections made in that stream system in 1964. A similar decline may have occurred in the Osage system. At present the striped shiner is confined to the southern part of the Osage system, but Jordan and Meek (1885:17) reported it from South Grand River many miles north of recent records. The reasons for decline of the striped shiner are not apparent. The present scarcity of this fish in the Gasconade system is particularly puzzling, because *N. chrysocephalus* remains abundant just across the divide in the Meramec system, where stream conditions seem to be similar.

In Missouri the striped shiner is most abundant in clear, permanent-flowing streams with clean gravel or rubble bottoms. It frequently occurs just below riffles in a slight to moderate current but is more often found in nearby backwaters or short, rocky pools with little or no current. Gilbert (1964:185) stated that *N. chrysocephalus* is more tolerant of warm, turbid conditions than *N. cornutus,* but the reverse relationship seems to exist in Missouri, where *N. cornutus* occupies the warmer, more turbid prairie streams, and *N. chrysocephalus* inhabits the cooler and clearer streams of the Ozark Uplands.

Zoogeography.—Gilbert (1964:106) suggested that *N. chrysocephalus* had its origin in the Mississippi system and was brought into contact with *N. cornutus* when the latter species gained access to the Mississippi system during the Pleistocene. If this explanation is correct, *N. chrysocephalus* or its progenitor long may have occupied the Ozark Uplands.

Notropis chalybaeus (Cope)—ironcolor shiner

Distribution and habitat.—The ironcolor shiner is known in Missouri only from the lowlands (Map 55). It is not widespread, but where it occurs it is usually abundant. Because it was formerly present in eastern Iowa (Harlan and Speaker, 1956:95), it may also have occurred along the Mississippi River in Missouri. It has not been taken in Iowa for more than 50 years. *Notropis chalybaeus* is found only in the clearest ditches, where there is little or no current and an abundance of submergent aquatic vegetation.

Zoogeography.—*Notropis chalybaeus* may have inhabited the Mississippi Valley in preglacial time or entered from the east by way of stream connectives formed with eastern Gulf coastal drainages during the Pleistocene. The broadly disjunct populations around the lower end of Lake Michigan indicate a more widespread northern distribution in the past; possibly these populations are southern relicts that date from the post-glacial Climatic Optimum. However, Gerking (1947) suggested that *N. chalybaeus* followed the Wisconsin ice sheet into northern Indiana and southwestern Michigan soon enough to take advantage of minor glacial connectives in its dispersal. If this interpretation is correct, *N. chalybaeus* may have achieved its present northern distribution before the Climatic Optimum. It is also possible that this disjunct range results from the extirpation of intervening populations within historic time.

Notropis texanus (Girard)—weed shiner

Distribution and habitat.—The weed shiner is widespread in the lowlands, and penetrates into adjacent sections of the Ozarks along the larger streams (Map 56). It is more widespread in the lowlands than the ironcolor shiner, but does not seem to attain as high a population density. Like *N. chalybaeus,* the weed shiner occurs northward in the Mississippi Basin to Iowa and southern Wisconsin (Suttkus and Raney, 1955:24) and should occur along the Mississippi River in northeastern Missouri. An old record for St. Louis suggests that formerly this may have been the case. Harlan and Speaker (1956:95) reported it from two localities on the Mississippi River in northeastern Iowa and predicted that it "probably occurs throughout the downstream slough areas of the Mississippi River." The weed shiner occurs most abundantly in large ditches and lowland rivers having noticeable current, a sandy bottom, and little or no aquatic vegetation. Therefore, it is separated ecologically from the ironcolor shiner.

Zoogeography.—The present distribution of *N. texanus* suggests that it inhabited the Teays-Mississippi system in preglacial time. This species and *N. chalybaeus* seem to have had a similar history of postglacial redispersal into the upper Mississippi Valley and southwestern Great Lakes Region; the northern disjunct populations of both are perhaps subject to the same explanation.

Notropis hudsonius (Clinton)—spottail shiner

Notropis hudsonius: Forbes and Richardson, 1920:141-143, map XXXVIII (abund.; Mississippi R. local.).

Distribution and habitat.—The spottail shiner is uncommon but generally distributed in the Mississippi River above the mouth of the Missouri River (Map 57). In the lower Mississippi it is known only from a few scattered localities. It is not known from the Missouri River system in Missouri but occurs farther upstream in the Missouri system of northwestern Iowa (Cleary, 1956:map 45), southwestern Minnesota (Underhill, 1957:map 16), and South Dakota (Bailey and Allum, 1962:62). *Notropis hudsonius* inhabits moderately clear waters, over a bottom of sand, gravel or rubble. It seldom occurs where there is a strong current. In Missouri it is strictly a fish of the larger rivers, but elsewhere it commonly occurs in lakes.

Zoogeography.—This northern species may have been localized in northern drainages in preglacial time, gaining access to the Mississippi Valley by way of connectives that developed during

the Pleistocene. Bailey and Allum (1962:123) indicated that *N. hudsonius* and a number of other species probably gained access to the upper Missouri system by way of headwater stream connections with the upper Mississippi. All species so considered by Bailey and Allum occur in the Missouri River system of South Dakota but have a restricted distribution elsewhere in the Missouri Basin.

Notropis blennius (Girard)—river shiner

Notropis jejunus: Forbes and Richardson, 1920:map XLII (Mississippi R. local.).

Notropis blennius: Cleary, 1956:298, map 46 (Des Moines R. local.). Fisher, 1962:427 (Missouri R. local). Metcalf, 1966:table 11 (char.; Missouri R., Platte Co.; Mississippi R., Grand Tower, Ill.). Cross, 1967:117 (Missouri R. local. mapped).

Distribution and habitat.—The river shiner is widespread in the Missouri and Mississippi rivers, but it occurs only occasionally in tributary streams (Map 58). In the Mississippi River, it is exceeded in abundance only by the emerald shiner. In the Missouri River it is common from the northern border of the state downstream to Lexington but is known from only one collection between Lexington and the river mouth. In a series of collections I made in 1963, this species occurred abundantly in a collection made near the mouth of the Missouri River but was not taken again below Lexington, 322 river miles upstream. From Lexington upstream to the state line it occurred in every collection, making up 6 per cent by number of all fishes in drag seine hauls. That this distribution pattern has persisted for 20 years or more is indicated by the fact that Fisher (1962:table 1) reported the river shiner from only two Missouri River collections, both above Kansas City. I can think of no plausible explanation for this unusual distribution. *Notropis blennius* inhabits the main channels of large rivers. It avoids strong currents and occurs over all types of bottom. It is tolerant of continuous high turbidity but reaches its greatest abundance in moderately clear waters.

Variation and zoogeography.—Hubbs and Bonham (1951:103-107) tentatively recognized two subspecies of *N. blennius.* They reported the nominate subspecies from the Arkansas (except for the Neosho and Illinois drainages) and Red River systems in Oklahoma and from the Arkansas and Missouri systems in Kansas. The wide-ranging subspecies (*N. b. jejunus*) was reported to occupy most of the remainder of the range, with populations from Nebraska being intermediate, in some respects, between the two subspecies. Metcalf (1966:120) reported intermediate specimens from the Kansas River system. I have not attempted a variational analysis of *N. blennius* in Missouri, but a superficial comparison of specimens from the Missouri River in northwestern Missouri with those from the Mississippi River suggests slight phenotypic differences.

Metcalf (1966:122) suggested that the "*N. b. blennius*" phenotype may have differentiated in the preglacial drainage of the central and southern plains and subsequently came into contact with eastern populations when these streams were deflected into the central Mississippi Valley.

Notropis greenei Hubbs and Ortenburger—wedgespot shiner

Notropis boops: Meek, 1891:121 (char.; Gasconade R. and Little Piney Cr. near Arlington; Jones Cr. near Dixon).

Notropis greenei: Hubbs and Ortenburger, 1929:78-81 (orig. descr.; paratypes from trib. of Big R., 6 mi. S Potosi). Martin and Campbell, 1953 (abund.; hab.; Black R.). Patriarche and Campbell, 1958:255-256 (abund.; Clearwater Res.).

Distribution and habitat.—The wedgespot shiner is confined to the Ozarks and reaches its greatest abundance in the Gasconade and Meramec systems (Map 59). It is common in most streams of the southern Ozarks but is not known from Eleven Point River. It is rare and highly localized in distribution in the Neosho and Osage systems. The reference by Meek (1891:121) to the wedge-shaped spot at the base of the caudal, the smaller eye, and more posterior position of the dorsal fin in his specimens of "*Notropis boops*" from the Gasconade system, compared with specimens from the Meramec system, strongly suggests that he had this species. *Notropis greenei* is most abundant in clear streams with permanent strong flow and gravelly or rocky bottoms. It never occurs in small headwater streams. The wedgespot shiner is usually found near riffles in a slight to moderate current, where the bottom is mostly sand and fine gravel.

Zoogeography.—The wedgespot shiner is endemic to, and may have evolved in, the Ozark Uplands. Unlike some other Ozark endemics, it seems to have no near-relatives in uplands east of the Mississippi River.

Notropis boops Gilbert—bigeye shiner

Notropis scabriceps: Call, 1887:76 (West Fork Black R. and Barren Fork, Reynolds Co.; Jacks Fork and Spring Valley Cr., Shannon Co.).

Notropis boops: Meek, 1891:117 (Meramec R. and Big Dry Fork near St. James; Little Dry Fork near Rolla). Martin and Campbell, 1953 (abund.; hab.; Black R.). Patriarche and Campbell, 1958:255-256 (abund.; Clearwater Res.).

Notropis illecebrosus: Evermann and Kendall, 1895:470 (spring branch at Neosho).

Notropis shumardi: Evermann and Kendall, 1895:470 (Indian Cr. near Neosho).

Distribution and habitat.—The bigeye shiner is present in most parts of the Ozarks and northeastern Ozark border (Map 60). It is one of the most abundant minnows in the Meramec and Neosho systems. The most unusual feature of its distribution is its absence from the Osage system and extreme rarity in the Gasconade system. Both of these streams appear to contain an abundance of habitat of the type occupied by *N. boops* elsewhere. In this respect, the distribution of the bigeye shiner is like that of the striped shiner, a species with which the bigeye shiner is commonly associated. *Notropis boops* is characteristic of quiet pools having clear, warm water, a firm bottom that is relatively free of silt, and much aquatic vegetation. Such habitat is abundant in small creeks draining undissected uplands of the central Ozarks. These streams have not cut down into the rock strata from which the major springs of the Ozarks originate; hence they tend to be warmer and more intermittent than deeply incised Ozark streams. Along larger and cooler streams, the bigeye shiner invariably is found in quiet backwaters and overflow pools that are several degrees warmer than the main stream.

Zoogeography.—*Notropis boops* was probably present in the preglacial Teays-Mississippi system; it may have long inhabited the Ozark Uplands.

Notropis dorsalis (Agassiz)—bigmouth shiner

(?) *Notropis gilberti:* Jordan and Meek, 1885:16 (Grand R. at Clinton and/or Tebo Cr. at Calhoun).

Notropis dorsalis: Cleary, 1956:map 47 (Des Moines R. local.). Fisher, 1962: 427 (Missouri R. local.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.). Cross, 1967:130 (Missouri R. local. mapped).

Distribution and habitat.—The bigmouth shiner is widespread and abundant in the till plains (Map 61). It is the only Missouri fish with a distribution that seems to be correlated with the glacial border. Except for one doubtful early report for the South Grand River near Clinton (Jordan and Meek, 1885:16), *N. dorsalis* has never been taken more than a few miles south of the Missouri River, which approximates the southern limit of glaciation in Missouri. Failure of early collectors to report the bigmouth shiner from Missouri (except as noted above), and its absence from collections made in northwestern Missouri in the early 1940's, suggests that this species is expanding its range in Missouri. The bigmouth shiner occurs most abundantly in small streams with permanent flow and unstable sandy bottoms. It is usually found in open, shallow channels having slight current. It is rare or absent in larger streams, where it is replaced by the sand shiner. Extensive channelization of prairie streams in the till plains since the turn of the century created conditions favorable to the bigmouth shiner.

Zoogeography.—Western populations of *N. dorsalis* are sometimes referred to a distinct subspecies (*N. d. piptolepis*), which differs from the wide-ranging eastern subspecies (*N. d. dorsalis*) primarily in having the nape naked or with minute and embedded scales. All Missouri specimens have the nape well scaled; thus they are referable to the nominate subspecies. This pattern of variation suggests that *N. dorsalis* was separated into eastern and western populations at some time in the past. Perhaps ancestral stocks of *N. d. piptolepis* survived the last glacial period in the unglaciated western tributaries of the Missouri River, while ancestral stocks of *N. d. dorsalis* survived not far south of the glacial front in the central or eastern part of the Mississippi system. Trautman (1957: 376) attributed disjunct eastern populations of *N. dorsalis* to range adjustments during and subsequent to the Xerothermic Interval.

Notropis amnis Hubbs and Greene—pallid shiner

Notropis amnis: Hubbs and Greene *in* Hubbs, 1951 (orig. descr.; hab.; Missouri local. mapped).

Distribution and habitat.—As recently as 1941 the pallid shiner occurred at many localities in eastern Missouri (Map 62). Its main areas of occurrence were streams and ditches of the lowlands, and the Salt and Meramec stream systems. Recent efforts to collect *N. amnis* in these areas have not been successful, indicating a marked decline in abundance or complete extirpation from Missouri. The pallid shiner inhabits streams of medium to large size. It seems intolerant of siltation and turbidity, and it avoids strong currents. The reasons for its decline in Missouri are not known.

Zoogeography.—Probably *N. amnis* has inhabited the Mississippi Valley continuously since preglacial time. Hubbs (1951) recognized a southwestern subspecies (*N. a. pinnosus*) and a northern subspecies (*N. a. amnis*) with a broad zone of intergradation in the central Mississippi Valley. Perhaps ancestral stocks of *N. a. pinnosus* occupied the ancestral Red or other southwestern drainages, while those of *N. a. amnis* occupied the central and northern part of the Mississippi Valley. The presence of *N. a. pinnosus* in Gulf coastal streams of Texas provides further evidence for former connections between these streams and the Red River.

Such a connection was suggested by Gilbert and Bailey (1962:817) to explain a similar distribution pattern in *N. shumardi.*

Notropis whipplei (Girard)—steelcolor shiner

Notropis whipplii: Meek, 1891:117 (in part (?); Big Dry Fork near St. James). Gibbs, 1963:511-520 (syn.; char.; compar.; hab.; Missouri local. mapped).

Distribution and habitat.—The steelcolor shiner is common and widespread in the Meramec, Headwater Diversion, and St. Francis stream systems and occurs occasionally in the southern Ozarks as far west as the upper White River (Map 63). North of the Missouri River it occurs only in the Cuivre River system. The habitat requirements of this minnow are similar to those of the spotfin shiner; the two are often taken together in the eastern Ozarks. The steelcolor shiner seems less tolerant of high turbidity than the spotfin shiner, and avoids the Mississippi and Missouri rivers, where the spotfin shiner occurs in small numbers.

Zoogeography.—Gibbs (1963:525-526) suggested that the common ancestral stock of *N. whipplei* and *N. analostanus* (Girard) differed little from the present *N. whipplei* and had its center of dispersal in the Mississippi Valley. If this is the case, *N. whipplei* or its ancestral stock may have occupied the Ozark Uplands continuously since at least the late Tertiary.

Notropis spilopterus (Cope)—spotfin shiner

Notropis whipplei: Meek, 1891:117,121 (in part (?) Big Dry Fork near St. James; Gasconade R. near Arlington; Osage Fork 6 mi. SE Marshfield).

Notropis notatus: Call, 1887:76 (Piney R., Texas Co.).

Notropis whipplii: Fowler, 1910:282 (Carthage, Mo.).

Notropis spilopterus hypsisomatus: Gibbs, 1957b:195-198 (syn.; char.; compar.; Missouri local. mapped).

Distribution and habitat.—The spotfin shiner is common in the Gasconade and Meramec systems, and occurs in lesser numbers in the upper Mississippi River and in the Spring River system of southwestern Missouri (Map 64). Strays occur in the lower Missouri River, and in the lower Mississippi River as far south as Cape Girardeau County. *Notropis spilopterus* inhabits moderately clear, permanent-flowing streams ranging in size from small creeks to large rivers. It is most often found near riffles over a clean gravel or rubble bottom.

Zoogeography.—Gibbs (1957b) recognized two subspecies within the rather broad range of this species. The subspecies to which Missouri populations are assigned (*N. s. hypsisomatus* Gibbs) occupies tributaries of the Mississippi River north of the Ohio River, with disjunct populations in the upper Arkansas system. Gibbs (1957b:204) suggested that subspecific differentiation was initiated when the Nebraskan or Kansan ice sheet split the range into western and eastern segments and that the Ozark region was the most likely center of origin for the western subspecies. He further suggested that disjunct populations in the Arkansas are the result of stream capture from the Osage or White river systems. *Notropis spilopterus* is found in neither of the latter two stream systems today, so this explanation assumes a former more widespread distribution in the Ozark Uplands. I can think of no plausible reason for the persistence of *N. spilopterus* in the upper Arkansas system, if it was eliminated from the White and Osage systems. Perhaps *N. spilopterus* was never present in the Osage or White river systems, but instead dispersed into the upper Arkansas by way of the lower Mississippi and lower Arkansas rivers. The Wisconsin glacial period, with the consequent southward displacement of northern species and initiation of an erosional cycle in the Mississippi Embayment, would have provided an opportunity for such dispersal. Climatic changes and alluviation subsequent to retreat of the Wisconsin ice sheet would have favored the related species *N. venustus* in the lower Mississippi Valley, permitting it to replace its northern counterpart in that area.

Notropis venustus (Girard)—blacktail shiner

(?) *Notropis notatus:* Call, 1887:76 (very abund.; West Fork Black R. and Toms Cr., Reynolds Co.; Jacks Fork, Spring Valley Cr., Barren Cr., and Sinking Cr., Shannon Co.).

Notropis venustus: Patriarche, 1953:247 (Lake Wappapello).

Notropis venustus venustus: Gibbs, 1957a:175-189 (syn.; char.; compar.; hab.; Missouri local. mapped).

Distribution and habitat.—The blacktail shiner is the most abundant minnow in the lowlands and penetrates for considerable distances into the Ozarks along the larger streams (Map 65). In Ozark streams it is much less abundant than the closely related whitetail and steelcolor shiners. *Notropis venustus* occupies a variety of habitats but shows a decided preference for flowing waters. It is most abundant in the large, sparsely vegetated lowland ditches, where there is a strong current and a firm sand or gravel bottom.

Zoogeography.—This species is most closely allied to *N. spilopterus,* and the distributional relationship of the two suggests an origin for *N. venustus* in Gulf coastal drainages (Gibbs, 1957a: 195-200).

Notropis galacturus (Cope)—whitetail shiner

Notropis galacturus: Call, 1887:76 (Jacks Fork and Spring Valley Cr., Shannon Co.). Meek, 1891:129 (James R. near Springfield). Martin and Campbell, 1953 (abund.; hab.; Black R.). Patriarche and Campbell, 1958: 255-256 (abund.; Clearwater Res.). Gibbs, 1961:338-343 (syn.; char.; compar.; hab.; Missouri local. mapped).

Distribution and habitat.—The whitetail shiner is one of the most abundant minnows in streams draining the southern slope of the Ozarks (Map 66). *Notropis galacturus* inhabits the swifter sections of clear, high-gradient streams with permanent strong flow and firm, silt-free bottoms. It avoids small headwater creeks.

Zoogeography.—Notropis galacturus occurs disjunctly in the Ozark and Appalachian uplands. A report of this species from Wyatt, Missouri, about halfway between the eastern and western segments of the range (Gibbs, 1961:342), seems to be based on faulty locality data. Gibbs subsequently informed me that the jar containing this collection (USNM 63029) bears an external label and a catalog entry reading "Wyatt, Mo.," but the label in the jar reads "Wyatt Cr., Wyatt, Ark." According to Gibbs, the letters interpreted as "W" on the pencil label in the jar could as well be interpreted as "M," and the locality becomes "Myatt Cr., Myatt, Ark." in the White River system, well within the known range of *N. galacturus.* Gibbs (1961:351) suggested that *N. galacturus* differentiated in the Tennessee system, and then dispersed westward into the Ozarks, probably during one of the glacial periods of the Pleistocene.

Notropis camurus (Jordan and Meek)—bluntface shiner

Notropis galacturus: Meek, 1891:126 (Shoal Cr. near Neosho).
Notropis camurus: Gibbs, 1961:343-351 (syn.; char.; compar.; hab.; Missouri local. mapped).

Distribution and habitat.—The bluntface shiner is confined to the Neosho system on the southwestern slope of the Ozark Uplands (Map 67). It has been reported from the upper White River system (Gibbs, 1961:350), but this report is probably based on faulty locality data. The collection was made by personnel of the Missouri Department of Conservation in 1942. An examination of the field sheet for this collection reveals that the locality was originally recorded as "Shoal Creek-White R. near Protem, Taney Co., near Ark. state line." It was later changed to read "Shoal Cr.-(Spring R. watershed) near Kansas state line." Also included in this collection was *N. lutrensis,* a fish known in Missouri from the Spring River but not from the White River. *Notropis camurus* inhabits moderately clear, permanent-flowing streams with strong current and clean gravel or rubble bottoms. It is most often found near riffles in a moderate current.

Zoogeography.—According to Gibbs (1961:350), *N. camurus* was derived from a western stock of the same ancestral form that gave rise to *N. galacturus* in the Tennessee River system. Isolated populations in the lower Mississippi Valley indicate a former more widespread distribution in that region for *N. camurus.* Possibly this species was localized preglacially on the western slope of the Ozark-Ouachita uplands; probably it gained access to the lower Mississippi Valley when the lower Arkansas River breached the Ozark-Ouachita divide and captured upper Arkansas drainage. Perhaps *N. camurus* was then able to cross the lower Mississippi Embayment during one of the erosional cycles that accompanied glaciation, only to be isolated in eastern drainages during the subsequent period of alluviation.

Notropis lutrensis (Baird and Girard)—red shiner

Cyprinella Billingsiana: Cope, 1871:439 (orig. descr.; type local. Missouri R. at St. Joseph).
Moniana Jugalis: Cope, 1871:439-440 (orig. descr.; type local. Missouri R. at St. Joseph).
Notropis lutrensis: Meek, 1891:118,121,125,129 (Big Dry Fork near St. James; Little Piney Cr. near Arlington; Maries R. near Dixon; (?) James R. near Springfield). Jordan and Meek, 1885:11,14,15,17 (Hundred and Two R. at Maryville; Tabo Cr. 6 mi. E Lexington; Flat Cr. near Sedalia and/or Blackwater R. at Brownsville; Grand R. at Clinton and/or Tebo Cr. at Calhoun). Fowler, 1910:279-280, figs. 19 and 20 (syn.; char.; Clinton; Osage R.; Brownsville; Sedalia; Marshfield; Greenfield; types of *Cyprinella Billingsiana* and *Moniana Jugalis* figured). Forbes and Richardson, 1920: map XXXIX (Mississippi R. local.). Fisher, 1962:427 (Missouri R. local.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.). Cross, 1967:126 Missouri R. local. mapped).

Distribution and habitat.—The red shiner is the most abundant and widely distributed minnow in the prairie region (Map 68). It is common in most streams of the Ozark border and occurs occasionally in the lowlands. Its distribution largely complements that of its close relatives (whitetail, bluntface, spotfin, and steelcolor shiners), and competition from these species may be an important factor in controlling its distribution. In the Neosho system, for example, it is confined primarily to the warmer, more turbid North Fork of Spring River and the lower main stream of Spring River, leaving the cooler, clearer Ozark streams to the bluntface shiner. *Notropis lutrensis* scarcely enters lowland ditches, where the blacktail shiner is abundant, but penetrates the short tributaries of the Mississippi River immediately to the north, where no other species

of this group occurs. Along the northern Ozark border it is found throughout most of the Osage system, where no other species of the *Cyprinella* group occurs, but scarcely enters the Gasconade and Meramec systems, where *N. spilopterus* and *N. whipplei* are found.

Notropis lutrensis occurs in streams of all sizes, but it is most abundant in large creeks and rivers. It inhabits a variety of habitats, including quiet pools and backwaters as well as riffles. Although it sometimes thrives when introduced into impoundments, in natural waters it is abundant only in streams. The red shiner is tolerant of high turbidity and siltation but avoids waters that are continuously clear and cool.

Zoogeography.—Metcalf (1966:118-119) suggested a southwestern origin for *N. lutrensis,* because of its distribution and habitat preferences, and the presence of closely related forms in northeastern Mexico.

Notropis sabinae Jordan and Gilbert—Sabine shiner

Distribution and habitat.—The Sabine shiner has been collected in Missouri only from Black River where it descends into the lowlands (Map 69). In 1964, the Sabine shiner was found to be fairly common a few miles below Poplar Bluff, but only one specimen was contained in a collection made several miles farther upstream. None occurred in collections from Black River above and below these localities. Black River at the point where the Sabine shiner was collected is clear, narrow, and deep, with a bottom composed entirely of fine, silt-free sand. The Sabine shiner was taken over sand bars in slight to moderate current.

Zoogeography.—This southern species may have inhabited the lower Mississippi Valley in preglacial time or dispersed into the Mississippi from western Gulf coastal drainages during the Pleistocene. Disjunct populations in the White River system may indicate a more widespread northern distribution in the past, perhaps during the postglacial Climatic Optimum.

Notropis stramineus (Cope)—sand shiner

Hybopsis missuriensis: Cope, 1871:437-38 (orig. descr.; types from "near St. Joseph, Missouri.")

Notropis deliciosus: Jordan and Meek, 1885:11,13,14,15,16 (Hundred and Two R. at Maryville; Missouri R. at St. Joseph; Tabo Cr. 6 mi. E Lexington; Flat Cr. near Sedalia and/or Blackwater R. at Brownsville; Grand R. at Clinton and/or Tebo Cr. at Calhoun). Call, 1887:76 (Piney R., Texas Co., rare). Meek, 1891:124 (Sac R. near Springfield). Hanson and Campbell, 1963 (linear distr.; Perche Cr.).

Notropis deliciosus missouriensis: Call, 1887:80 (Bear Cr., Boone Co.).

Notropis stramineus: Fisher, 1962:426 (Missouri R. local.). Bailey and Allum, 1962:table 5 (var.; Missouri local.). Metcalf, 1966:table 12 (var.; Missouri local.). Cross, 1967:133 (Missouri R. local. mapped).

Distribution and habitat.—The sand shiner is widespread in the prairie region (Map 70). This species and the red shiner comprise the bulk of the minnows in many streams of the prairie region. The only real difference in the distribution of these two species in Missouri is the absence of the sand shiner from the Neosho system and its greater abundance and more widespread distribution in the Gasconade and Meramec systems. As its name implies, *N. stramineus* shows a strong affinity for sandy bottoms. It is tolerant of a wide range of turbidities and occurs in streams of all sizes. However, it is seldom abundant in the largest rivers, and it is replaced towards the headwaters of many streams by the bigmouth shiner, another minnow exhibiting an affinity for sandy bottoms. The sand shiner is most abundant in the shallow, sandy pools of moderately large creeks having permanent flow, moderately clear water, and low or moderate gradient.

Variation and zoogeography.—Bailey and Allum (1962:64) recognized two subspecies of the sand shiner in the northern plains, distinguishing them primarily on the basis of the number of circumferential scales. They reported the coarse-scaled *N. s. stramineus* from most of eastern South Dakota and northwestern Iowa, whereas the small-scaled *N. s. missuriensis* (Cope) occupies the remainder of the Missouri system as far downstream as the Niobrara River in Nebraska. They found little evidence of intergradation in South Dakota, but reported intergrades in southeastern Nebraska and northwestern Missouri. They also noted (p. 68) that the type locality for *Hybopsis missuriensis* near St. Joseph, Missouri, was within the zone of intergradation. Metcalf (1966: 124-131) extended this comparison to include most of Kansas and Missouri. He concluded that intergradation in the Kansas River system was "slight and mosaic in nature."

Since the Arkansas River system is occupied by *N. s. missuriensis* almost exclusively, Metcalf (1966:125) concluded that this subspecies had its origin in the central plains and utilized former connections between the Arkansas and Kansas systems in attaining its present distribution. Isolated populations of *N. s. stramineus* in the Missouri River system of eastern South Dakota have apparently resulted from westward dispersal by way of connections between the Missouri and the Minnesota and/or Des Moines rivers (Bailey and Allum, 1962:64).

Notropis topeka Gilbert—Topeka shiner

Notropis topeka: Jordan and Meek, 1885:11 (Hundred and Two R. at Maryville). Fisher, 1962:427 (Missouri R. tribs. near Hermann and Rocheport). Bailey and Allum, 1962:69-70 and fig. 6 (Missouri local. compiled and mapped). Hanson and Campbell, 1963 (linear distr.; Perche Cr.).

Distribution and habitat.—The main area of occurrence for the Topeka shiner is in small, direct tributaries of the Missouri River in central Missouri, with scattered populations northwestward in the prairie region (Map 71). An early report for the Hundred and Two River near Maryville (Jordan and Meek, 1885:11) indicates a possible former more widespread distribution in northwestern Missouri. The Topeka shiner is nowhere abundant, but is a characteristic element in the fish fauna of small streams in central Missouri. The Topeka shiner inhabits quiet pools of small, clear upland creeks, having bottoms composed mostly of sand, gravel, or rubble. These streams often cease to flow during dry seasons, but permanent pools are maintained by the movement of ground water through deep beds of sand and gravel. Increased siltation as a result of intensive cultivation may have reduced the abundance of the Topeka shiner in Missouri. At present this minnow is largely restricted to direct tributaries of the Missouri River that have sufficient gradient to prevent extensive deposition of silt.

Zoogeography.—Metcalf (1966:132-133) suggested an origin for *N. topeka* in the "Pleistocene south-draining stream of the Great Plains." I think it is more likely that this species had its origin in the western Mississippi Valley and that it achieved its present highly localized distribution in the Arkansas River system by way of connectives that existed between the Arkansas and Kansas river systems one or more times during the Pleistocene.

Notropis maculatus (Hay)—taillight shiner

Distribution and habitat.—The taillight shiner reaches the northern limits of its range in southeastern Missouri, where it has not been collected since 1941 (Map 72). Its habitat is the sluggish sections of lowland rivers and creeks.

Zoogeography.—Perhaps *N. maculatus* has inhabited the lower Mississippi Valley continuously since preglacial time. Alternatively, it may have entered the Mississippi Valley from eastern Gulf coastal drainages by way of stream connections that developed during the Pleistocene.

Notropis heterolepis Eigenmann and Eigenmann—blacknose shiner

Notropis cayuga: Meek, 1891:117,121,124 (char.; abund.; Meramec R. near St. James; Big Piney R. at Cabool; Osage Fork 6 mi. SE Marshfield; Lick Fork at Mansfield; Niangua R. near Marshfield).

Distribution and habitat.—The blacknose shiner is nowhere abundant in Missouri, where it is confined to the northern Ozarks and adjacent Ozark border (Map 73). Although the blacknose shiner was reported as "scarce in southern Missouri" by one early collector (Meek, 1891:121) it occurred with much greater frequency in collections then than it does today. Even some streams where *N. heterolepis* occurred in the early 1940's no longer seem to support populations. The few remaining populations in Missouri seem on the verge of extinction; if the present trend continues *N. heterolepis* will soon be eliminated from the state. The blacknose shiner is characteristic of quiet pools of small, clear prairie streams having bottoms composed mostly of muck and organic debris (often overlying sand or gravel), and moderate to large amounts of aquatic vegetation. A secondary area of occurrence is in the quiet, weedy backwaters of large Ozark streams. Continuous turbidity and the covering of organic sediments by inorganic silt seem to be especially unfavorable to this species, and may be the most important factors in its declining abundance. The largest remaining populations are in streams of the Ozark border that drain level uplands underlain by thin, rocky soils. These soils are not conducive to intensive cultivation, and large areas of native grasses that retard siltation are being maintained for hay production and pasture.

Zoogeography.—Perhaps this northern species was localized preglacially in the Laurentian or other northern drainages, and entered the Mississippi Valley by way of glacial connectives. Occurrence in the upper Arkansas system (Cross, 1967:142) may have resulted from southwestward dispersal by way of Pleistocene connections between the Kansas and Arkansas systems.

Notropis ozarcanus Meek—Ozark shiner

Notropis ozarcanus: Meek, 1891:129 (orig. descr.; type local. North Fork White R. S Cabool). Martin and Campbell, 1953 (abund.; hab.; Black R.).

Distribution and habitat.—The Ozark shiner is endemic to the southern Ozark Uplands (Map 74). It is common in Current River and North Fork of White River; elsewhere it seems to be rather rare. It was formerly abundant in the section of White River

now inundated by Bull Shoals and Table Rock reservoirs. The Ozark shiner inhabits large, clear streams having high gradients and permanent strong flow. It occurs most abundantly near riffles in a slight to moderate current, over a firm, silt-free bottom.

Zoogeography.—Notropis ozarcanus is represented in the Tennessee system by the related mirror shiner, *N. spectrunculus* (Cope). Perhaps their common ancestral stock had a continuous preglacial distribution, and became localized in the two uplands during an early ice advance of the Pleistocene. Alternatively, east-west dispersal of the common stock may have occurred during the Pleistocene, by way of the lower Ohio and Mississippi rivers.

Notropis volucellus (Cope)—mimic shiner

Notropis volucellus wickliffi: Trautman, 1931 (orig. descr.; hab.; St. Louis, Missouri).

Distribution and habitat.—Three well-marked forms of the mimic shiner occur in Missouri (Map 75). One of these, *N. v. wickliffi* Trautman, is confined to the Missouri and Mississippi rivers and the lower few miles of their major tributaries. Another, *N. v. volucellus* (Cope), occurs abundantly in the larger lowland ditches, in major Ozark streams draining into the lowlands, and in the Osage and Meramec systems of east-central Missouri. The two are usually isolated ecologically; *N. v. volucellus* inhabits clear streams ranging in size from medium-sized creeks to rather large rivers, and *N. v. wickliffi* inhabits the main channels of very large, moderately clear to highly turbid rivers. The zone of intergradation between the two is exceedingly narrow and is limited to the lower reaches of larger tributaries of the Missouri and Mississippi rivers. A third form has no available name and occurs in the Neosho system of southwestern Missouri. This is the "unnamed creek subspecies" referred to by Hubbs and Bonham (1951:103). As indicated by these authors, it differs from typical *N. volucellus* in the only moderate elevation of the lateral line scales, the large eye, the high dorsal fin, the chubby body, and the smaller size.

Zoogeography.—Until a thorough study has been made, conclusions concerning the distributional history of this complex must be tentative. The distributional relationship of the unnamed southwestern subspecies and *N. v. volucellus* suggests that the former had its origin in streams draining the southern plains, at a time when *N. v. volucellus* was localized in the preglacial Teays-Mississippi or Laurentian systems. *Notropis v. wickliffi* seems to have evolved from stock that became specialized for life in large rivers of the Teays-Mississippi system.

Notropis buchanani Meek—ghost shiner

Notropis volucellus: Fisher, 1962:427 (Missouri R. local.).
Notropis buchanani: Cross, 1967:139 (Missouri R. local. mapped).

Distribution and habitat.—The ghost shiner reaches its greatest abundance in the prairie and Ozark border streams of west-central, central and northeastern Missouri (Map 76). It is common in the Missouri River as far upstream as Boone County but is rare in the upper Missouri and in the Mississippi River. *Notropis buchanani* inhabits the low-gradient sections of large creeks and rivers having permanent flow and moderately clear water. It is a quiet-water species, inhabiting the larger pools and the lower reaches of tributaries or other protected backwaters, where there is no noticeable current.

Zoogeography.—Notropis buchanani is most closely allied to *N. volucellus,* with which it was long considered to be conspecific. The widespread southwestern distribution of *N. buchanani* suggests an origin in Gulf coastal drainages west of the Mississippi River.

Dionda nubila (Forbes)—Ozark minnow

Dionda nubila: Call, 1887:75 (Toms Cr., Reynolds Co.; Piney R., Texas Co.). Hubbs and Ortenburger, 1929:90 (trib. Big R. S Potosi; Sarcoxie). Martin and Campbell, 1953 (abund.; hab.; Black R.).
(?) *Hybognathus meeki:* Call, 1887:75 (West Fork Black R., Reynolds Co.; Jacks Fork, Shannon Co.).
Hybognathus nubila: Meek, 1891:117,121,124,126,129 (Meramec R. near St. James; Little Dry Fork near Rolla; Little Piney Cr. near Arlington and/or Newburg; Jones Cr. and Maries R. near Dixon; Lick Fork and Bryants Cr. near Mansfield; Osage Fork and Niangua R. near Marshfield; Sac R. and James R. near Springfield; Shoal Cr. near Neosho; North Fork White R. S Cabool). Evermann and Kendall, 1895:470 (Indian Cr. near Neosho).

Distribution and habitat.—With respect to its distribution in Missouri the Ozark minnow is well named, for it occurs only in the Ozark Uplands, where it is one of the most abundant fishes (Map 77). Although it is widespread elsewhere in the Meramec system, *D. nubila* is absent from the Bourbeuse River and the upper Dry Fork. It occurs north of the Missouri River only in a few small streams in southern Montgomery and Warren counties, and it is not found in any tributary of the Missouri River above the mouth of the Osage River. The Ozark minnow is almost invariably found in association with either the bleeding shiner or the duskystripe shiner, and its distribution in the state parallels the combined distribution of these two closely related species to a remarkable degree. The Ozark minnow inhabits streams with silt-free bottoms and a permanent strong flow of clear, cool water. It is usually found in

protected backwaters near riffles, or in pools just below riffles where the current slackens.

Zoogeography.—Dionda nubila seems to be autochthonous to the Mississippi Valley, and has probably long occupied the Ozark Uplands. Disjunct populations in the Driftless Area may have been established by dispersal from an Ozark refugium postglacially, but it is equally plausible that *D. nubila* was present in or near the Driftless Area throughout the Wisconsin glacial period. G. R. Smith (1963:285) reported this species in a late-Illinoian fauna in southwestern Kansas, thus providing evidence of a more western distribution during glaciation.

Ericymba buccata Cope—silverjaw minnow

Distribution and habitat.—The silverjaw minnow occurs in the Meramec River and other tributaries of the Mississippi River southward to the Headwater Diversion (Map 78). Although not widely distributed, it is common at most localities where it occurs. *Ericymba buccata* inhabits the sandy stretches of small, clear, permanent-flowing streams. It seems to be the ecological counterpart of the plains-inhabiting *N. dorsalis* in the clearer and more stable streams in the eastern and southern parts of the Mississippi Valley. Trautman (1957:376) noted the similarity in requirements of these two species and presented data indicating interspecific competition between them in Ohio. I have found them together only in a single collection from the lower Meramec River, where both were rare.

Zoogeography.—The distribution of *E. buccata* suggests an origin in the preglacial Teays-Mississippi system. It probably survived the last ice advance in the lower Mississippi Valley and redispersed northward solely from that area. Trautman (1957:376) indicated that this species is still extending its range northeastward.

Hybognathus hankinsoni Hubbs—brassy minnow

Hybognathus hankinsoni: Bailey, 1954 (Missouri local. mapped). Cross, 1967: 144 (Missouri R. local. mapped).

Distribution and habitat.—The brassy minnow is common in small tributaries of the upper Chariton River and occurs rarely in the Missouri River and its tributaries westward in the Dissected Till Plains (Map 79). It inhabits small, moderately clear, low-gradient streams with permanent pools and bottoms of sand or fine gravel.

Zoogeography.—Possibly this northern species was localized preglacially in the Hudson Bay or Laurentian systems. Bailey (1954:291) concluded that *H. hankinsoni* is "of Mississippi derivation" and "survived the Wisconsin glaciation in the Missouri and Upper Mississippi drainages." That it has had a more southerly distribution in the past is indicated by its presence in Illinoian fossil deposits from southwestern Kansas (G. R. Smith, 1963:279).

Hybognathus nuchalis Agassiz—central silvery minnow

Hybognathus nuchalis: Agassiz, 1855:224 (orig. descr.; type local. Quincy, Ill.; St. Louis, Mo.). Garman, 1890:143 (Mississippi R. near Quincy, Ill.). Hubbs, 1951:17 (Mississippi R. at St. Louis). Forbes and Richardson, 1920:map XXV (Mississippi R. local.).

Taxonomic considerations.—At present, most workers recognize four species of *Hybognathus*, all of which occur in Missouri. Two of these (*H. hankinsoni* and *H. hayi*) appear to present no taxonomic difficulties. The other two (*H. nuchalis* and *H. placitus*) are superficially similar, and until recently there was no consensus regarding their taxonomic relationship. At different times and by different workers they have been treated as distinct species, as subspecies, and as environmental variants. The discovery of striking differences in the pharyngeal apparatus of the two forms (Niazi and Moore, 1962; Bailey and Allum, 1962:72 and plate I) seems to leave little doubt that they are distinct species.

Hybognathus nuchalis is commonly divided into two subspecies: *H. n. regius* Girard of the Atlantic Slope, and *N. n. nuchalis* of the Mississippi Valley. The two were formerly thought to intergrade along the eastern Gulf Coast (Hubbs and Lagler, 1947:68), but they are now known to be entirely allopatric (Bailey, 1954:291). In addition to the slight differences in external morphology used to separate the two forms in the past, they are now known to differ in the shape of the basioccipital process; the process of *regius* is most nearly like that of *placitus* (Al-Rawi and Cross, 1964). Considering the nature of the differences and the absence of opportunity for gene exchange, *nuchalis* and *regius* could be considered as different species.

In examining numerous series of *nuchalis* from the Mississippi Valley, I find that the "*H. n. nuchalis*" of previous workers is a complex of two forms. One of these occurs sympatrically with *H. placitus* in the Missouri River system; the other occupies the remainder of the *nuchalis* range in the Mississippi Valley and Gulf coastal drainages. Both occur in the Mississippi River from the mouth of the Missouri River downstream to the mouth of the Ohio River. There seems to be no lessening of differences between the two forms in the zone of sympatric occurrence, and I tentatively

consider them to be distinct species. I resurrect the name *Hybognathus argyritis* Girard for the form in the Missouri River system, and restrict the name *Hybognathus nuchalis* Agassiz to the form in the central Mississippi Valley. The types of *argyritis* consist of seven specimens (USNM 87) from Milk River, Montana, and one specimen (MCZ 1788) from Arkansas River near Fort Smith (Girard, 1856). *Hybognathus argyritis* seems to be the only name available for a species of *Hybognathus* from the Missouri River system that is not applicable to *H. placitus.* The specimen from Fort Smith is undoubtedly *nuchalis; H. argyritis* is not known from the Arkansas River. The types of *H. nuchalis* are from Quincy, Illinois. Fingermann and Suttkus (1961) designated a lectotype (MCZ 1926); other syntypes originally sharing that number were recatalogued (MCZ 40697).

The only truly diagnostic character for separating *nuchalis* and *argyritis* is the shape of the basioccipital process. That of *nuchalis* is greatly expanded posteriorly, and the posterior margin is deeply emarginate (see Niazi and Moore, 1962:fig. 21). The process of *argyritis* is less expanded posteriorly, and the posterior margin is truncate or only shallowly emarginate (see Bailey and Allum, 1962: plate ID). In *nuchalis* the greatest width of the process exceeds its length (measured from its base to the center of the emargination); in *argyritis* the width is less than the length (Fig. 15). Specimens from the zone of sympatric occurrence are as different in this character as specimens from allopatric populations. External differences between *nuchalis* and *argyritis* are slight, but a practiced observer can identify most specimens without dissection. These differences involve eye length (greater in *nuchalis* than in *argyritis*), interorbital width and gape width (less in *nuchalis* than in *argyritis*), and pigmentation (dark margins of scale pockets more pronounced in *nuchalis* than in *argyritis*).

The differences in external morphology of the two forms need to be quantified, and more material of *argyritis* is needed from the zone of sympatric occurrence; I have examined many *nuchalis* but only 14 specimens of *argyritis* (mostly young of the year) from that area. Both species were found in collections from four localities.

Distribution and habitat.—Hybognathus nuchalis, as here restricted, is abundant in the lower Current, Black, and St. Francis rivers, and the lower sections of some of the larger ditches of the lowlands (Map 80). It occurs along the full length of the Mississippi River, but is far more common below the mouth of the Ohio River than above. It now seems to be rare in the upper Mississippi

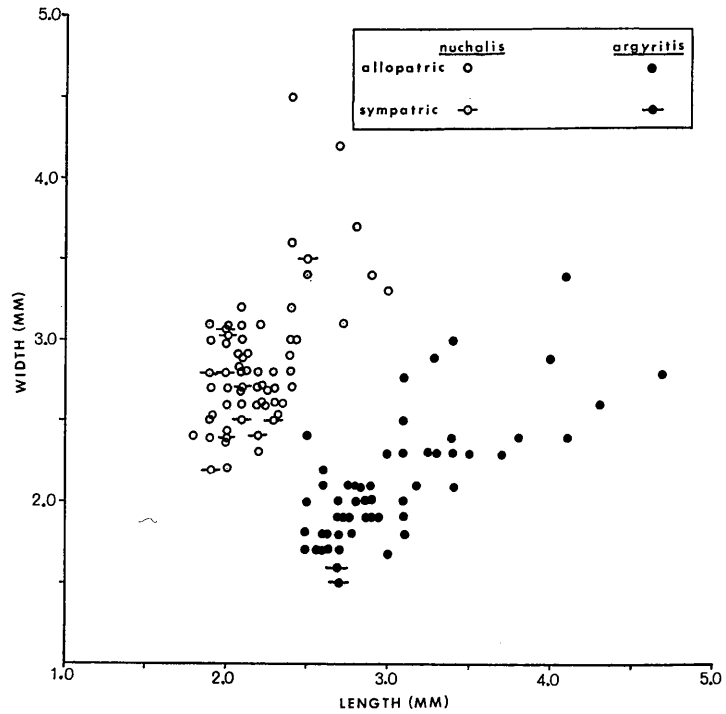

FIGURE 15. Relationship of basioccipital process width to basioccipital process length in *Hybognathus nuchalis* and *Hybognathus argyritis.* The graph is based on data from the following specimens:

Hybognathus nuchalis.—Wisconsin: Chippewa R., Eau Claire Co. (KU 2012, 10 spec.). *Illinois:* Mississippi R. at Quincy (UMMZ 150029, 3 spec.); Piasa Cr., Madison and Jersey Co. (uncat., 13 spec.); Mississippi R., Grand Tower (UMMZ 111579, 5 spec.). *Missouri:* Sugar Cr., Lewis Co. (UMMZ 149435, 1 spec.); Missouri R. at its mouth, St. Charles Co. (KU 9697, 2 spec.); Meramec R. 1 mi. S Pacific, Jefferson Co. (MU 1307, 1 spec.); Mississippi R. at Claryville, Perry Co. (uncat., 1 spec.); Apple Cr., Perry Co. (UMMZ 152946, 1 spec.); Brazeau Cr., Perry Co. (UMMZ 149878, 1 spec.); Current R., Ripley Co. (uncat., 10 spec.). *Indiana:* Wabash R., New Harmony (UMMZ 81316, 5 spec.). *Alabama:* Town Cr.. Wilson L. (UMMZ 122851, 5 spec.). *Texas:* Neches R. above Beaumont, Hardin Co. (UMMZ 166490, 1 spec.).

Hybognathus argyritis.—Alberta: Milk R. 3 mi. S Groton PO, 8 mi. N and 1 mi. W Alden PO (National Museum Canada 66-431, 1 spec.). *North Dakota:* Little Missouri R. below Marmarthen (UMMZ 94800, 3 spec.). *South Dakota:* Moreau R. 14 mi. N Eagle Butte, Dewey Co. (UMMZ 178956, 3 spec.). *Nebraska:* Elkhorn R. 1 mi. N Winslow, Dodge Co. (UMMZ 135765, 2 spec.); Platte R., Bellwood, Butler Co. (UMMZ 134702, 2 spec.). *Missouri:* Tarkio R. 4 mi. S Tarkio, Atchison Co. (uncat., 20 spec.); Missouri R. at Gasconade, Gasconade Co. (KU 9627, 11 spec.); Meramec R. 1 mi. S Pacific, Jefferson Co. (MU 1307, 1 spec.); Mississippi R. at Claryville, Perry Co. (uncat., 1 spec.).

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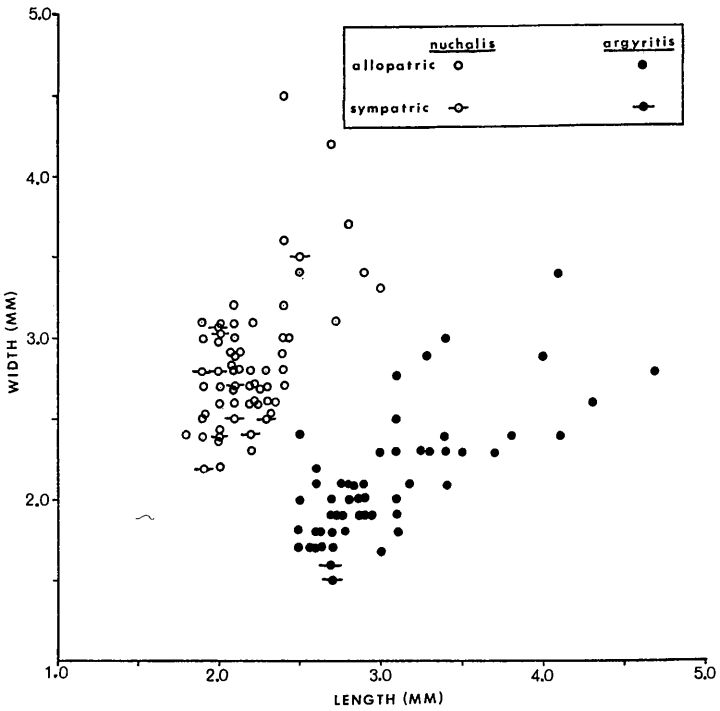

FIGURE 15. Relationship of basioccipital process width to basioccipital process length in *Hybognathus nuchalis* and *Hybognathus argyritis*. The graph is based on data from the following specimens:

Hybognathus nuchalis.—Wisconsin: Chippewa R., Eau Claire Co. (KU 2012, 10 spec.). *Illinois:* Mississippi R. at Quincy (UMMZ 150029, 3 spec.); Piasa Cr., Madison and Jersey Co. (uncat., 13 spec.); Mississippi R., Grand Tower (UMMZ 111579, 5 spec.). *Missouri:* Sugar Cr., Lewis Co. (UMMZ 149435, 1 spec.); Missouri R. at its mouth, St. Charles Co. (KU 9697, 2 spec.); Meramec R. 1 mi. S Pacific, Jefferson Co. (MU 1307, 1 spec.); Mississippi R. at Claryville, Perry Co. (uncat., 1 spec.); Apple Cr., Perry Co. (UMMZ 152946, 1 spec.); Brazeau Cr., Perry Co. (UMMZ 149878, 1 spec.); Current R., Ripley Co. (uncat., 10 spec.). *Indiana:* Wabash R., New Harmony (UMMZ 81316, 5 spec.). *Alabama:* Town Cr., Wilson L. (UMMZ 122851, 5 spec.). *Texas:* Neches R. above Beaumont, Hardin Co. (UMMZ 166490, 1 spec.).

Hybognathus argyritis.—Alberta: Milk R. 3 mi. S Groton PO, 8 mi. N and 1 mi. W Alden PO (National Museum Canada 66-431, 1 spec.). *North Dakota:* Little Missouri R. below Marmarthen (UMMZ 94800, 3 spec.). *South Dakota:* Moreau R. 14 mi. N Eagle Butte, Dewey Co. (UMMZ 178956, 3 spec.). *Nebraska:* Elkhorn R. 1 mi. N Winslow, Dodge Co. (UMMZ 135765, 2 spec.); Platte R., Bellwood, Butler Co. (UMMZ 134702, 2 spec.). *Missouri:* Tarkio R. 4 mi. S Tarkio, Atchison Co. (uncat., 20 spec.); Missouri R. at Gasconade, Gasconade Co. (KU 9627, 11 spec.); Meramec R. 1 mi. S Pacific, Jefferson Co. (MU 1307, 1 spec.); Mississippi R. at Claryville, Perry Co. (uncat., 1 spec.).

River and its tributaries, but it was common in collections made in that area in the early 1940's. The reasons for this decline are not known. The central silvery minnow is most abundant in the low-gradient sections of clear, moderately large streams. It seems to be rather intolerant of continuous high turbidity, as indicated by marked reduction in abundance in the Mississippi River above the point where that stream receives the clear waters of the Ohio River. The central silvery minnow avoids strong currents and occurs most abundantly in pools and backwaters over a silt or sand bottom.

Zoogeography.—Hybognathus nuchalis, H. argyritis, and *H. placitus* constitute a close-knit group having recent distributional relationships that seem to reflect their distribution in preglacial time. Each species has its distribution centered in an area drained in preglacial time by one of the principal stream systems that were modified during the Pleistocene to form the present Mississippi River system. *Hybognathus nuchalis* is widespread in the central Mississippi Valley; probably it inhabited the preglacial Teays-Mississippi system. *Hybognathus argyritis* has its distribution centered in the upper Missouri system, which drained in preglacial time into Hudson Bay. *Hybognathus placitus* is widespread in the central and southern plains, and probably inhabited the preglacial drainage of that region. The distributional relationships of these three species still can be discerned, because they seem to have made only modest invasions of each other's range since disruption of the preglacial drainage patterns. The most overlap is between *argyritis* and *placitus. Hybognathus nuchalis* is represented southwestward into the Pecos and Rio Grande drainages by another nominal form (*Hybognathus amarus* Girard) of uncertain relationship. Some workers have treated this form as a subspecies of *H. placitus,* but the shape of the basioccipital process suggests that its relationships are with *H. nuchalis.*

Hybognathus argyritis Girard—western silvery minnow

Hybognathus nuchalis: Jordan and Meek, 1885:11 (Hundred and Two R. at Maryville). Call, 1887:75 (in part (?); "two specimens only"; Piney R., Texas Co.; Meramec R., Dent Co.). Fisher, 1962:427 (Missouri R. local.). Cross, 1967:148 (Missouri R. local. mapped).

Hybognathus placita: Hanson and Campbell, 1963 (in part (?); linear distr.; Perche Cr.).

Distribution and habitat.—The western silvery minnow is restricted to the Missouri system and the Mississippi River from the mouth of the Missouri River downstream to about Scott County

(Map 81). It is abundant in the Missouri River and some large prairie streams of the till plains but is rare in the Mississippi River. In a series of collections made in 1963, it occurred at every locality studied in the Missouri River, but it was less abundant than *H. placitus.* In tributaries of the Missouri River from the Grand River system westward it is generally less abundant than *H. placitus,* but it is more abundant than that species in collections from the clearer streams of central Missouri. The specimen reported by Call (1887: 75) from Big Piney River is probably this species, whereas that from the Meramec River could be this species or *H. nuchalis.* The presence of any species of *Hybognathus* at either of the localities reported by Call is surprising, because they are far removed from any other Missouri localities for *Hybognathus.* The habitat requirements of this minnow are similar to those of the central silvery minnow, except that it seems more tolerant of high turbidity. It is generally found over a silt or sand bottom in the quiet backwaters and pools of large streams, and in the ponded lower reaches of smaller tributaries.

Hybognathus placitus Girard—plains minnow

Hybognathus nuchalis placita: Jordan and Meek, 1885:13 (Missouri R. at St. Joseph).

Hybognathus placita: Hanson and Campbell, 1963 (in part (?); linear distr.; Perche Cr.). Fisher, 1962:427 (Missouri R. local.).

Hybognathus placitus: Al-Rawi and Cross, 1964 (char.; var.; Missouri local. mapped). Cross, 1967:146 (Missouri R. local. mapped).

Distribution and habitat.—The distribution of the plains minnow (Map 82) is similar to that of the western silvery minnow. The plains minnow is abundant in the Missouri River and in prairie streams of north Missouri from Grand River westward. Its abundance declines in the Missouri River toward its mouth, and *H. placitus* is uncommon in the lower Mississippi River. Like several other species inhabiting turbid plains streams, *H. placitus* occurs downstream in the Mississippi River from the mouth of the Missouri but not upstream. It is far more abundant than the western silvery minnow in the Missouri River and most of its tributaries in the till plains of northwestern Missouri from Grand River westward. Although the two species occur at the same locality, they tend to be segregated ecologically; the plains minnow predominates in the main channel where there is a sandy bottom and some current, whereas the western silvery minnow is more abundant in the mouths of tributary streams and other protected backwaters where there is little or no current and a silt bottom.

Hybognathus hayi Jordan—cypress minnow

Distribution and habitat.—In the early 1940's the cypress minnow was common in collections made in the lower Black and St. Francis rivers, but it has not been taken since anywhere in Missouri (Map 83). The cypress minnow often occurs with the central silvery minnow, and its habitat requirements are probably similar.

Zoogeography.—This southern species may have had its origin in the lower Mississippi Valley, because it has only a limited distribution in other Gulf drainages.

Pimephales vigilax (Baird and Girard)—bullhead minnow

Ceratichythys vigilax: Fowler, 1924:404 (char.; Carthage, Mo.).
Ceratichthys perspicuus: Hubbs and Black, 1947:5-31; map 1 (char.; syn.; Missouri local. mapped).
Pimephales perspicuus: Patriarche, 1953:247 (abund.; Lake Wappapello).

Distribution and habitat.—The bullhead minnow is widespread in the lowlands, and occurs northward in the Mississippi River and its direct tributaries to the Iowa line (Map 84). In the lowlands it is second in abundance only to *Notropis venustus.* It is common in the sluggish prairie streams of northeastern Missouri and in the upper Mississippi River, but it is scarce in the swifter and more turbid Mississippi River below the mouth of the Missouri. The bullhead minnow has not occurred in recent collections from the Neosho River system, but an old literature record indicates its former presence there. It still occurs in the Neosho system of Kansas. *P. vigilax* was reported from South Grand River and Tabo Creek as *Cliola vigilax* by Jordan and Meek (1885:16), but the specimens on which this report is based are *Pimephales notatus* (Hubbs and Black, 1947:21). Records for this minnow plotted by Hubbs and Black (1947:map 1) in the Missouri River system of Iowa, Nebraska, and South Dakota are based on erroneous locality data or misidentifications (Bailey and Allum, 1962:109). The bullhead minnow inhabits sluggish pools and backwaters of medium-sized to large streams with continuous flow and low to moderate gradients. It avoids strong current but is rather tolerant of turbidity and siltation.

Zoogeography.—Hubbs and Black (1947:33) recognized two subspecies of *P. vigilax,* with the nominate subspecies occupying that portion of the species range from the upper Red River southwestward. These authors suggested that *P. v. perspicuus* (Girard) had its origin in the Mississippi Valley and that it has replaced *P. v. vigilax* in much of the Red River system and in other coastal streams of Texas as far west as the Trinity River.

Pimephales tenellus (Girard)—slim minnow

Ceratichthys tenellus tenellus: Hubbs and Black, 1947:35-38, map 2 (char.; syn.; Missouri local. mapped).
Ceratichthys tenellus parviceps: Hubbs and Black, 1947:36-43, map 2 (orig. discr.; type local. White R. 3 mi. S Kissee Mills, Taney Co.; Missouri local. mapped).
Ceratichthys callarchus: Hubbs and Black, 1947:43-47, map 2 (orig. descr.; only the type known; Castor R., Bollinger Co.).

Taxonomic considerations.—Two well marked subspecies of the slim minnow occur in Missouri. These are *P. t. tenellus* (Girard) and *P. t. parviceps* (Hubbs and Black). Hubbs and Black (1947:37) regarded populations of *P. t. parviceps* in the St. Francis and Black river systems as "nongeographic intergrades," because they are in some respects intermediate between this subspecies and the nominate subspecies. Hubbs and Black (1947:43-47) described *Ceratichthys callarchus,* which they regarded as a species closely related to *P. tenellus,* from a single specimen collected in the Castor River, Bollinger County, Missouri. A series of 9 specimens that I collected recently from Castor River differ in no important respect from *P. t. parviceps* from the adjacent St. Francis and Black river systems, thereby suggesting that the type of *callarchus* is merely an aberrant specimen of *P. tenellus,* as suggested by Moore (1957:136).

Distribution and habitat.—*Pimephales t. tenellus* is confined to the Neosho River system, and *P. t. parviceps* occurs disjunctly in the upper White, Black, St. Francis, and Castor rivers (Map 85). *Pimephales t. tenellus* is fairly common within its area of occurrence, but *P. t. parviceps* is rare. The latter subspecies now may be absent from the upper White River, since most localities from which it has been recorded are covered by Bull Shoals and Table Rock reservoirs.

The streams in which *P. t. tenellus* occurs are warmer and more sluggish than typical Ozark streams. Its habitat preferences seem to be much like those of the bullhead minnow, but it occupies smaller streams and is less tolerant of turbidity. *Pimephales t. parviceps* inhabits clearer and higher gradient streams than *P. t. tenellus,* suggesting that the two are differentiated ecologically as well as morphologically.

Zoogeography.—At the time the two subspecies of *P. tenellus* were diverging, *P. t. tenellus* may have been localized in streams draining the Flint Hills of Kansas and the western slope of the Ozark-Ouachita uplands, while *P. t. parviceps* was localized farther east in the White River and other streams draining the

southern and southeastern Ozark Uplands. If this theory is correct, breaching of the Ozark-Ouachita divide by the lower Arkansas River during the Pleistocene (Quinn, 1958) brought the two subspecies into contact, but their original distributional relationship has remained essentially intact.

Pimephales notatus (Rafinesque)—bluntnose minnow

Pimephales notatus: Jordan and Meek, 1885:11,15,16 (Hundred and Two R. at Maryville; Flat Cr. near Sedalia and/or Blackwater R. at Brownsville; Grand R. at Clinton and/or Tebo Cr. at Calhoun). Call, 1887:80 (Bear Cr., Boone Co.). Meek, 1891:117,121,124,126,129 (Meramec R. and Big Dry Fork near St. James; Lick Fork near Mansfield; Big Piney R. and North Fork White R. near Cabool; Niangua R. and Osage Fork near Marshfield; James R. and Sac R. near Springfield; Shoal Cr. and Hickory Cr. near Neosho; Maries R. near Dixon; Little Piney Cr. at Newburg). Evermann and Kendall, 1895:470 (Indian Cr. near Neosho). Fowler, 1921:399 (St. Louis). Martin and Campbell, 1953 (Black R.). Patriarche and Campbell, 1958:255-256 (Clearwater Res.). Fisher, 1962:427 (Missouri R. local.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.).

Cliola vigilax: Jordan and Meek, 1885:16 (Grand R. at Clinton and/or Tebo Cr. at Calhoun).

Hyborhynchus notatus: Hubbs and Black, 1947:21,23 (reident. of spec. reported by Jordan and Meek, 1885:16 as *Cliola vigilax*).

Distribution and habitat.—The bluntnose minnow is virtually statewide in distribution, but it is rare in the northwestern part of the prairie region (Map 86). Only the ubiquitous green sunfish has occurred in more collections. *P. notatus* is common over most of its Missouri range, but reaches its greatest abundance in and adjacent to the Ozark border. This minnow occurs in a variety of habitats but is most numerous in the quiet pools and backwaters of medium-sized to moderately large streams having clear, warm waters, permanent flow, and moderate amounts of aquatic vegetation. In the cooler Ozark streams it is most often found in backwaters that are a few degrees warmer than the main channel. In the more turbid and intermittent prairie streams it is largely replaced by the fathead minnow, and in the larger rivers and lowland ditches it is outnumbered by the bullhead minnow.

Zoogeography.—In preglacial time, this wide-ranging species probably inhabited the preglacial Teays-Mississippi system, and perhaps also the Laurentian system.

Pimephales promelas Rafinesque—fathead minnow

Pimephales promelas: Agassiz, 1855:221 (smaller brooks west of St. Louis). Smiley, 1885:347 (salt springs, Saline Co.). Jordan and Meek, 1885:11 (Hundred and Two R. at Maryville). Call, 1887:80 (Bear Cr., Boone Co.). Coker, 1930:201 (Mississippi R. near Warsaw, Ill.). Fisher, 1962:427 (Missouri R. local.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.). Cross, 1967:150 (Missouri R. local. mapped).

Coliscus parietalis: Cope, 1871:437 (orig. descr.; Missouri R. near St. Joseph).

Pimephales promelas promelas: Martin and Campbell, 1953:47 (abund.; Black R.).

Distribution and habitat.—The fathead minnow is abundant and widespread in the prairie region (Map 87). Although it is propagated at several hatcheries and is commonly used as bait in Ozark reservoirs, the fathead minnow is rare in natural waters of the Ozarks. *Pimephales promelas* occurs occasionally in streams of all sizes but is abundant only in the pools of small, intermittent headwater creeks. Because of its tolerance of high temperature, extreme turbidity, and low oxygen, the fathead minnow is well suited for survival in the stagnant pools that provide the only refuge for fish in many small prairie streams during extended dry periods. In such situations the fathead minnow, along with a few other hardy species such as the creek chub, black bullhead, and green sunfish, usually comprise the entire fish population. The fathead minnow seems intolerant of competition and is seldom abundant in habitats that support a variety of other fishes.

Zoogeography.—This wide-ranging species exhibits a trend from north to southwest in several characters, and Metcalf (1966: 136-137) concluded that these trends could be environmentally induced, or could have arisen in ancestral stocks that were present in all three of the principal drainages that were integrated to form the present Mississippi River system.

Campostoma oligolepis Hubbs and Greene—largescale stoneroller

Taxonomic considerations.—Most workers recognize three subspecies of the wide-ranging *Campostoma anomalum.* These are: *C. a. anomalum* (Rafinesque) of the Ohio River system; *C. a. oligolepis* Hubbs and Greene, occurring disjunctly in the Driftless Area of Wisconsin and Ozark Uplands; and the wide-ranging *C. a. pullum* (Agassiz). A fourth subspecies, *C. a. plumbeum* (Girard) of the western plains is recognized by some workers. Subspecific allocation has been made principally on the basis of the number of scales, supplemented by differences in morphometrics and coloration.

Two of these forms (*pullum* and *oligolepis*) occur in Missouri, and their taxonomic relationship is the subject of the present discussion. Hubbs and Greene (1935) considered *pullum* and *oligolepis* to be conspecific, although they found little evidence of intergradation where the two forms occur together in Wisconsin. Their decision was based on the fact that subspecies *anomalum* is intermediate in certain characters (most notably scutellation) between

pullum and *oligolepis*. Known at the time of its original description only from Wisconsin, *oligolepis* has since been found to be widespread in the Ozark Uplands. Here as in Wisconsin, *oligolepis* remains distinct although it is sympatric with *pullum*. In Wisconsin there is only moderate overlap in the ranges of the two forms; in the Ozark Uplands *oligolepis* is wholly sympatric with *pullum*. Bailey (1956:334) pointed out the inconsistency of treating sympatric forms as subspecies, and suggested that *oligolepis* is either a full species or an environmental variant. He favored the latter explanation, pointing out that *oligolepis* usually is found in regions having numerous springs, and that fishes spawned in the relatively uniform temperatures of streams emerging from large springs might be structurally different from those exposed to wider fluctuations in environmental conditions.

Scale counts of the two forms in Missouri are presented and compared with Wisconsin populations in Table 5. Counts for *oligolepis* from the northern and southeastern Ozarks (Osage, Gasconade, Meramec and Headwater Diversion systems) are similar to those of Wisconsin populations, but are consistently lower than those for populations from the southern Ozarks (White, Black, and St. Francis systems). Variation is not clinal; scale counts for the Headwater Diversion are as low as those for drainages in the northern Ozarks, in spite of the proximity of populations with high scale counts in the adjacent St. Francis system. Scale counts for *pullum* vary from stream system to stream system with no definite pattern. The number of circumferential scales varies more than the number of lateral line scales, and variation of the two counts is discordant. Counts for Wisconsin *pullum* are comparable with those of Missouri populations. The relatively high number of scales in *oligolepis* in the southern Ozarks could result from present or past gene exchange with *pullum*, but this seems unlikely, because there is no increased variability (as indicated by the coefficient of variation) in scale counts of populations from that region.

In other characters Missouri populations of *pullum* and *oligolepis* agree rather well with the list of differential characters given by Hubbs and Greene (1935:table I). Hubbs and Greene did not note differences between breeding males of the two forms, but Missouri specimens differ consistently in tubercle pattern and fin color. Males of *pullum* typically have a crescent-shaped row of 1-3 tubercles mesial to each nostril and a prominent black band in

TABLE 5.—Scale Counts in Selected Populations of *Campostoma* from Missouri and Wisconsin.*

Population	Circumferential Scales					Lateral Line Scales					Circumf. + L.L. Scales				
	N	$\bar{X}$	Range	S.D.	C.V.	N	$\bar{X}$	Range	S.D.	C.V.	N	$\bar{X}$	Range	S.D.	C.V.
Missouri:															
White River															
pullum	67	42.2	38-47	2.06	4.88	66	50.2	46-54	1.88	3.75	66	92.4	85-98	3.10	3.36
oligolepis	80	36.8	33-40	1.43	3.90	80	47.2	44-50	1.34	3.03	80	84.0	79-89	1.96	2.33
Black River															
pullum	71	42.7	38-47	2.29	5.36	70	48.8	44-55	2.17	4.45	70	91.5	85-98	3.25	3.56
oligolepis	73	36.0	32-40	1.75	4.85	73	46.4	43-50	1.44	3.11	73	82.4	77-89	2.62	3.18
St. Francis River															
pullum	74	43.6	37-49	2.42	5.54	74	50.6	46-57	2.43	4.79	74	94.2	84-101	3.68	3.90
oligolepis	78	36.9	34-40	1.47	3.97	78	47.4	45-51	1.32	2.78	78	84.4	81-91	2.14	2.53
Headwater Diversion															
pullum	54	40.5	37-45	2.08	5.13	54	51.1	47-57	2.47	4.83	54	91.5	85-99	3.35	3.66
oligolepis	71	34.6	32-38	1.40	4.04	71	45.0	42-49	1.69	3.76	71	79.6	75-86	2.56	3.22
Meramec River															
pullum	65	41.6	38-46	1.92	4.62	65	49.7	45-55	2.08	4.19	65	91.3	85-99	2.94	3.22
oligolepis	60	34.6	32-39	1.56	4.52	60	44.3	41-47	1.41	3.19	60	78.9	74-86	2.48	3.15
Gasconade River															
pullum	63	43.9	39-49	2.01	4.57	63	52.1	48-58	2.34	4.49	63	96.0	88-103	3.64	3.80
oligolepis	59	34.9	32-38	1.53	4.36	59	45.4	41-48	1.48	3.26	59	80.5	76-85	2.22	2.76
Osage River															
pullum	51	42.2	38-46	2.20	5.21	51	50.0	46-55	2.00	3.99	51	92.2	84-101	3.66	3.97
oligolepis	57	34.9	32-38	1.33	3.81	57	44.6	41-48	1.38	3.09	57	79.5	74-84	2.23	2.81
Wisconsin:															
pullum	168	42.3	38-50	2.81	6.65	197	52.0	47-58	2.15	4.14	165	94.5	86-107	3.81	4.03
oligolepis	258	33.3	29-38	1.62	4.86	249	45.2	41-49	1.37	3.03	233	78.4	72-85	2.22	2.83

* Wisconsin statistics computed from counts by Hubbs and Greene, 1935:table II.

the anal fin; in males of *oligolepis* these characters are seldom developed.

I doubt that *oligolepis* is an environmental variant as proposed by Bailey. Largescale stonerollers occur in Missouri at localities so remote from springs that dispersal there after hatching is unlikely. The differences between *oligolepis* and *pullum* are slight, but involve so many characters that they could hardly all be the result of differing conditions during development (in particular, I doubt that conditions during embryonic development determine the distinctive characters of breeding males). I have stripped and artificially fertilized eggs of *oligolepis,* hatched them in the laboratory, and reared the offspring in ponds. Scale counts of pond-reared *oligolepis* were within the range of those for naturally occurring populations.

The widespread sympatric occurrence of *oligolepis* and *pullum* with no indication of intergradation leaves little doubt that they are reproductively isolated. If it were not for the supposed potential for gene exchange between *oligolepis* and *anomalum,* there would be no basis for treating *oligolepis* and *pullum* as anything but distinct species. Evidence of reproductive compatability between *oligolepis* and *anomalum* is lacking, because the two forms are allopatric. In the absence of such evidence it seems more realistic to recognize reproductive isolation between *oligolepis* and *pullum* by treating them as different species than to recognize an undemonstrated potential for gene exchange between *anomalum* and *oligolepis* by treating them as conspecific.

Distribution and habitat.—The largescale stoneroller occurs throughout the Ozarks except for the Neosho River system (Map 88). The habitats of the largescale and central stonerollers seem to be similar, except for the preference of the latter species for smaller streams. The largescale stoneroller is the more abundant of the two species in most large Ozark streams, but often there is a shift in abundance in favor of the central stoneroller toward the headwaters. I have found no localities where the largescale stoneroller occurred to the exclusion of the central stoneroller.

Zoogeography.—The present distribution of the largescale stoneroller suggests that it inhabited the Mississippi Valley in preglacial time and has long inhabited the Ozark Uplands. Perhaps the disjunct occurrence of *C. oligolepis* in the Ozark Uplands and the Driftless Area of Wisconsin resulted from the fragmentation of a widespread preglacial distribution. The lack of strong differentiation between populations of the Driftless Area and the northern Ozark Uplands suggests that this range disjunction is quite recent.

Campostoma anomalum pullum (Agassiz)—central stoneroller

Campostoma anomalum: Jordan and Meek, 1885:15,16 (Flat Cr. near Sedalia and/or Blackwater R. at Brownsville; Grand R. at Clinton and/or Tebo Cr. at Calhoun). Call, 1887:74,75,79 (West Fork Black R., Reynolds Co.; Jacks Fork, Shannon Co.; Piney R., Texas Co.; Meramec R., Dent Co.; Bear Cr. and Hinkson Cr., Boone Co.). Meek, 1891:117,121,124,126,129 Meramec R., Meramec Spring and Big Dry Fork near St. James; Little Dry Fork near Rolla; Jones Cr. near Dixon; Big Piney R. near Cabool; Lick Fork at Mansfield; Osage Fork SE Marshfield; Niangua R. near Marshfield; Sac R. and James R. near Springfield; Maries R. near Dixon; Shoal Cr. near Neosho; North Fork White R. S Cabool). Evermann and Kendall, 1895: 470 (Indian Cr. and spring branch near Neosho). Fowler, 1921:398 (St. Louis). Hubbs and Ortenburger, 1929:95 (creeks 2 mi. W Shepard, 2 mi. S DeSoto, and 4 mi. S Potosi). Martin and Campbell, 1953 (abund.; hab.; Black R.). Fisher, 1962:428 (Missouri R. local.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.).

Distribution and habitat.—The central stoneroller occurs in all of Missouri except for the lowlands and the extreme northwestern part of the prairie region (Map 89). It is most abundant in the Ozarks and northern Ozark border. It is generally less abundant than the largescale stoneroller in the Ozarks but in some places occurs to the exclusion of that species in small headwater streams. The central stoneroller inhabits the rocky pools and riffles of clear, permanent-flowing streams with moderate or high gradients. It is tolerant of moderate turbidity, if there is sufficient current to keep the bottom mostly free of silt.

Previous workers did not distinguish the central and largescale stonerollers, and some published records cited above may apply to either or both forms.

Zoogeography.—Metcalf (1966:139) suggested that *C. a. pullum* had a preglacial origin west, south or southwest of the central Teays-Mississippi system and cited the occurrence of the small-scaled *Campostoma ornatum* Girard in southwestern drainages as proof that fine-scaled stonerollers have long inhabited that region. However, Ross (1958:18) suggested that occurrence of *pullum* in the upper Allegheny River, a former tributary of the preglacial Laurentian system, may date from pre-Pleistocene times. If this is correct, *pullum* must have had an eastern or a mixed origin. The presence of an east-west cline in scale size (Metcalf 1966:138) may have resulted from intergradation between partially differentiated forms that were localized preglacially in the central Mississippi Valley and in plains drainages that were later diverted into the central Mississippi Valley.

Catostomidae

Cycleptus elongatus (Lesueur)—blue sucker

Cycleptus elongatus: Forbes and Richardson, 1920:65 (Mississippi R. at Cairo and Grafton, Ill.). Barnickol and Starrett, 1951:292-293 (abund.; utiliz.; Mississippi R. local.). Fisher, 1962:428 (Missouri R. local.). Cross, 1967: 166 (Missouri R. local. mapped).

Distribution and habitat.—The blue sucker is scarce but widely distributed in the Missouri and Mississippi rivers and their largest tributaries (Map 90). It seems to be less abundant now than in the early 1900's. Probably it is more generally distributed than our records indicate, because it is difficult to capture with the gear used in making most of the collections. This sucker inhabits deep, swift channels. It is tolerant of turbidity if current is sufficient to prevent deposition of silt on the firm sand, gravel, and rubble bottoms over which the blue sucker is usually found. Construction of dams, with the attendant decrease in current velocity and increase in siltation, is unfavorable to the blue sucker. Coker, 1930:183 noted the decline of *C. elongatus* in the upper Mississippi River following the construction of a dam at Keokuk, Iowa.

Zoogeography.—Perhaps *C. elongatus* has inhabited the Mississippi Valley continuously since preglacial time. It is also possible that it entered the Mississippi Valley during the Pleistocene, when the lowering of sea levels that accompanied glaciation may have created connections with Gulf coastal drainages to the west.

Ictiobus cyprinellus (Valenciennes)—bigmouth buffalo

Ichthyobus stolleyi: Agassiz, 1855:81 (orig. descr.; Osage R.).

Ictiobus cyprinella: Garman, 1890:145 (Mississippi R. near Quincy, Ill.). Jordan and Meek, 1885:13 (Missouri R. at St. Joseph). Meek, 1891:124 (Maries R. near Dixon). Forbes and Richardson, 1920:map IX (Mississippi R. local.). Cleary, 1956:map 17 (Des Moines R. local.). Berner, 1951:9,10 (commer. catch; food; Missouri and Mississippi R.).

Megastomatobus cyprinella: Barnickol and Starrett, 1951:293-298 (abund.; utiliz.; Mississippi R. local.). Patriarche, 1953 (abund.; Lake Wappapello).

Ictiobus cyprinellus: Funk and Campbell, 1953 (abund.; Black R. local.). Fisher, 1962:428 (Missouri R. local.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.). Cross, 1967:169 (Missouri R. local. mapped).

Distribution and habitat.—The bigmouth buffalo occurs in large streams and reservoirs over most of the state, but it is most abundant in the Missouri and Mississippi rivers and the larger streams of the till plains (Map 91). In the Missouri River and its major tributaries the bigmouth far outnumbers the other two species of buffalofishes. In collections made by Fisher (1962:table 1), from the Missouri River, *I. cyprinellus* outnumbered the smallmouth buffalo about three to one. Long-term population inventories conducted by the Missouri Department of Conservation reveal that the bigmouth buffalo is the prevalent buffalofish in the Grand River watershed. Similar inventories in Salt River (tributary of the upper Mississippi River) indicate that the bigmouth buffalo is slightly more abundant than the black buffalo there but is far less abundant than the smallmouth buffalo. In the Mississippi River Barnickol and Starrett (1951:294-296) ranked the three species of buffalofishes in the same order as indicated above for the Salt River; this has also been the case in our collections.

The habitat requirements of the three species of buffalofishes are similar, but their distributional relationships in Missouri and elsewhere suggest that the bigmouth buffalo is more tolerant of high turbidity than the other species. *Ictiobus cyprinellus* is primarily an inhabitant of quiet waters, especially the pools of large streams, natural lowland lakes, and impoundments. The young are sometimes found in rather small creeks where these flow directly into large rivers.

Zoogeography.—The preglacial distributional relationships of the buffalofishes probably have been profoundly altered by events during the Pleistocene, making their distributional history difficult to discern. Large rivers are ready avenues for dispersal by these species; they probably were quick to take advantage of the stream connections made available to them by glaciation. The bigmouth buffalofish is less widespread in Gulf coastal drainages and occurs farther north than the other buffalofishes. Perhaps it invaded the Mississippi Valley from northern drainages during the Pleistocene, and has had less time to disperse along the Gulf coast.

Ictiobus niger (Rafinesque)—black buffalo

Bubalichthys bonasus: Agassiz, 1855:80 (orig. descr.; Osage R.).

Ictiobus urus: Jordan and Meek, 1885:13 (Missouri R. at St. Joseph). Garman, 1890:145 (Mississippi R. near Quincy, Ill.). Forbes and Richardson, 1920:map X (Mississippi R. local.).

Ictiobus niger: Borges, 1950 (vert. distr.; Niangua Arm, Lake Ozark). Barnickol and Starrett, 1951:293-298 (abund.; utiliz.; Mississippi R. local.). Berner, 1951:table 5 (commer. catch; Missouri and Mississippi R.). Funk and Campbell, 1953 (abund.; Black R. local.). Patriarche, 1953 (abund.; Lake Wappapello). Fisher, 1962:428 (Missouri R. local.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.). Cross, 1967:171 (Missouri R. local. mapped).

Distribution and habitat.—This species is less common in Missouri than the other buffalofishes (Map 92). In our collections the black buffalo outnumbered the other two species only in the lower Current River. It is slightly more abundant than the bigmouth buffalo in the streams and ditches of the lowlands but is less abun-

dant there than the smallmouth buffalo. In the Mississippi River it is more abundant in the unimpounded section below the mouth of the Missouri River than in the impounded section above (Barnickol and Starrett, 1951:294). The habitat requirements of *I. niger* are much like those of the other buffalofishes, but it more often occurs in strong current (Cross, 1967:172).

Ictiobus bubalus (Rafinesque)—smallmouth buffalo

Ictiobus bubalus: Jordan and Meek, 1885:13 (Missouri R. at St. Joseph). Garman, 1890:144-145 (Mississippi R. near Quincy, Ill.). Meek, 1891:124 (Maries R. near Dixon). Forbes and Richardson, 1920:map XI (Mississippi R. local.). Borges, 1950 (vert. distr.; Niangua Arm, Lake Ozark). Barnickol and Starrett, 1951:292-293 (abund.; utiliz.; Mississippi R. local.). Berner, 1951:9-10 (commer. catch; food; Missouri and Mississippi R.). Martin and Campbell, 1953:46 (abund.; Black R.). Funk and Campbell, 1953 (abund.; Black R. local.). Patriarche, 1953 (abund.; Lake Wappapello). Purkett, 1958a:123-124 (growth; Salt. R.). Fisher, 1962:428 (Missouri R. local.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.). Cross, 1967:173 (Missouri R. local. mapped).

Distribution and habitat.—The smallmouth buffalo is nearly as widespread in Missouri as the bigmouth buffalo (Map 93). It is the most abundant buffalofish in the Mississippi River and its major tributaries in northeast Missouri, in the lowland ditches of the southeast, and in large reservoirs of the Ozarks. Elsewhere in the state it is usually less prevalent than the bigmouth buffalo but is more abundant than the black buffalo. *Ictiobus bubalus* seems to require clearer waters than *I. cyprinellus,* and it is less often found in strong currents than *I. niger.*

Zoogeography.—The smallmouth and black buffalofishes are more southern and southwestern in distribution than the bigmouth buffalo. It seems likely that they inhabited the preglacial Teays-Mississippi system and perhaps also other Gulf coastal drainages to the west. C. L. Smith (1962:509) tentatively identified *I. bubalus* in Pliocene fossil deposits from Oklahoma and suggested that this species has long inhabited the Mississippi Valley.

Carpiodes cyprinus (Lesueur)—quillback

(?) *Ictiobus velifer:* Jordan and Meek, 1885:11,15,16 (Hundred and Two R. at Maryville; Flat Cr. and/or Blackwater R. at Brownsville; Grand R. at Clinton and/or Tebo Cr. at Calhoun).

Carpiodes cyprinus heinei: Trautman, 1956 (orig. descr.; Missouri local. mapped).

Carpiodes cyprinus: Barnickol and Starrett, 1951:292-293 (abund.; utiliz.; Mississippi R.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.).

Carpiodes forbesi: Trautman, 1956 (Missouri local. mapped). Hanson and Campbell, 1963 (linear distr.; Perche Cr.).

Quillback: Fry, 1962 (harv.; Taneycomo Res. tailwater).

Taxonomic considerations.—Until recently many workers have recognized *Carpiodes forbesi* Hubbs as a distinct species closely allied to *C. cyprinus.* However, Bailey and Allum (1962:81) placed *C. forbesi* in the synonymy of *C. cyprinus,* suggesting that "the slender fish with a low dorsal fin are likely the product of their environment." This conclusion was based on the assumption that the *C. forbesi* phenotype "is found chiefly in prairie and plains areas where high turbidity and scanty food supplies in the rivers are characteristic" (Bailey and Allum, *op. cit.*). I do not agree with this assumption, because I have encountered the *C. forbesi* phenotype in the Ozark Uplands of Missouri (Big Piney River, Texas County and Lake Taneycomo, Taney County), as well as in the prairie regions. Furthermore, the conclusion that prairie and plains streams are unproductive is unwarranted, because these streams drain areas with highly productive soils and support large populations of other fishes that do not differ phenotypically from populations in streams of other areas. However, I concur that the evidence is insufficient to retain *C. forbesi* as a valid species. Among Missouri specimens I have noted all degrees of variation in development of the anterior dorsal rays with no apparent bimodality that would permit the recognition of two types. Furthermore, there seems to be no obvious correlation between body depth and development of the anterior dorsal ray in Missouri specimens. It is possible that *C. forbesi* and *C. cyprinus* are sibling species, but if this is the case, additional characters will have to be found if they are to be recognized.

Distribution and habitat.—The quillback is most abundant in the Ozark border and in the clearer prairie streams of central and northeastern Missouri (Map 94). It is fairly common in the upper Mississippi River, but it is rare elsewhere in the Mississippi River and in the Missouri River. The quillback is taken frequently in the large reservoirs of the central Ozarks, but it is seldom encountered in the streams of that region. *Carpiodes cyprinus* is characteristic of moderately clear streams having low or moderate gradients, well defined pools and riffles, and stable bottoms of gravel and other coarse material. Like other carpsuckers, the quillback inhabits quiet water, except when spawning. It is most abundant in moderately large streams but also occurs in creeks if large, permanent pools are present.

Zoogeography.—Until the *C. cyprinus* complex has been subjected to a thorough variational analysis, and the basis for this variation has been established, little can be said concerning its

zoogeographic history. The widespread distribution of *C. cyprinus* suggests that it could have been present preglacially in all the principal drainages that were integrated to form the present Mississippi River system, with the possible exception of the ancestral Hudson Bay system.

Carpiodes carpio (Rafinesque)—river carpsucker

Carpiodes bison: Agassiz, 1854:356 (orig. descr.; type local. Osage R., Mo.).
Ictiobus carpio: Jordan and Meek, 1885:13 (Missouri R. at St. Joseph).
Carpiodes carpio: Forbes and Richardson, 1920:map XII (Missisippi R. local.). Funk and Campbell, 1953 (abund.; Black R. local.). Purkett, 1958a:121 (growth; Salt R.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.). Cross, 1967:177 (Missouri R. local. mapped).
Carpiodes carpio carpio: Barnickol and Starrett, 1951:292-293 (abund.; utiliz.; Mississippi R. local.). Martin and Campbell, 1953:46 (abund.; Black R.). Brezner, 1958 (food habits; Lake Ozark).
River carpsucker: Purkett, 1958b:5,23 (growth; Missouri streams).

Distribution and habitat.—The river carpsucker is by far the most abundant and widely distributed carpsucker in Missouri (Map 95). In the larger prairie streams of north and west Missouri it is the must abundant large fish at many localities or is second in abundance only to the carp or gizzard shad. It rarely occurs in the lowland and Ozark regions. The preferred habitat of the river carpsucker is the quiet, silt-bottomed pools, backwaters, and oxbows of large streams having moderate or low gradients. It usually thrives in impoundments. *Carpiodes carpio* is tolerant of high turbidity and is replaced in clearer waters by the quillback or highfin carpsucker.

Zoogeography.—*Carpiodes carpio* may have inhabited the Teays-Mississippi system, as well as other preglacial drainages to the southwest. The presence of a distinct subspecies (*C. c. elongatus* Meek) in Gulf coastal drainages from eastern Texas to northwestern México suggests that ancestral stocks of this species have long been present in southwestern drainages.

Carpiodes velifer (Rafinesque)—highfin carpsucker

Carpiodes difformis: Forbes and Richardson, 1920:map XIII (Mississippi R. local.).
Carpiodes velifer: Barnickol and Starrett, 1951:292-293 (abund.; utiliz.; Mississippi R.). Cleary, 1956:map 23 (Des Moines R. local.).

Distribution and habitat.—The highfin carpsucker is rare in Missouri. At present it seems to be confined to the Ozarks, where it is more common in large reservoirs than in streams (Map 96). Formerly it may have been more widespread and abundant in the state. Cross (1967:180-181) noted a marked decline in abundance

of the highfin carpsucker in Kansas. The habitat requirements of the highfin carpsucker are similar to those of the river carpsucker, but the highfin is generally found in clearer waters and over firmer bottoms. It is much less tolerant of high turbidity and siltation than other carpsuckers, and this intolerance probably explains its restricted distribution in Missouri.

Zoogeography.—The present distribution of *C. velifer* suggests that it was present in the preglacial Teays-Mississippi system (Metcalf, 1966:142).

Catostomus commersoni (Lacépède)—white sucker

Catostomus teres: Jordan and Meek, 1885:11,15,16 (Hundred and Two R. at Maryville; Flat Cr. near Sedalia and/or Blackwater R. at Brownsville; Grand R. at Clinton and/or Tebo Cr. at Calhoun). Call, 1887:74,79 (Jacks Fork, Shannon Co.; Toms Cr., Reynolds Co.; Hinkson Cr., Boone Co.). Meek, 1891:117,121,124,126 (Meramec Spring and Meramec R. near St. James; Little Dry Fork near Rolla; Big Piney R. near Cabool; Niangua R. near Marshfield; Maries R. near Dixon; Shoal Cr. near Neosho). Evermann and Kendall, 1895:470 (Indian Cr. and spring branch near Neosho).
Catostomus commersoni: Purkett, 1958a:125 (growth; Salt R.). Fisher, 1962: 428 (Missouri R. local.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.).

Distribution and habitat.—The white sucker is common in the clearer prairie streams of central and northeastern Missouri but becomes increasingly rare toward the northwest (Map 97). It is locally common but spotty in distribution in the Ozarks and is absent from the lowlands. The white sucker is decidedly a small-creek fish, occurring only rarely in the main channels of large rivers. In the Ozarks *C. commersoni* is generally found in spring branches and in clear, heavily vegetated spring pools along large streams. In the prairie region it is most abundant in high-gradient headwater creeks having gravelly or rocky bottoms and well defined riffles. These creeks tend to be intermittent, but permanent pools are maintained by seepage through gravel of the stream bed. The habitats in which the white sucker is abundant are largely devoid of other suckers, suggesting that competition with these may be a factor in limiting its distribution. Its requirements are most like those of the creek chub, a minnow with which it is commonly associated.

Zoogeography.—Preglacially this widespread northern species may have been confined to drainages north of the Mississippi Valley. However, Metcalf (1966:144-147) discussed a trend in eye size and number of rows of lip papillae from east to west and in scale size from north to south in western populations of *C. commersoni;* he suggested that this fish was represented preglacially

by three geographically separated and morphologically different stocks that occupied the Hudson Bay, Teays-Mississippi and "Ancestral Plains" systems. Mixing of these three stocks as a result of drainage alterations and distributional changes during the Pleistocene presumably resulted in the present variational patterns.

Hypentelium nigricans (Lesueur)—northern hog sucker

Catostomus nigricans: Agassiz, 1855:77,92 (Osage R., Missouri). Meek, 1891: 117,121,124,126,129 (Meramec R., Meramec Spring and Big Dry Fork near St. James; Little Piney Cr. at Newburg and Arlington; Osage Fork SE Marshfield; Lick Fork at Mansfield; Jones Cr. and Maries R. near Dixon; Niangua R. near Marshfield; Sac R. and James R. near Springfield; Shoal Cr. near Neosho; North Fork White R. S Cabool). Evermann and Kendall, 1895:470 (Indian Cr. and Shoal Cr. near Neosho).

Hypentelium nigricans: Call, 1887:74 (Toms Cr., Reynolds Co.; Meramec R., Dent Co.). Coker, 1930:186 (Mississippi R. near Warsaw, Ill.). Martin and Campbell, 1953 (abund.; hab.; Black R.). Funk and Campbell, 1953 (abund.; Black R. local.). Metcalf, 1966:163 (Richland Cr., Morgan Co.).

Hog sucker: Purkett, 1958b:6,24,43 (growth; length-weight relat.; Missouri streams).

Distribution and habitat.—The hog sucker is one of the most abundant stream fishes in the Ozarks (Map 98). Among suckers of that region it is exceeded in abundance only by the black and golden redhorses. Its distribution in Missouri is remarkably similar to that of the black redhorse. *Hypentelium nigricans* is an inhabitant of clear streams with clean gravelly or rocky bottoms and permanent flow. It is most often found in or near riffles, or in pools where there is noticeable current.

Zoogeography.—Hypentelium nigricans probably was an inhabitant of the preglacial Teays-Mississippi system and has long inhabited the Ozark Uplands. Its only close relatives are *H. roanokense* Raney and Lachner from the Roanoke River in Virginia and *H. etowanum* (Jordan) from the Alabama River system.

Moxostoma duquesnei (Lesueur)—black redhorse

Moxostoma duquesnei: (?) Meek, 1891:117,121,126,129 (Meramec Spring, Meramec R. and Big Dry Fork near St. James; Little Dry Fork near Rolla; Osage Fork SE Marshfield; Lick Fork at Mansfield; Little Piney Cr. at Newburg; Gasconade R. at Arlington; Shoal Cr. near Neosho; James R. near Springfield; North Fork White R. S Cabool). (?) Evermann and Kendall, 1895:470 (Indian Cr. near Neosho). Patriarche, 1953 (abund.; Lake Wappapello). Funk, 1957 (mov.; Missouri streams). Patriarche and Campbell, 1958:251 (abund.; growth; Clearwater Res.).

Moxostoma duquesnei duquesnei: Martin and Campbell, 1953 (abund.; hab.; Black R.).

Black redhorse: Purkett, 1958b:7,25,43 (growth; length-weight relat.; Missouri streams).

Distribution and habitat.—The black redhorse is restricted in Missouri to the Ozark Uplands (Map 99). In many Ozark streams

the total poundage of this fish and the golden redhorse equals that of all other large fishes combined. The species of *Moxostoma* were confused by workers prior to 1900, and literature records for that period have been plotted only where specimens were examined.

The black redhorse inhabits clear streams having permanent flow and clean gravelly or rocky bottoms. It is most abundant in streams of medium size, being replaced by the white sucker in headwater creeks and spring branches and by the northern redhorse and golden redhorse in the larger rivers. Generally it is more abundant than the golden redhorse in the cooler and swifter streams. Where the two occur together, the black redhorse tends to occupy short, rocky pools with considerable current, whereas the golden redhorse is most abundant in larger pools and backwaters with little or no current.

Zoogeography.—Moxostoma duquesnei probably inhabited the preglacial Teays-Mississippi system. It may have survived the Wisconsin ice advance in both the Ozark and Appalachian uplands and possibly also in the Driftless Area. *Moxostoma duquesnei* is known from late-Illinoian fossil deposits in southwestern Kansas (G. R. Smith, 1963:281), indicating a more western distribution in the past.

Moxostoma erythrurum (Rafinesque)—golden redhorse

Ptychostomus bucco: Cope, 1871:437 (orig. descr.; St. Joseph, Mo.).

Moxostoma macrolepidotum duquesnei: (?) Jordan and Meek, 1885:15 (Flat Cr. near Sedalia and/or Blackwater R. at Brownsville). (?) Meek, 1891 (Niangua R. near Marshfield; Maries R. near Dixon).

Moxostoma macrolepidotum: (?) Call, 1887:74,80 (West Fork Black R., Reynolds Co.; Jacks Fork, Shannon Co.; Meramec R., Dent Co.; Big Cr. and Piney R., Texas Co.; Hinkson Cr., Boone Co.).

Moxostoma erythrurum: Martin and Campbell, 1953 (abund.; hab.; Black R.). Patriarche, 1953 (abund.; Lake Wappapello). Funk, 1957 (mov.; Missouri streams). Patriarche and Campbell, 1958:251 (abund.; growth; Clearwater Res.). Fisher, 1962:428 (Missouri R. local.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.).

Golden Redhorse: Purkett, 1958b:8,26,43 (growth; length-weight relat.; Missouri streams).

Distribution and habitat.—The golden redhorse occurs throughout the Ozarks and northeastern Ozark border (Map 100). It is rare in the western part of the prairie region, where it may have declined in abundance since settlement. It is the most abundant redhorse in many Missouri streams. The habitat requirements of this fish are similar to those of the black redhorse, except that *M. erythrurum* prefers slightly warmer waters and less current, and is more tolerant of turbidity and intermittent flow. It reaches its

greatest abundance in moderately clear, unpolluted streams having large, permanent pools and well defined gravelly or rocky riffles.

Zoogeography.—Except for a more widespread occurrence west of the Mississippi River, *M. erythrurum* is distributed much like *M. duquesnei,* and the two probably had a similar distributional history during the Pleistocene.

Moxostoma anisurum (Rafinesque)—silver redhorse

Catostomus anisurus: Agassiz, 1854:87 (St. Louis).
Silver redhorse: Purkett, 1958b:27 (growth; Missouri streams).

Distribution and habitat.—The silver redhorse is widespread but seldom abundant in the northern and eastern Ozarks (Map 101). I have found this species to be most abundant in the Salt River of northeastern Missouri. There it is the most abundant redhorse. It may also be abundant in other streams of the northeastern Ozark border, but most of these have not been sampled with the kind of collecting gear that is effective for sampling redhorse. The silver redhorse inhabits the larger and deeper pools of medium to large streams having moderately clear water, rocky or gravelly bottoms, and permanent flow. It avoids swift-flowing streams having high gradients and those that are excessively turbid.

Zoogeography.—*Moxostoma anisurum* is northern and eastern in distribution. Perhaps it was localized in the Hudson Bay or Laurentian systems preglacially, and entered the Mississippi Valley by way of stream connections that developed during the Pleistocene.

Moxostoma macrolepidotum (Lesueur)—northern redhorse

Moxostoma breviceps: Forbes and Richardson, 1920:map XXII (Mississippi R. local.).

Moxostoma aureolum: Hubbs, 1930:30 (Osage R.). Barnickol and Starrett, 1951:292-293 (abund.; utiliz.; Mississippi R. local.). Purkett, 1958a:124-125 (growth; Salt R.).

Moxostoma aureolum pisolabrum: Trautman and Martin, 1951 (orig. descr.; type local. Coon Cr., Jasper Co.; Missouri local. mapped). Martin and Campbell, 1953:46 (abund.; Black R.). Patriarche, 1953 (abund.; Lake Wappapello).

Moxostoma macrolepidotum: Hanson and Campbell, 1963 (linear distr.; Perche Cr.). Cross, 1967:189 (Missouri R. local. mapped).

Northern redhorse: Purkett, 1958b:9,28,43 (growth; length-weight relat.; Missouri streams).

Taxonomic considerations.—Trautman and Martin (1951) recognized *Moxostoma macrolepidotum pisolabrum* from the Ozark Uplands and adjacent parts of the Arkansas and Osage river systems in Kansas and Oklahoma. They indicated that *M. m. pisolabrum* differed notably from the nominate subspecies only in the enlargement of the upper lip, which in adults is developed into a prominent bulbous knob. They treated all populations from Missouri south of the Missouri River as typical *M. m. pisolabrum* and restricted the zone of intergradation between the two subspecies to Missouri north of the Missouri River. Minckley and Cross (1960) subsequently extended the zone of intergradation to include all of the Missouri River system in Kansas, except for the Osage drainage. Since 1961 I have examined much additional material of *M. macrolepidotum* from Missouri, and I can see no basis for treating populations in Ozarkian tributaries of the Missouri River as typical *M. m. pisolabrum,* while treating populations in the same drainage system north of the Missouri River as intergrades. Specimens I have examined from the Osage, Gasconade and Meramec systems south of the Missouri River seem to exhibit as much variability in the development of the bulbous knob as do specimens from Chariton River, Perche Creek and Loutre River to the north. Specimens from Mississippi River tributaries north of the Missouri River are likewise quite variable in this character but are much closer to the nominate subspecies than populations in the Missouri River system. Thus, it would appear that the zone of intergradation is much broader than that indicated by Trautman and Martin and perhaps includes all of the Missouri River system in Missouri. Probably populations in tributaries of the Mississippi River from Salt River northward are typical *M. m. macrolepidotum.*

Distribution and habitat.—The northern redhorse is widespread in the Ozarks, but is rare in the White River system (Map 102). It is abundant in the northeastern Ozark border but becomes increasingly scarce and spotty in distribution westward in the prairie region. *Moxostoma macrolepidotum* inhabits streams of all sizes, but it achieves its greatest abundance in moderately large rivers. It is the most abundant redhorse in the lower sections of large Ozark streams. In the prairie region it frequents small streams to a much greater extent than in the Ozarks. In rivers the northern redhorse is most abundant in deep, swift chutes; in small streams it is sometimes found in pools with no noticeable current. No other Missouri redhorse seems as plastic in its habitat requirements as the northern redhorse.

Zoogeography.—Metcalf (1966:144) suggested that *M. m. macrolepidotum* may have been localized in the pregacial Hudson Bay system and came into contact with *M. m. pisolabrum* after deflection of the upper Missouri River southward into the Mississippi

Valley. *Moxostoma m. pisolabrum* has probably long inhabited the Ozark Uplands. Perhaps it had a widespread preglacial distribution in the northern and western part of the Mississippi Valley. Following retreat of the Wisconsin ice sheet, the upper Mississippi and Great Lakes drainages may have been invaded by *M. m. macrolepidotum* from a glacial refugium in the upper Missouri River by way of temporary connections between the upper Mississippi and middle Missouri systems (Bailey and Allum, 1962:113-114). *Moxostoma m. pisolabrum* and its close relative *M. m. breviceps* represent another example of the geminate forms inhabiting the Ozark and Appalachian uplands. *Moxostoma m. breviceps* was probably localized preglacially in the Teays, Ohio, and/or Tennessee systems.

Moxostoma carinatum (Cope)—river redhorse

Placopharynx carinatus: Patriarche, 1953 (abund.; Lake Wappapello).
Moxostoma carinatum: Martin and Campbell, 1953:46 (abund.; Black R.).
River redhorse: Purkett, 1958b:29, 43 (growth; length-weight relat.; Missouri streams).

Distribution and habitat.—The river redhorse occurs throughout the Ozarks but is nowhere abundant (Map 103). In most collections it is represented by one or a few individuals. *Moxostoma carinatum* has declined markedly over much of its range within the last century, but there seems to have been no changes in distribution in Missouri for at least the last 30 years. This sucker inhabits the pools of clear, medium-sized or large streams with permanent strong flow and clean gravelly or rocky bottoms. It seems to be less tolerant of turbidity, siltation, and intermittent flow than any other Missouri redhorse.

Zoogeography.—The distribution of *M. carinatum* suggests that it inhabited the preglacial Teays-Mississippi system, and has long been present in the Ozark Uplands. Disjunct populations in southern Michigan and in the St. Lawrence River may date from a more widespread distribution to the northeast during the Climatic Optimum. Alternatively, the intervening populations may have been extirpated by man's activities within historic time.

Minytrema melanops (Rafinesque)—spotted sucker

Minytrema melanops: Meek, 1891:117 (Meramec Spring near St. James). Patriarche, 1953 (abund.; Lake Wappapello). Martin and Campbell, 1953: 46 (abund.; Black R.). Funk and Campbell, 1953 (Black R. local.).

Distribution and habitat.—The spotted sucker occurs mainly in the lowlands with scattered populations in the eastern and southwestern Ozarks (Map 104). It is known from the upper Mississippi River and the Salt River system but has not been taken there for nearly 30 years. Cross (1967:182) mapped early records of the spotted sucker in the Missouri drainage of Kansas, but this species has not been reported anywhere else in the Missouri system. If the spotted sucker is native to the Missouri system, it is surprising that it does not occur in the Gasconade and Osage drainages of Missouri, where there seems to be an abundance of habitat suitable for this species. In the lowlands the spotted sucker is most often found in clear ditches having little or no current and with thick growths of submergent aquatic vegetation. In the Ozarks it inhabits the sluggish pools of small creeks draining level areas along the major divides, and the quiet backwaters and overflow pools of larger streams.

Zoogeography.—*Minytrema melanops* is widespread in the central and southeastern United States. Perhaps it has inhabited the lower Mississippi Valley continuously since preglacial time.

Erimyzon sucetta Lacépède—lake chubsucker

Erimyzon sucetta kennerlyi: Martin and Campbell, 1953 (abund.; Black R.).

Distribution and habitat.—The lake chubsucker occurs in the lowlands, and has isolated populations along the Current and upper Meramec rivers in the Ozarks (Map 105). Specimens collected near St. Louis in 1853 suggest a former more widespread distribution along the Mississippi River. This fish is nowhere abundant in Missouri, and may have declined in recent years. The lake chubsucker is most often found in clear, quiet pools having a thick growth of submerged aquatic vegetation and bottoms composed of sand or silt mixed with organic debris. In the lowlands it is found in the smaller and more sluggish ditches, and in the Ozarks it occurs in overflow pools and quiet backwaters along the larger streams. It is likely that the habitat of this species was more prevalent in the lowlands before the swamps were drained than is now the case.

Zoogeography.—The range and requirements of *E. sucetta* and *Minytrema melanops* are much alike, suggesting a similar distributional history for the two species.

Erimyzon oblongus (Mitchill)—creek chubsucker

(?) *Erimyzon sucetta:* Meek, 1891:129 (North Fork White R. S Cabool).
Erimyzon oblongus claviformis: Martin and Campbell, 1953:46 (abund.; Black R.). Funk and Campbell, 1953 (Black R. local.).

Distribution and habitat.—The creek chubsucker is widespread

in the southern and eastern Ozarks but is absent from the Neosho and Missouri stream systems (Map 106). It is nowhere abundant and tends to occur as small, widely scattered populations.

The habitat of *E. oblongus* is similar to that of the lake chubsucker, but it is less strictly associated with submergent vegetation, and occurs more frequently in the main channels of flowing streams. The two species may be highly competitive, as suggested by their complementary distribution patterns in Missouri.

Zoogeography.—Two subspecies of *E. oblongus* are recognized. *Erimyzon o. oblongus* (Mitchill) occupies the eastern part of the Lake Ontario Basin and Atlantic coastal drainages as far south as Virginia (Hubbs and Lagler, 1947:51), and *E. o. claviformis* (Girard) occupies the remainder of the range as mapped (Map 106). Intergrades occur in Atlantic coastal drainages of Georgia (Bailey, Winn and Smith, 1954:123). The distributional relationships of these two subspecies are similar to those of the subspecies of *Esox americanus*, and perhaps are subject to the same explanation. *Erimyzon o. claviformis* and *E. o. oblongus* probably evolved from ancestral stocks that were localized in the Mississippi Valley and Atlantic coastal drainages respectively. Possibly the progenitor of *E. o. oblongus* occupied the preglacial Laurentian system. Gulf and Atlantic coastal drainages of the southeastern United States were probably occupied at that time by ancestral stocks of *Erimyzon tenuis* (Agassiz). The lowering of sea levels during Pleistocene ice advances may have created stream connections that permitted eastward movement of *E. o. claviformis* along the Gulf Coast and southward movement of *E. o. oblongus* along the Atlantic Coast, bringing the three previously isolated forms into contact. After retreat of Wisconsin ice *E. o. claviformis* entered the Great Lakes system through the outlets of glacial lakes Chicago and Maumee (Greene, 1935:63), and came into contact with *E. o. oblongus* in the Lake Ontario Basin.

Ictaluridae

Ictalurus melas (Rafinesque)—black bullhead

Ameiurus melas: Jordan and Meek, 1885:10,13,14,15,16 (Hundred and Two R. at Maryville; Missouri R. at St. Joseph; Tabo Cr. 6 mi. E Lexington; Flat Cr. at Sedalia and/or Blackwater R. at Brownsville; Grand R. at Clinton and/or Tebo Cr. at Calhoun). Meek, 1891:120,124 (Big Piney R. at Cabool; Maries R. near Dixon). Fowler, 1915:208 (St. Joseph). Forbes and Richardson, 1920:map LV (Mississippi R. local.). Patriarche and Campbell, 1958 (abund.; Clearwater Res.).

Ameiurus melas melas: Barnickol and Starrett, 1951:303-311 (abund.; Mississippi R. local.). Martin and Campbell, 1953 (abund.; Black R.). Funk and Campbell, 1953 (abund.; Black R. local.).

Ictalurus melas: Fisher, 1962:428 (Missouri R. local.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.). Cross, 1967:198 (Missouri R. local. mapped).

Distribution and habitat.—The black bullhead probably occurs at least occasionally in every principal stream system of Missouri (Map 107). It is the most abundant bullhead in the prairie region. In the Ozark and lowland regions it is usually less abundant than the yellow bullhead. *Ictalurus melas* has broad environmental tolerances. The habitats in which it is abundant are characterized by turbid water, a silt bottom, the absence of noticeable current or strong flow, and a lack of diversity in the fish fauna. Especially favorable are the permanent pools of small, low-gradient creeks having intermittent flow, and the muddy oxbows and backwaters of large streams in the prairie region. In these habitats the black bullhead, fathead minnow, green sunfish, and golden shiner often comprise the bulk of the fishes present.

Zoogeography.—Ictalurus melas is wide-ranging, but is more western in distribution than the other bullheads. This, along with its tolerance of extremes of temperature, turbidity, and flow, suggests an origin in streams of the Great Plains. Some workers have recognized a northern and a southern subspecies. Metcalf (1966: 149) suggested that the subspecies may have resulted from initial isolation of ancestral stocks in the southwestern part of the Hudson Bay system and in preglacial drainage of the central and southern plains. Subsequent mixing of the two stocks and the formation of a broad zone of intergradation occurred when part of the Hudson Bay drainage was diverted into the Mississippi Valley. The black bullhead has been reported from Illinoian fossil deposits from southwestern Kansas and northwestern Oklahoma (C. L. Smith, 1954:285; 1958:178; G. R. Smith, 1963:281).

Ictalurus nebulosus (Lesueur)—brown bullhead

Ameiurus nebulosus: Meek, 1891:120 (Osage Fork Gasconade R. 6 mi. SE Marshfield). Fowler, 1915:207-208 ("Paw Paw, Mo.").

Ictalurus nebulosus marmoratus: Barnickol and Starrett, 1951:303-311 (abund.; Mississippi R. local.).

Ictalurus nebulosus: Fisher, 1962:428 (Moniteau Cr. near Rocheport).

Distribution and habitat.—I have confirmed locality records for the brown bullhead in Missouri only from Duck Creek Wildlife Area in Bollinger County, where this fish is common, and a roadside ditch in Stoddard County, where a single specimen was taken in 1946 (Map 108). I have not reexamined specimens for the references cited above; any or all of them may be based on misidentifications, because the species of bullheads have often been

confused. The "Paw Paw, Mo." referred to by Fowler (1915:207-208) may be Paw Paw Creek in Sullivan County. The brown bullhead has been stocked in a few ponds in Missouri, but none of these stockings is known to have resulted in the establishment of populations in natural waters. The habitat requirements of the brown bullhead are similar to those of the yellow bullhead, except that *nebulosus* is less often found in flowing waters.

Zoogeography.—Ictalurus nebulosus is eastern in distribution, reaching the western limit of its present range in Missouri. C. L. Smith (1962:512) tentatively identified this species from Middle Pliocene deposits in Logan County, Kansas, thereby indicating a former more westerly distribution.

Ictalurus natalis (Lesueur)—yellow bullhead

Ameiurus natalis: Jordan and Meek, 1885:13 (Missouri R. at St. Joseph). Meek, 1891:116 (Little Dry Fork near Rolla). Fowler, 1915:207 (Marshfield). Martin and Campbell, 1953 (abund.; Black R.). Funk and Campbell, 1953 (abund.; Black R. local.). Funk, 1957 (mov.; Missouri streams). Patriarche and Campbell, 1958 (abund.; Clearwater Res.).

Ameiurus natalis natalis: Barnickol and Starrett, 1951:303-311 (abund.; Mississippi R. local.).

Ictalurus natalis: Fisher, 1962:428 (Missouri R. local.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.).

Distribution and habitat.—The yellow bullhead is nearly as widespread in Missouri as the black bullhead (Map 109). It is the commonest bullhead in the Ozark and lowland regions, and it is nearly as common as the black bullhead in the clearer prairie streams of central and northeastern Missouri. The yellow bullhead prefers clearer waters than the black bullhead and is usually found in or near streams with permanent flow. Like the other bullheads, this fish avoids strong currents. In the Ozarks it is almost invariably found in quiet, heavily vegetated backwaters and overflow pools. Elsewhere it is less restricted and often occurs in the open pools of the stream channel.

Zoogeography.—This species possibly had a more eastern origin than *I. melas,* but its present widespread distribution provides no clues to the drainages in which its ancestral stocks were localized.

Ictalurus punctatus (Rafinesque)—channel catfish

Ictalurus punctatus: Jordan and Meek, 1885:11,13,14,16 (Hundred and Two R. at Maryville; Missouri R. at St. Joseph; Tabo Cr. at Lexington; Grand R. at Clinton and/or Tebo Cr. at Calhoun). Call, 1887:74 (Piney R., Texas Co.). Meek, 1891:120 (Gasconade R. near Newburg). Fowler, 1915:206 (Brownsville and St. Louis). Forbes and Richardson, 1920:map LII (Mississippi R. local.). Coker, 1930:174-177 (abund.; life hist.; Mississippi R. at Canton). Martin and Campbell, 1953:47 (abund.; Black R.). Funk and Campbell, 1953 (abund.; Black R. local.). Marzolf, 1957 (reprod.; Missouri ponds). Funk, 1957 (mov.; Missouri streams). Purkett, 1958a:127-129 (growth; import.; Salt R.). Fisher, 1962:428 (Missouri R. local.). Burress, 1962 (abund.; Bull Shoals Res.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.). Morris, 1967 (prop.; Missouri ponds). Cross, 1967:206 (Missouri R. local. mapped).

Ictalurus anguilla: Forbes and Richardson, 1920:179-180 (Mississippi R. at Alton and Grafton, Ill.).

Ictalurus lacustris punctatus: Borges, 1950 (Niangua Arm, Lake Ozark). Barnickol and Starrett, 1951:303-311 (abund.; growth; Mississippi R. local.). Marzolf, 1955 (growth; Niangua Arm, Lake Ozark).

Ictalurus lacustris: Berner, 1951:9,10 (food; Missouri and Mississippi R.). Patriarche, 1953 (abund.; Lake Wappapello).

Channel catfish: Purkett, 1958b:31,43 (growth; length-weight relat.; Missouri streams). Fry, 1962 (harv.; Table Rock, Taneycomo, and Clearwater Res. tailwaters).

Distribution and habitat.—In Missouri the channel catfish is the most abundant and widely distributed of the larger catfishes; it occurs over all of the state except for the central Ozarks (Map 110). It is found in a variety of habitats but attains its greatest abundance in large streams and impoundments. It avoids clear or cool streams, and those with high gradients. Adults are found in the larger pools, in deep water or near cover. The young often occur in riffles and in shallow pools.

Zoogeography.—Ictalurus punctatus ranges widely in the central United States, and could have been present in all of the principal preglacial drainages of the region. It is known from Pliocene (C. L. Smith, 1962:507) and Pleistocene (C. L. Smith, 1954:285; 1958:179 and G. R. Smith, 1963:281) fossil deposits in the southern plains, thereby indicating that it has long occurred in or near Missouri.

Ictalurus furcatus (Lesueur)—blue catfish

Ameiurus ponderosus: Bean, 1880a:286-290 (orig. descr.; Mississippi R. near St. Louis).

Ictalurus furcatus: Jordan and Meek, 1885:13 (Missouri R. at St. Joseph). Forbes and Richardson, 1920:179 (abund.; Mississippi R. at Alton, Ill.). Coker, 1930:174-175 (Mississippi R. at Warsaw, Ill.). Berner, 1951:table 5 (commer. catch; Missouri and Mississippi rivers). Fisher, 1962:428 (Missouri R. local.). Cross, 1967:209-213 (size records; Missouri R. local. mapped).

Ictalurus f. furcatus: Borges, 1950 (vert. distr.; Niangua Arm, Lake Ozark). Barnickol and Starrett, 1951:303-311 (abund.; Mississippi R. local.).

Distribution and habitat.—In Missouri the blue catfish is known only from the Missouri, Mississippi, Osage and Grand rivers (Map 111). In these streams it is much less common than the other large catfishes. *Ictalurus furcatus* is principally an inhabitant of swift chutes and of pools having noticeable current. It also occurs in the open waters of large reservoirs.

Zoogeography.—An extinct species (*Ictalurus lambda* Hubbs

and Hibbard) related to *I. furcatus* has been reported from early Pliocene fossil deposits in Kansas (Hubbs and Hibbard, 1951:8-14; C. L. Smith, 1962:510). This suggests that *I. furcatus* or its ancestral stocks long have been present in or near Missouri.

Noturus gyrinus (Mitchill)—tadpole madtom

Noturus gyrinus: Hanson and Campbell, 1963 (linear distr.; Perche Cr.). Taylor, 1969:35-54, map 1: (syn.; char.; compar.; Missouri local. mapped).

Distribution and habitat.—The tadpole madtom occurs in the lowlands and in a broad northeastward-trending zone from Spring River in southwestern Missouri into tributaries of the Mississippi River in northeastern Missouri (Map 112). *Noturus gyrinus* may have been more abundant in Missouri before settlement than it is today, particularly in the prairie streams of west-central Missouri. Trautman (1957:444-445) noted a decrease in the abundance of this species in Ohio as a result of the drainage of marshes, stream channelization, and increased turbidity and siltation; similar environmental changes have occurred in Missouri. The tadpole madtom inhabits clear to moderately turbid waters with little current and an abundance of cover, such as thick growths of submergent aquatic vegetation or accumulations of organic debris. In the lowlands *N. gyrinus* is most abundant in ditches having no noticeable current and along the vegetated margins of ditches with current. In the prairie region it inhabits quiet pools of small, sluggish creeks draining flat upland areas, and backwaters and overflow pools along the larger streams.

Zoogeography.—The present distribution of this wide-ranging species provides few clues to its place of origin. Perhaps it has inhabited the Mississippi Valley continuously since preglacial time.

Noturus exilis Nelson—slender madtom

Noturus exilis: Bean, 1880:112 (South Grand R.). Call, 1887:79 (Hinkson Cr., Boone Co.). Meek, 1891:117,120,124,126,129 (Little Dry Fork near Rolla; Jones Cr. near Dixon; Little Piney Cr. near Arlington and/or Newburg; Niangua R. near Marshfield; Shoal Cr. near Neosho; James R. near Springfield). Evermann and Kendall, 1895:470 (Indian Cr. near Neosho). Metcalf, 1966:151 (Moniteau Cr., Moniteau Co.; Moreau Cr., Morgan Co.). Taylor, 1969:57-68, map 2 (syn.; char.; compar.; Missouri local. mapped).

Schilbeodes exilis: Jordan and Evermann, 1900:3236, fig. 65 (*sic.*) (Ozark Fork Gasconade R., Marshfield).

Schilbeodes insignis: Fowler, 1915:209 (Carthage). Hubbs and Raney, 1944: 18-24 (char.; syn.; compar.; Missouri local. mapped). (?) Martin and Campbell, 1953 (abund.; Black R.).

Distribution and habitat.—The slender madtom is common over most of the Ozarks, and it occurs at scattered localities in the northeastern Ozark border (Map 113). Elsewhere in the state it is known only from the Blue River in Jackson County, and tributaries of the Osage River in Vernon County. Over much of the Ozarks it is the most abundant madtom. However, it is scarce in the southeastern Ozarks, perhaps as a result of competition from the Ozark madtom, a species with similar habits. The slender madtom is characteristic of small to medium-sized streams with moderate or high gradients and permanent flow of clear water. It is usually found on rocky riffles, or in rocky pools where there is sufficient current to keep the bottom free of silt.

Zoogeography.—The present distribution of *N. exilis* suggests that its origin was in the central Mississippi Valley, and that it probably has long occupied the Ozark Uplands. Disjunct populations in the Tennessee and Cumberland basins (Taylor, 1969:64) may owe their isolated position to eastward dispersal during one of the Pleistocene ice advances, when the lowering of sea levels produced conditions in the Mississippi Embayment more suitable for upland fishes.

Noturus nocturnus Jordan and Gilbert—freckled madtom

Noturus nocturnus: Taylor, 1969:74-83; map 4 (syn.; char.; compar.; Missouri local. mapped).

Distribution and habitat.—The distribution of the freckled madtom in Missouri is similar to that of the tadpole madtom, but the two are seldom found together (Map 114). *Noturus nocturnus* is nowhere abundant, but it is frequently found in the upper Osage and Mississippi rivers, as well as streams and ditches of the lowlands. It inhabits clear to moderately turbid streams having permanent flow and low or moderate gradients. *Noturus nocturnus* occupies sluggish riffles over a gravel or rubble bottom. Cross (1967: 219) reported it from among leaves and other woody material over a muddy bottom in Kansas, but I have not found it in such habitats in Missouri.

Zoogeography.—*Noturus nocturnus* is primarily southern in distribution and perhaps is autochthonous to the lower Mississippi Valley.

Noturus flavus Rafinesque—stonecat

Noturus flavus: Jordan and Meek, 1885:10,15,16 (Hundred and Two R. at Maryville; Flat Cr. near Sedalia and/or Blackwater R. at Brownsville; Grand R. at Clinton and/or Tebo Cr. at Calhoun). Fowler, 1915:208 (Clinton). Taylor, 1969:111-128, map 8 (syn.; char.; var.; compar.; Missouri local. mapped).

Distribution and habitat.—The stonecat occurs over most of the northern two-thirds of Missouri, but is most abundant in the north-

ern Ozark border and the prairie region (Map 115). It is common in the upper Mississippi, but it is rare in the lower Mississippi and Missouri rivers. *Noturus flavus* occurs in varied stream types but avoids those with intermittent flow or extremely high gradients. It usually occupies rocky riffles in swift current. In the Missouri River I have found it over sandy bottoms in swift current.

Variation and zoogeography.—Stonecats from the Missouri and lower Mississippi rivers have the eyes much reduced in size, but otherwise appear to be typical of *flavus* (Taylor, 1969:123). These differences may be environmentally induced, but it is also possible that the Missouri-lower-Mississippi population is a genetic variant adapted for survival in the distinctive habitat of large, continuously turbid streams. *N. flavus* has a widespread northern distribution and could have been present preglacially in all of the principal drainages that were integrated to form the present Mississippi system.

Noturus albater Taylor—Ozark madtom

(?) *Noturus flavus:* Martin and Campbell, 1953:47 (abund.; Black R.).

Noturus albater: Taylor, 1969:144-150, map 10 (orig. descr.; type local. White R., Taney Co.; Missouri local. mapped).

Distribution and habitat.—The Ozark madtom is the most abundant small catfish in the southern Ozarks (Map 116). It inhabits riffles and rocky pools of clear, high-gradient streams with permanent strong flow.

Zoogeography.—The Ozark madtom is endemic to the southern Ozarks, and probably had its origin in or near its present area of occurrence. It is a distinctive species without close affinity to other species of the subgenus *Rabida* (Taylor, 1969:149).

Noturus placidus Taylor—Neosho madtom

Distribution and habitat.—The Neosho madtom was included only in a collection from the Spring River just upstream from the Kansas state line (Map 117). This collection contained 60 slender madtoms and 23 stonecats, but only two Neosho madtoms. Collections elsewhere in the Spring River in Missouri have yielded an abundance of other madtoms, but not the Neosho madtom; Cross (1967: 233) reported it from the Spring River in Kansas. *N. placidus* inhabits gravelly or rocky riffles of medium-sized to moderately large streams with permanent flow, moderate gradients, and fairly clear water. Deacon (1961:396) noted a marked decrease in the abundance of the Neosho madtom in Kansas during a period

of extreme drought, when the Neosho River became intermittent for the first time since flow records were kept.

Zoogeography.—The Neosho madtom is endemic to the Neosho and Illinois stream systems of northeastern Oklahoma and adjoining states. It seems to be most closely allied to madtoms of the *furiosus* species group (Taylor, 1969:172) and may have evolved from a common ancestral stock that has long been isolated west of the Mississippi Embayment. No other species of this group occurs west of the Mississippi River.

Noturus miurus Jordan—brindled madtom

Schilbeodes miurus: Martin and Campbell, 1953 (abund.; Black R.).

Noturus miurus: Taylor, 1969:190-201, map 14 (syn.; char.; compar.; Missouri local. mapped).

Distribution and habitat.—The brindled madtom occurs in the lowland ditches and adjacent portions of the southeastern Ozarks, and in the Spring River of southwestern Missouri (Map 118). It is much more common in the lowlands than in Spring River. Other observers (Cross, 1967:225; Trautman, 1957:441) reported the brindled madtom to be primarily an inhabitant of pools with little current and an abundance of organic debris, but in Missouri *N. miurus* is most often found on gravelly or rocky riffles in a slight or moderate current. The streams where it occurs are characterized by moderate or low gradients, permanent flow, and bottoms that are mostly free of silt.

Zoogeography.—The origin of the *miurus* species group (*N. miurus, N. flavater* and *N. flavipinnis*) was probably in the central Mississippi Valley, where all are found today (Taylor, 1969:189).

Noturus flavater Taylor—checkered madtom

Noturus flavater: Taylor, 1969:204-208, map 14 (orig. descr.; type local. Flat Cr., Barry Co.; Missouri local. mapped).

Distribution and habitat.—The checkered madtom occurs on the southern slope of the Ozark Uplands, where it is similar in distribution to but generally less abundant than the Ozark madtom. The principal difference in their ranges is the absence of the checkered madtom from the St. Francis and Black rivers (Map 119). The checkered madtom inhabits moderately large, clear streams having high gradients and permanent strong flow. It occurs in quiet pools or backwaters where the bottom is composed of gravel and rocks overlain by thick deposits of sticks, leaves, and other organic debris.

Zoogeography.—The checkered madtom is endemic to the White and Black stream systems of the southern Ozarks. It is most

closely allied to *N. miurus* and *N. flavipinnis* (Taylor, 1969:188), and probably evolved from a common ancestral stock that has long been localized in its present area of occurrence.

Pylodictis olivaris (Rafinesque)—flathead catfish

Leptops olivaris: Jordan and Meek, 1885:13,16 (Missouri R. at St. Joseph; Grand R. at Clinton and/or Tebo Cr. at Calhoun). Meek, 1891:120 (Gasconade R. near Newburg).

Pylodictis olivaris: Borges, 1950 (vert. distr.; Niangua Arm, Lake Ozark). Barnickol and Starrett, 1951:303-311 (abund.; growth; Mississippi R. local.). Berner, 1951:table 5 (commer. catch; Missouri and Mississippi rivers). Patriarche, 1953 (abund.; Lake Wappapello). Martin and Campbell, 1953:47 (abund.; Black R.). Funk and Campbell, 1953 (abund.; local.; Black R.). Patriarche and Campbell, 1958 (abund.; Clearwater Res.). Fisher, 1962:428 (Missouri R. local.). Burress, 1962 (abund.; harv.; Bull Shoals Res.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.). Cross, 1967:213 (Missouri R. local. mapped).

Flathead catfish: Purkett, 1958b:31 (growth; Missouri streams). Fry, 1962 (harv.; Taneycomo and Clearwater res. tailwaters).

Distribution and habitat.—The flathead catfish occurs in most of the large streams of Missouri (Map 120). It is most abundant in the Missouri and Mississippi rivers and their major tributaries in the prairie and Ozark border regions. It is common in large reservoirs of the Ozarks, but is rare or absent in many streams of that region. Barnickol and Starrett (1951:303) reported that the total poundage of flatheads in their collections from the Mississippi River exceeded that of any other species of catfish. Flathead catfishes inhabit medium to large streams having moderate or low gradients and permanent flow. The young are often found among rocks in swift water, occupying essentially the same habitats as the stonecat and other riffle-inhabiting madtoms. Adults occur in pools, almost invariably near submerged logs, piles of drift, or other cover.

Zoogeography.—The present distribution of *P. olivaris* suggests an origin in the Mississippi Valley, or in other Gulf drainages to the southwest.

Percopsidae

Percopsis omiscomaycus (Walbaum)—trout perch

Percopsis omiscomaycus: Hanson and Campbell, 1963 (linear dist.; Perche Cr.).

Distribution and habitat.—The trout perch is widespread in the Grand and Chariton stream systems, and occurs eastward along the Missouri and Mississippi rivers to St. Charles and Perry counties (Map 121). It is fairly common in parts of the Chariton, Lamine, Petite Saline and Perche stream systems, but it is rare elsewhere in the state. Its distribution and abundance seem to

have remained unchanged since at least the early 1940's. In Missouri the trout perch is common only in the unstraightened sections of prairie streams having permanent flow and deep pools floored by sand and fine gravel. Possibly the trout perch was more widespread in northern and western Missouri before extensive channelization of the prairie streams.

Zoogeography.—The trout perch is widespread in the northern United States and Canada, and could have been present preglacially in all the principal drainages of that region. Perhaps it was absent from the Mississippi Valley in pre-Pleistocene time, and dispersed southward by way of stream connections that developed with glaciation.

Aphredoderidae

Aphredoderus sayanus (Gilliams)—pirate perch

Distribution and habitat.—The pirate perch is widely distributed in the lowlands and adjacent sections of the southeastern Ozark border (Map 122). It is also known from Peruque Creek in St. Charles County, and probably occurs elsewhere along the Mississippi River. In spite of its general occurrence in the lowlands, *A. sayanus* is seldom abundant. The pirate perch inhabits bottomland lakes, overflow ponds, and the quiet pools and backwaters of low-gradient streams and ditches. The habitats it occupies are characterized by clear water, absence of current, and an abundance of aquatic vegetation, organic debris, or other cover.

Zoogeography.—The pirate perch is the only living species of its family. It may have occupied the lowlands of the Mississippi Valley throughout the Cenozoic Era.

Amblyopsidae

Amblyopsis rosae (Eigenmann)—Ozark cavefish

Typhlichthys subterraneous: Garman, 1889:226 (wells in Jasper Co.; Wilson's and Day's caves, Jasper Co.).

Typhlichthys rosae: Eigenmann, 1898:231 (original descr.; Day's Cave, Jasper Co.). *Ibid.*, 1899:247-251 (descr.; compar.).

Troglichthys rosae: Cox, 1905 (subterranean waters in southern Missouri, northern Arkansas, and probably eastern Kansas).

Amblyopsis rosae: Woods and Inger, 1957:245-247 (syn.; char.; Missouri local. compiled and mapped).

Distribution and habitat.—The Ozark cavefish is known at present only from the Ozark Uplands of southwestern Missouri (Map 123), but it also may occur in portions of adjoining states. No element in the Missouri fish fauna is less well known than the cavefishes, and future efforts directed at correcting this deficiency will

probably reveal a more widespread distribution for this and the following species. *Amblyopsis rosae* is confined to unglaciated uplands underlain by limestone bedrocks that were not extensively deformed by internal stresses during uplift. The highly soluble limestone bedrocks are honeycombed by subsurface drainageways. The Ozark cavefish ventures rarely, if ever, into surface waters; it has been collected only from caves, wells, and the outlets of springs.

Zoogeography.—*Amblyopsis rosae* is well isolated from its closest relative, *A. spelaea* DeKay, which occurs east of the Mississippi Embayment. Woods and Inger (1957:252-255) suggested that the common ancestor of the family Amblyopsidae entered subterranean waters of the limestone plateaus of the central United States during the Tertiary. They envisioned two waves of dispersal. The first wave involved *Amblyopsis,* which spread through the limestone pleateaus and was then split into two isolated populations by the more competitive *Typhlichthys.* One of these isolated populations was localized in the limestone regions of the Ozark Uplands, where it gave rise to *A. rosae.* Amblyopsids presumably disperse primarily through subterranean channels which are largely independent of surface drainage. Consequently, they may disperse across major drainage divides, and perhaps also beneath the channels of large streams, such as the Mississippi River. Perhaps the successive waves of dispersal envisioned by Woods and Inger are related to the repeated cycles of erosion and sedimentation in the Mississippi Embayment that resulted from fluctuations in sea level during the Pleistocene. Such changes might create ecological conditions in subterranean waters that would favor alternate periods of dispersal and isolation of cavefishes east and west of the Mississippi Embayment.

Typhylichthys subterraneus Girard—southern cavefish

Typhlichthys eigenmanni: Hubbs, 1938:265 (*nomen nudum,* central Missouri).

Typhlichthys subterraneus: Woods and Inger, 1957:240-243, fig. 10 (syn.; char.; Missouri local. compiled and mapped).

Distribution and habitat.—The southern cavefish inhabits subterranean waters of the central and southeastern Ozarks (Map 124). It has not been found in the same caves as the Ozark cavefish, but both species occur in Greene County. The habitat of *T. subterraneus* seems to be like that of *A. rosae.*

Zoogeography.—Populations of *T. subterraneus* in the Ozark Uplands are broadly disjunct from those east of the Mississippi River. The potential therefore exists for the divergence of two kinds, as has occurred in the genus *Amblyopsis.* Probably *T. subterraneus* is a recent invader of the Ozark Uplands, and may have dispersed westward during the erosional cycle that accompanied the Wisconsin ice advance.

Gadidae

Lota lota (Linnaeus)—burbot

Lota lota: Gilbert, 1886:210 (Missouri R. at Leavenworth, Kans.). Fisher, 1962 (Missouri R. local.). Metcalf, 1966:153 (Missouri R. 8 mi. S Atchison, Kans.). Cross, 1967:228 (Missouri R. local. mapped).

Distribution and habitat.—All records for the burbot in Missouri are based on single specimens, usually adults, that probably strayed into Missouri from the north along the Missouri and Mississippi rivers (Map 125). Most have been caught by commercial fishermen. In some years there are many reports, whereas in other years none are reported. This suggests that population pressure or other factors result in occasional influx of this fish into Missouri waters. I have examined a small burbot reported by Dr. Leonard Durham to have been taken by him and his students at Duck Creek Refuge, Bollinger County, Missouri, on May 10 or 11, 1964. Durham told me that the specimen, a small individual, was not noticed at the time the collection was made, but was later found when the collection was being sorted. This record is in need of further substantiation, since it is far south of any previous Missouri locality, and is the only report outside of the mainstream of the Missouri and Mississippi rivers.

Zoogeography.—This holarctic species reaches the southern limit of its range in Missouri. Its presence in the Mississippi Valley may date from the Pleistocene, when drainage derangements that accompanied glaciation permitted faunal exchange with other stream systems to the north.

Cyprinodontidae

Fundulus catenatus (Storer)—northern studfish

Fundulus catenatus: Call, 1887:77 (West Fork of Black R. and tribs., Reynolds Co.; Jacks Fork and tribs., Shannon Co.). Meek, 1891:118,122,130 (Meramec R. and Big Dry Fork near St. James; Jones Cr. near Dixon; Gasconade R. and Little Piney Cr. near Arlington; James R. near Springfield). Martin and Campbell, 1953 (abund.; Black R.). Patriarche and Campbell, 1958 (abund.; Clearwater Res.). Smith, 1965:11 (St. Louis, Ste. Genevieve, Perry, and Cape Girardeau counties). Branson, 1964:746 Shoal Cr., Newton Co.).

Distribution and habitat.—The northern studfish is one of the most common and widely distributed Ozark stream fishes (Map

126). Occurrence of *F. catenatus* in Elk River of extreme southwestern Missouri is presumably the result of introduction. All records are recent, and Hall (1956:20-21) suggested that occurrence of the northern studfish in the Neosho system of Oklahoma is the result of introduction. *Fundulus catenatus* inhabits streams of all sizes, having moderate or high gradients, permanent flow of clear water, and bottoms composed mostly of silt-free sand, gravel, or rubble. *Fundulus catenatus* is most often found in shallow water, along the margins of pools and riffles.

Zoogeography.—*Fundulus catenatus* occurs disjunctly in the Ozark and Appalachian uplands. Presence of the closely related or conspecific *F. stellifer* (Jordan) in the Alabama River system suggests that *F. catenatus* has long occupied the uplands east of the Mississippi River. Perhaps *F. catenatus* was localized preglacially east of the Mississippi River, and dispersed westward into the Ozark Uplands during one of the Pleistocene ice advances. Absence of *F. catenatus* from Ozarkian tributaries of the Arkansas River until its introduction by man (Hall, 1956:20-21) suggests a recent invasion of the Ozark Uplands. The occurrence of other disjunct populations of *F. catenatus* both north and south of its two main areas of occurrence indicates a former more widespread distribution. Possibly these isolated populations have resulted from range adjustments that accompanied climatic fluctuations during late-Pleistocene and Recent time.

Fundulus kansae Garman—plains killifish

Fundulus kansae: Miller, 1955:1 (Clay Co.; Boone's Lick Spring, Howard Co.). Fisher, 1962:428 (Missouri R. local.). Cross, 1967:235 (Missouri R. local. mapped).

Distribution and habitat.—In recent collections the plains killifish has occurred abundantly only in Salt Creek near Boone's Lick Spring, Howard County (Map 127), where it is the predominant fish. In the early 1940's, George V. Harry collected many specimens in Clear Creek, Clay County, and in 1945 Fisher (1962:table 1) found it in the Missouri River as far downstream as Franklin County. No specimens were collected by me during a rather extensive survey of the Missouri River in 1963, suggesting that this species is not now as abundant there as it was in 1945. No collections have been made in Clear Creek in recent years, so the present status of the plains killifish in that stream is not known. *Fundulus kansae* normally inhabits streams with alkaline or saline waters and few other kinds of fish. Its distribution may be limited by a requirement for high salinity, or by inability to compete in the more diverse fish populations that occur in most Missouri streams. Where it is abundant, this topminnow is found in all types of habitats, from pools and backwaters to shallow sandy areas with considerable current.

Zoogeography.—Metcalf (1966:152) suggested that *F. kansae* originated in preglacial drainages of the central and southern plains. This is suggested by its present widespread distribution there and occurrence of the closely related or conspecific *F. zebrinus* Jordan and Gilbert in adjacent southwestern drainages. *Fundulus kansae* now occurs, presumably as the result of introduction, in parts of South Dakota (Miller, 1955:11-12), and Montana (C. J. D. Brown, pers. comm. to F. B. Cross).

Fundulus chrysotus (Günther)—golden topminnow

Distribution and habitat.—The golden topminnow is known in Missouri from only five specimens collected at two localities in the lowlands in 1944 and 1946 (Map 128). *Fundulus chrysotus* did not occur in collections made at these localities in 1964. The habitat of the golden topminnow is much like that of the starhead topminnow.

Zoogeography.—*Fundulus chrysotus* is southeastern in its affinities. Perhaps it has occupied the lower Mississippi Valley continuously since preglacial time, or entered from Gulf coastal drainages to the east when lower sea levels created stream connections that favored dispersal.

Fundulus sciadicus Cope—plains topminnow

Zygonectes macdonaldi: Meek, 1891:122,126-127 (orig. descr.; Jones Cr. near Dixon; Osage Fork Gasconade R. 6 mi. SE Marshfield; spring branch at Neosho). Evermann and Kendall, 1895:471 (spring branch at Neosho).
Fundulus sciadicus: Gosline, 1949 (sensory canals; Miller Co.). Metcalf, 1966: 153 (Missouri R. tribs. in central Missouri).

Distribution and habitat.—The plains topminnow occurs disjunctly in the Neosho and Missouri river systems of the north-central and southwestern Ozarks (Map 129). It is locally abundant but tends to occur as scattered, isolated populations. *Fundulus sciadicus* inhabits quiet pools of small creeks, and the backwaters and overflow pools of larger streams. It is invariably found where the water is clear and without noticeable current, and there are dense growths of aquatic vegetation. The plains topminnow seems to have declined in abundance or disappeared from parts of the Neosho and Osage stream systems since the early 1940's.

Zoogeography.—The distribution of *F. sciadicus* suggests that pre-

glacially it may have inhabited either the Iowa and lower Missouri systems, or the Ancestral Plains system. Occurrence in the Neosho system may date from preglacial time, but could as plausibly have resulted from southward dispersal through Pleistocene connections between the Arkansas and middle Missouri systems.

Fundulus notti (Agassiz)—starhead topminnow

Distribution and habitat.—The starhead topminnow is known only from the lowlands and from one locality in St. Charles County (Map 130). Although limited in distribution, *F. notti* is usually abundant where it occurs. This fish is an inhabitant of quiet, weedy backwaters and oxbows along the courses of major streams.

Zoogeography.—Two subspecies of *F. notti* are recognized: *F. n. dispar*, occurring from the southwestern Great Lakes southward in the Mississippi Valley to northeastern Arkansas and western Tennessee, and *F. n. notti*, occurring southward in the Mississippi Valley and along the Gulf coastal plain from western Florida west to Louisiana and eastern Texas. A distinct but closely related species (*F. lineolatus*) occurs along the Atlantic Coast, coming into contact with *F. notti* in northwestern Florida. The presence of a distinct subspecies of *F. notti* in the Mississippi Valley suggests that it is not a recent invader from the south, but rather has long been established there.

Fundulus olivaceus (Storer)—blackspotted topminnow

Zygonectes notatus: Call, 1887:77 (West Fork of Black R., Reynolds Co.; Jacks Fork, Shannon Co.). Meek, 1891:130 (James R. near Springfield; North Fork White R. S Cabool).

Fundulus olivaceus: Gosline, 1949 (sens. can.; Ozark Co.). Martin and Campbell, 1953 (abund.; Black R.). Brown, 1956 (char.; compar.; Little Gravois Cr. 2½ mi. NE Gravois Mills, Morgan Co.; Little Black R. 2.4 mi. E Fairdealing, Butler Co.). Patriarche and Campbell, 1958:255-256 (abund.; Clearwater Res.). Braasch and Smith, 1965 (char.; hab.; relat.; Missouri local. mapped). Thomerson, 1966 (distr.; var.; ecol.; Missouri local. mapped). Setzer, 1970:141 (karyotype; Niangua R.).

Distribution and habitat.—The blackspotted topminnow is abundant and widely distributed in the Ozark and lowland regions (Map 131). In the lowlands it is the most abundant topminnow, and in the Ozarks it is second in abundance to the studfish. *Fundulus olivaceus* inhabits clear streams and ditches having permanent strong flow, clean sand, gravel, or rocky bottoms, and thick stands of water willow or other aquatic vegetation.

In Missouri, as elsewhere in the central and lower Mississippi Valley, *F. olivaceus* and its close relative, *F. notatus*, tend to exclude each other microgeographically and ecologically. In Missouri

they have occurred together only in collections from the lowlands, and from Clear Creek, a tributary of the Osage River in St. Clair County. In a series of collections made in the lowlands in 1964, both species occurred in nine of 36 collections in which one or the other occurred. In eight of the nine collections *F. olivaceus* outnumbered *F. notatus*, often by a significant margin. In the Clear Creek collection, *F. notatus* predominated. The largely allotopic distribution of these two closely related topminnows may result from competition. Their requirements seem to be similar, but they may differ to the extent that, at any given locality, conditions favor one species over the other.

The distributional relationships of *F. olivaceus* and *F. notatus* and the factors determining these relationships in the area where their ranges overlap have been the subject of two recent studies (Braasch and Smith, 1965; Thomerson, 1966). Braasch and Smith concluded that *F. notatus* occurred in "low-gradient streams and sloughs in relatively level areas," and that *F. olivaceus* inhabited "fast gravelly streams in upland areas." They also indicated that the species have occurred together for 60 years or more in several stream systems in southern Illinois. Thomerson studied the two species over a wider area and indicated that their ecological preferences are not uniform throughout their ranges, but *F. notatus* seldom occurs in "blackwater." He also concluded that syntopic associations at a particular locality are "unstable and transient" rather than relatively stable, as indicated by Braasch and Smith.

My observations on the ecological preferences of the two species are in general agreement with Braasch and Smith, except that *F. olivaceus* is not confined to upland areas in Missouri. There *F. olivaceus* seems to occupy clearer and perhaps cooler waters than *F. notatus*. This relationship is apparent in the Meramec system, where *F. notatus* is confined to the upper portions of the Bourbeuse and Meramec mainstem, whereas *F. olivaceus* occupies most of the remainder of the Meramec system. The Bourbeuse and upper Meramec drain undissected uplands, underlain principally by shales and sandstones, whereas the remainder of the Meramec system drains uplands that are intricately dissected and underlain by cherty dolomites and limestones. Springs are virtually absent from the upper Bourbeuse and Meramec drainages, and the streams are more turbid and have lower base flows than those elsewhere in the Meramec system. In the lowlands, *F. notatus* is confined principally to the larger, more turbid ditches, whereas *F. olivaceus* is more widespread.

Concerning the stability of syntopic populations, it appears that the area of syntopic occurrence in southeastern Missouri has remained stable for at least 25 years. Perhaps syntopy is maintained there by influx of *F. notatus* from the Mississippi River and adjacent waters, where this species apparently occurs to the exclusion of *F. olivaceus*. The same explanation could account for the syntopic occurrence of the two species in the upper Osage system. *Fundulus notatus* occurs to the exclusion of *F. olivaceus* in the prairie streams to the west of Clear Creek, whereas *F. olivaceus* occurs in streams immediately to the east.

Fundulus notatus (Rafinesque)—blackstripe topminnow

(?) *Zygonectes zonatus:* Agassiz, 1854:353 (orig. descr.; St. Louis).

(?) *Zygonectes notatus:* Meek, 1891 (Big Dry Fork near St. James).

Fundulus notatus: Forbes and Richardson, 1920:map XLV (Mississippi R. local.). Brown, 1956 (char.; compar.; Meramec R. 2 mi. NW Short Bend, Dent Co.). Braasch and Smith, 1965 (char.; hab.; relat.; Missouri local. mapped). Thomerson, 1966 (distr.; var.; ecol.; Missouri local. mapped).

Distribution and habitat.—The blackstripe topminnow is the most abundant and widely distributed topminnow in the Neosho system of the southwestern Ozarks and in the northeastern Ozark border (Map 132). In lowland ditches of the southeast it is less abundant than the blackspotted topminnow. The blackstripe topminnow was not collected in the Missouri River system before 1950, and its presence there may be due to introduction. The population in Perche Creek, Boone County, is definitely known to have been introduced since 1963. The habitat requirements of *F. notatus* are like those of the blackspotted topminnow except that it prefers slightly warmer and more turbid waters. The blackstripe topminnow avoids streams where the flow is strongly influenced by springs, and is most often found along large, lowland rivers and in the isolated pools of small, intermittent creeks draining level uplands.

Zoogeography.—The present distribution of *F. notatus* and *F. olivaceus* provides few clues to their distributional relationship in preglacial time. Probably one or both species inhabited the preglacial Teays-Mississippi system.

Poeciliidae

Gambusia affinis (Baird and Girard)—mosquitofish

Gambusia affinis affinis: Martin and Campbell, 1953 (abund.; hab.; Black R.). Fisher, 1962:428 (Missouri R. local.).

Gambusia affinis: Patriarche and Campbell, 1958 (abund.; Clearwater Res.).

Distribution and habitat.—In the early 1940's the mosquitofish was confined to the lowlands and the Mississippi flood plain northward from the lowlands to Pike County (Map 133). More recent collections reveal that this fish is now widely distributed in southwestern Missouri and occurs at scattered localities in central Missouri. These range extensions may result in part from stockings for mosquito control. *Gambusia affinis* is one of the most abundant fishes in the lowlands. Backwaters and adjacent oxbows of sluggish lowland streams are its preferred habitat. In such situations it is most abundant in shallow, marginal areas, where the water is clear and warm and there is considerable aquatic vegetation or other cover.

Zoogeography.—The widespread southern distribution of *G. affinis* suggests that it has long inhabited the lower Mississippi Valley and coastal drainages of the southeastern United States.

Atherinidae

Labidesthes sicculus (Cope)—brook silverside

Labidesthes sicculus: Jordan and Meek, 1885:16 (Flat Cr. near Sedalia and/or Blackwater R. at Brownsville). Meek, 1891:119,122,125,126 (Big Dry Fork near St. James; Osage Fork and Niangua R. near Marshfield; Big Piney R. at Cabool; Maries R. near Dixon; Hickory or Shoal Cr. near Neosho). Evermann and Kendall, 1895:471 (Indian Cr. near Neosho). Patriarche, 1953:247 (abund.; Lake Wappapello). Patriarche and Campbell, 1958:255-256 (abund.; Clearwater Res.).

Labidesthes sicculus sicculus: Martin and Campbell, 1953 (abund.; hab.; Black R.).

Distribution and habitat.—The brook silverside is widely distributed in the Ozark and lowland regions (Map 134). *Labidesthes sicculus* seems to be intolerant of siltation and continuous high turbidity; it is confined to clear, warm waters without noticeable current. In the Ozarks it is most often found in the permanent pools of small headwater creeks that receive little spring flow, and the warm backwaters and overflow pools of larger streams. It is one of the most abundant small fishes in Ozark reservoirs.

Zoogeography.—*Labidesthes sicculus* was probably derived from an atherinid stock that invaded freshwaters of eastern North America at an early date; probably it has inhabited the Mississippi Valley continuously since preglacial time.

Menidia audens Hay—Mississippi silverside

Menidia audens: Smith, 1965:12 (Mississippi Co.).

Distribution and habitat.—The Mississippi silverside is common in the Mississippi River downstream from the mouth of the Ohio

River (Map 135). It was not collected in Missouri until 1963. *Menidia audens* inhabits the open waters of large, moderately clear rivers. It is most readily seined at night, suggesting that it moves inshore during the hours of darkness and returns to deeper water in the daytime.

Zoogeography.—According to Gosline (1948:311), *M. audens* developed through invasion of the Mississippi River by *M. beryllina* (Cope) stock, and by subsequent isolation and differentiation in the lower Mississippi Valley.

Percichthyidae[1]

Morone chrysops (Rafinesque)—white bass

Lepibema chrysops: Borges, 1950 (vert. distr.; Niangua Arm, Lake Ozark). Barnickol and Starrett, 1951:319-320 (abund.; utiliz.; Mississippi R. local.).

Morone chrysops: Patriarche, 1953 (growth; abund.; Lake Wappapello).

Roccus chrysops: Cleary, 1956:map 73 (Des Moines R. local.). Burress, 1962 (abund.; Bull Shoals Res.). Cross, 1967:243 (Missouri R. local. mapped).

White bass: Hanson, 1962 (abund.; harv.; Bull Shoals Res.). Fry, 1962 (harv.; tailwaters of Table Rock, Taneycomo and Clearwater res.).

Distribution and habitat.—The centers of abundance for the white bass in Missouri are in the Mississippi River and the large reservoirs of the Ozarks (Map 136). It is seasonally abundant in major tributaries of these waters during its spring spawning migrations. In the Mississippi River *M. chrysops* is more abundant above the mouth of the Missouri River than below (Barnickol and Starrett, 1951:319). White bass are now fairly common in the Missouri River, but they were not found in 1945 by Fisher (1962). Perhaps the recent appearance of the white bass in the Missouri River reflects changes in turbidity and other factors resulting from impoundment of the river upstream from Missouri. Probably the white bass was absent from most parts of the Ozarks until construction of large reservoirs. The white bass inhabits the deeper pools of streams and the open waters of lakes and reservoirs. It tends to avoid waters that are continuously turbid and is most often found over a firm sandy or rocky bottom.

Zoogeography.—This species and *M. mississippiensis* were probably derived from marine stocks that invaded the Mississippi River system in Tertiary time.

Morone mississippiensis Jordan and Eigenmann—yellow bass

Labrax chrysops: Girard, 1858:31 (St. Louis).

[1] Gosline (1966) has recently restricted the family Serranidae to exclude the genus *Morone*, as well as some other groups, and he elevated the subfamily Percichthyinae to family rank.

Morone interrupta: Gill, 1860:118-119 (orig. descr.; St. Louis; New Orleans). Barnickol and Starrett, 1951:319-320 (abund.; utiliz.; Mississippi R. local.).

Distribution and habitat.—In Missouri the yellow bass is known only from the Mississippi River and its overflow waters (Map 137). It is nowhere abundant but seems to be more common above the mouth of the Missouri River than below. *Morone mississippiensis* is typically an inhabitant of lakes and the quiet pools and backwaters of large rivers.

Morone saxatilis (Walbaum), a species of this family not native to Missouri, has been stocked in recent years in Lake of the Ozarks and in Taum Sauk Reservoir on upper Black River. There is no evidence as yet of natural reproduction. Individuals stocked in Taum Sauk Reservoir have been caught below Clearwater Reservoir, many miles downstream.

Centrarchidae

Micropterus punctulatus (Rafinesque)—spotted bass

Micropterus punctulatus punctulatus: Hubbs and Bailey, 1940 (char.; syn.; hybrid.; Missouri local. mapped). Barnickol and Starrett, 1951:317 (Mississippi R. at Caruthersville).

Micropterus punctulatus: Funk and Campbell, 1953 (abund.; Black R.). Patriarche, 1953 (abund.; growth; Lake Wappapello). Funk, 1957 (mov.; Missouri streams). Burress, 1962 (abund.; Bull Shoals Res.).

Spotted bass: Purkett, 1958b:11,33 (growth; Missouri streams). Fry, 1962 (harv.; tailwaters of Table Rock, Taneycomo and Clearwater res.). Hanson, 1962 (abund.; harv.; Bull Shoals Res.).

Distribution and habitat.—The spotted bass has two distribution centers in Missouri (Map 138): (1) lowland ditches and the larger streams of the southeastern Ozarks; (2) the western periphery of the Ozarks, including parts of the White, Neosho, and Missouri systems. In the lowlands it is the most abundant species of *Micropterus;* elsewhere in its Missouri range it is the most abundant black bass in the larger streams. In the cool, spring-fed streams of the central Ozarks it is replaced by the smallmouth bass; in reservoirs and in the prairie streams it is replaced by the largemouth. Occurrence of the spotted bass in the Missouri River system seems to be due to introduction into the Osage drainage at a relatively recent date. Hubbs and Bailey (1940:map 1) plotted no records for this species anywhere in the Missouri River system. By the early 1940's, spotted bass were rather generally distributed in the upper Osage drainage, but it was not until some time later that it entered the Moreau River, which empties into the Missouri River not far upstream from the mouth of the Osage River. *Micropterus punctulatus* is now common in the Moreau, where it hybridizes exten-

sively with the native smallmouth bass. I have seen no spotted bass from Moniteau Creek, the next tributary of the Missouri westward, but I have seen several hybrids taken there since 1962.

Spotted bass have been stocked by Otto Fajen of the Missouri Department of Conservation in the Lamine, Grand, Chariton, Perche, Loutre, and Salt drainages since 1962. Reproduction has occurred in all of these streams. A single juvenile specimen was taken in a collection from the junction of the Missouri and Mississippi rivers in September, 1969. This locality is far removed from any streams where the spotted bass has been stocked, but the specimen is presumed to be a downstream straggler from one of these streams. Probably the spotted bass will eventually become established in all suitable streams of central Missouri.

The spotted bass generally occupies flowing waters that are warmer and slightly more turbid than those inhabited by the smallmouth bass. In the main channels of large rivers, the spotted bass commonly occurs almost to the exclusion of other black basses. It occurs abundantly in smaller streams only if these are not strongly influenced by springs.

Zoogeography.—*Micropterus punctulatus* has probably long inhabited the lower Mississippi Valley. After initial divergence from a common ancestral stock, *M. punctulatus* invaded the range of the closely related *M. coosae* in coastal drainages to the east, and there gave rise to subspecies *M. p. henshalli* (Hubbs and Bailey, 1940: 24).

Micropterus dolomieui Lacépède—smallmouth bass

Micropterus dolomieu: Call, 1887:78 (West Fork of Black R. and tribs., Reynolds Co.; Jacks Fork and tribs., Shannon Co.; Piney R., Texas Co.; Meramec R., Dent Co.). Meek, 1891 (Meramec R., Meramec Spring, and Big Dry Fork near St. James; Gasconade R. and Little Piney Cr. near Arlington; Osage Fork 6 mi. SE Marshfield; Maries R. near Dixon; James R. near Springfield; North Fork White R. S Cabool). Borges, 1950 (vert. distr.; Niangua Arm, Lake Ozark).

Micropterus dolomieu dolomieu: Hubbs and Bailey, 1940 (char.; syn.; Missouri local. mapped). Barnickol and Starrett, 1951:318 (Mississippi R. at Claryville).

Micropterus dolomieu velox: Hubbs and Bailey, 1940 (char.; syn.; hybrid.; Missouri local. mapped).

Micropterus dolomieui: Martin and Campbell, 1953 (abund.; hab.; Black R.). Funk and Campbell, 1953 (abund.; Black R. local.). Funk, 1957 (mov.; Missouri streams). Patriarche and Campbell, 1958 (abund.; growth; Clearwater Res.). Burress, 1962 (abund.; harv.; Bull Shoals Res.). Fajen, 1962 (homing; mov.; Little Saline Cr., Miller Co.; Big Buffalo Cr., Morgan Co.). Pflieger, 1966a (orangethroat darters on nest; Little Saline Cr., Miller Co.). Pflieger, 1966b (reprod.; Little Saline Cr.).

Smallmouth bass: Purkett, 1958b:12,34,43 (growth; length-weight relat.; Missouri streams). Fry, 1962 (harv.; tailwaters of Table Rock, Taneycomo, and Clearwater res.).

Distribution and habitat.—The smallmouth bass is abundant throughout the Ozarks and occurs sparingly in the northeastern Ozark border (Map 139). Only one specimen is known from the Missouri River, but the smallmouth is fairly common in swift water below navigation dams of the upper Mississippi. Its distribution seems to have remained essentially unchanged since the early 1940's, except for introduction into the Lamine River in 1952, and perhaps a reduction in abundance in streams of the Ozark border.

The smallmouth bass is the ecological replacement of the spotted bass and largemouth bass in the clear, cool, permanent-flowing streams of the Ozarks. It tolerates only moderate turbidity and siltation, and occurs only in streams that maintain flow in all but the most severe drouths. It is not usually found in swift current but is most abundant near riffles and in short pools where there is sufficient current to keep the bottom largely free of silt. *Micropterus dolomieui* is often associated with thick beds of water willow (*Justicia americana*), and prefers a coarse gravel, rubble, or boulder-strewn bottom. It also occurs along the rocky, wave-swept shores of large Ozark reservoirs.

Zoogeography.—The smallmouth bass is more northerly in distribution than the spotted bass, and may have been localized in the preglacial Teays or Laurentian systems. Invasion of the Ozark Uplands by the smallmouth bass may date from one of the ice advances of the Pleistocene, when climatic changes and drainage modifications provided conditions suitable for dispersal from the northeast. Hubbs and Bailey (1940) recognized two subspecies of the smallmouth bass in Missouri, but Bailey (per. comm.) no longer considers these to be valid.

Micropterus salmoides (Lacépède)—largemouth bass

Micropterus salmoides: Jordan and Meek, 1885:14,16,17 (Missouri R. at St. Joseph; Flat Cr. near Sedalia and/or Blackwater R. at Brownsville; Grand R. at Clinton and/or Tebo Cr. at Calhoun). Meek, 1891 (Meramec R. near St. James; Piney R. at Arlington and Newburg; Osage Fork 6 mi. SE Marshfield; Lick Fork at Mansfield). Forbes and Richardson, 1920:map LXXXI (Mississippi R. local.). Borges, 1950 (vert. distr.; Niangua Arm, Lake Ozark). Barnickol and Starrett, 1951:315-319 (abund.; Mississippi R. local.). Martin and Campbell, 1953 (abund.; hab.; Black R. local.). Funk and Campbell, 1953 (abund.; Black R. local.). Patriarche and Campbell, 1953 (abund.; growth; Clearwater Res.). Patriarche, 1953 (abund.; growth; Lake Wappapello). Funk, 1957 (mov.; Missouri streams). Burress, 1962 (abund.; harv.; Bull Shoals Res.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.).

Micropterus salmoides salmoides: Fisher, 1962:428 (Missouri R. local.).

Largemouth bass: Purkett, 1958b:13,35,43 (growth; length-weight relat.; Missouri streams). Hanson, 1962 (abund.; harv.; Bull Shoals Res.). Fry, 1962 (harv.; Table Rock, Taneycomo, and Clearwater res. tailwaters).

Distribution and habitat.—The largemouth bass is nearly statewide in distribution (Map 140). In the Ozarks it is common in the quiet backwaters and overflow pools of large streams but attains its greatest abundance in large reservoirs. In spite of widespread stocking in ponds throughout the state, the largemouth is rare in natural waters of northwestern Missouri. It is common in the lowlands, but drainage of the numerous swamps, sloughs, and natural lakes of that region has probably diminished its abundance.

The largemouth bass tolerates varied environmental conditions, but it is more characteristic of lentic habitats than of streams. It is intolerant of excessive turbidity and siltation; it is replaced by one of the other black basses in streams with high gradients and continuous strong flow. The largemouth is especially characteristic of backwaters and oxbows along major streams, permanent pools of intermittent upland creeks, and artificial impoundments.

Zoogeography.—The largemouth bass is widely distributed in the eastern United States, and may have been present in all or most of the major preglacial drainages of that region.

Lepomis gulosus (Cuvier)—warmouth

Chaenobryttus gulosus: Forbes and Richardson, 1920:map 74 (Mississippi R. local.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.).

Chaenobryttus coronarius: Barnickol and Starrett, 1951:319 (abund.; Mississippi R. local.). Martin and Campbell, 1953:47 (abund.; Black R.). Funk and Campbell, 1953:72-81 (abund.; Black R. local.). Patriarche and Campbell, 1953 (abund.; growth; Clearwater Res.).

Warmouth: Fry, 1962 (harv.; Clearwater Res. tailwater).

Distribution and habitat.—The warmouth is common and widespread in the lowlands, and it penetrates into the southeastern Ozarks along the major streams (Map 141). Elsewhere in the state it is known only from scattered localities, mostly along the Mississippi and lower Missouri rivers. The warmouth inhabits the backwaters of streams but is most abundant in adjacent oxbows. It is occasionally found in turbid, weedless waters, but the largest populations occur in clear waters having thick growths of submergent aquatic plants. In rivers it avoids areas with noticeable current.

Zoogeography.—The present distribution and ecological preferences of *L. gulosus* suggest a wide preglacial distribution in the lower Mississippi Valley and other stream systems of the Gulf and Atlantic coastal plains.

Lepomis cyanellus Rafinesque—green sunfish

Lepomis cyanellus: Jordan and Meek, 1885:12,14,16,17 (Hundred and Two R. at Maryville; Missouri R. at St. Joseph; Tabo Cr. 6 mi. E Lexington; Flat Cr. near Sedalia and/or Blackwater R. at Brownsville; Grand R. at Clinton and/or Tebo Cr. at Calhoun). Call, 1887:79 (Bear Cr. and Hinkson Cr., Boone Co.). Meek, 1891:119,122,125,130 (Big Dry Fork near St. James; Little Dry Fork near Rolla; Jones Cr. and Maries R. near Dixon; Gasconade R. and Little Piney Cr. near Arlington; Niangua R. near Marshfield; Big Piney R. and North Fork White R. near Cabool). Evermann and Kendall, 1895:471 (Indian Cr. and spring branch at Neosho). Borges, 1950 (vert. distr.; Niangua Arm, Lake Ozark). Barnickol and Starrett, 1951:318 (abund.; Mississippi R. local.). Martin and Campbell, 1953 (abund.; hab.; Black R.). Funk and Campbell, 1953 (abund.; Black R. local.). Funk, 1957 (mov.; Missouri streams). Patriarche and Campbell, 1958 (abund.; growth; Clearwater Res.). Purkett, 1958a:126-127 (growth; Salt R.). Burress, 1962 (abund.; harv.; Bull Shoals Res.). Fisher, 1962: 428 (Missouri R. local.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.). Cross, 1967:258 (Missouri R. local. mapped).

Green sunfish: Purkett, 1958b:14,36,43 (growth; length-weight relat.; Missouri streams). Fry, 1962 (harv.; tailwaters of Taneycomo and Clearwater res.).

Distribution and habitat.—The green sunfish is statewide in distribution, and has occurred in more collections than any other Missouri fish (Map 142). It is the most abundant centrarchid in streams of the prairie region and Ozark border. In the Ozark and lowland regions it is less abundant than the longear sunfish in most streams. It occurs only as strays in the open channels of the Missouri and Mississippi rivers, but is sometimes abundant in muddy ponds and ditches on their flood plains. The green sunfish tolerates a wide range of environmental conditions, but it thrives best where few other sunfishes occur. It tolerates extremes of turbidity, dissolved oxygen, temperature, and flow, and is well suited for survival in the fluctuating environment of small prairie streams. By late summer and fall these small streams often consist of a series of isolated, stagnant pools. Green sunfish commonly share this habitat with the creek chub, fathead minnow, and black bullhead.

Zoogeography.—I concur with Metcalf (1966:155-156) who suggested a western origin for the green sunfish. Its present distribution and ecological preferences indicate that it evolved under conditions not unlike those found on the Great Plains today. Fossil material referable to the green sunfish is known from late Pliocene deposits in the central plains (C. L. Smith, 1962:516).

Lepomis symmetricus Forbes—bantam sunfish

Distribution and habitat.—The bantam sunfish is known in Missouri only from the Duck Creek Wildlife Area in Bollinger County (Map 143), where it is common. Perhaps it was more widespread in the lowlands before the swamps were ditched and drained. At Duck Creek the bantam sunfish inhabits clear, quiet water having much submerged aquatic vegetation and standing timber.

Zoogeography.—The bantam sunfish seems to be autochthonous

to the lower Mississippi Valley. Disjunct populations along the lower Illinois River may date from range adjustments during, and subsequent to, the postglacial Climatic Optimum.

Lepomis punctatus (Valenciennes)—spotted sunfish

Lepomis punctatus miniatus: Martin and Campbell, 1953:47 (abund.; Black R.). Funk and Campbell, 1953 (abund.; Black R. local.). Patriarche and Campbell, 1958 (abund.; Clearwater Res.).

Distribution and habitat.—The spotted sunfish is common in the lowlands and penetrates into the southeastern Ozarks along the major streams (Map 144). In the lowlands *L. punctatus* is most often found in clear, heavily vegetated ditches; in Ozark streams it commonly occurs in quiet water near boulders and submerged logs.

Zoogeography.—Occurrence of a distinct subspecies (*L. punctatus miniatus*) in the Mississippi Valley suggests a rather long occupancy of the region. The presence of disjunct populations along the Illinois River perhaps result from a postglacial distributional history in the Mississippi Valley similar to that of *L. symmetricus.*

Lepomis gibbosus (Linnaeus)—pumpkinseed

Distribution and habitat.—Only two records are known for the pumpkinseed from streams in Missouri (Map 145). A single subadult was collected in 1963 from an overflow pool of the Meramec River in Crawford County, and five subadults were taken in 1967 from Salt Creek, a small tributary of Grand River in Chariton County. Perhaps these records are the result of escapement from near-by ponds, but there is no evidence for this. The pumpkinseed has been stocked in a few Missouri ponds, but none is known to have been stocked near either of the two localities cited above. I suspect that these records represent natural occurrences. Elsewhere in its range the pumpkinseed is reported to inhabit clear, quiet waters with dense aquatic vegetation; this is the habitat in which it was found along the Meramec River. Salt Creek is a small, turbid prairie stream with a silty bottom and no aquatic vegetation. Perhaps the pumpkinseeds collected in Salt Creek were strays from nearby Swan Lake or other natural lakes along lower Grand River. No fish collections are available from these lakes.

Zoogeography.—Missouri is on the southern edge of the range of *L. gibbosus* in the Mississippi Valley. The distributional relationship of this species and the related *L. microlophus* suggests a northeastern origin for *L. gibbosus,* perhaps in the preglacial Laurentian system.

Lepomis microlophus (Günther)—redear sunfish

(?) *Xystroplites heros.* Bean, 1880b:98 (St. Louis).

Distribution and habitat.—In natural waters, the redear sunfish is confined to the southern half of the state, where it is rare (Map 146). Self-sustaining populations occur as a result of stocking in many small artificial lakes and ponds elsewhere in Missouri. Like the pumpkinseed, this fish prefers quiet, clear waters having considerable aquatic vegetation.

Zoogeography.—The distributional relationship of this fish and the closely related pumpkinseed suggests an origin for the redear in the Mississippi Valley. *Lepomis microlophus* was tentatively identified from Pliocene deposits in Nebraska (C. L. Smith, 1962: 507). If valid, this report establishes the early presence of the redear in the Mississippi Valley, and indicates a more widespread distribution there preglacially.

Lepomis humilis (Girard)—orangespotted sunfish

(?) *Lepomis anagallinus:* Cope, 1871:440 (St. Joseph).

Lepomis humilis: Jordan and Meek, 1885:12,16,17 (Hundred and Two R. at Maryville; Flat Cr. and/or Blackwater R. at Brownsville; Grand R. at Clinton and/or Tebo Cr. at Calhoun). Call, 1887:79 (Bear Cr.; Boone Co.). Meek, 1891:125 (Maries R. near Dixon). Fowler, 1921:399 (St. Louis). Borges, 1950 (vert. distr.; Niangua Arm, Lake Ozark). Barnickol and Starrett, 1951:318 (abund.; Mississippi R. local.). Patriarche, 1953 (abund.; Lake Wappapello). Fisher, 1962:428 (Missouri R. local.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.). Cross, 1967:267 (Missouri R. local. mapped).

Distribution and habitat.—The orangespotted sunfish occurs over much of Missouri except for the central Ozarks (Map 147) but is abundant only in the prairie region and Ozark border. It is common in some silted ditches of the lowlands. *Lepomis humilis* is tolerant of siltation and high turbidity. It is commonly found in streams with low or intermittent flow, but occurs less frequently in the extreme headwaters of streams than does the green sunfish. It avoids streams with high gradient, clear or cool water, and continuous strong flow.

Zoogeography.—The distribution and ecological preferences of *L. humilis* suggest a western origin (Metcalf, 1966:156-157). This fish has extended its range eastward within historic time in response to increased siltation associated with clearing and tilling of the land (Trautman, 1957:506-508).

Lepomis megalotis (Rafinesque)—longear sunfish

Lepomis megalotis: Call, 1887:78 (Jacks Fork, Shannon Co.). Meek, 1891: 123,127,130 (Osage Fork Gasconade R. 6 mi. SE Marshfield; Shoal Cr. near Neosho; James R. near Springfield; North Fork White R. S Cabool). Evermann and Kendall, 1895:471 (Indian Cr. at Neosho). Patriarche, 1953 (abund.; Lake Wappapello). Funk, 1957 (mov.; Missouri streams). Patriarche and Campbell, 1958:247-250 (abund.; growth; Clearwater Res.). Burress, 1962 (abund.; harv.; Bull Shoals Res.).

Lepomis megalotis megalotis: Borges, 1950 (vert. distr.; Niangua Arm, Lake Ozark). Martin and Campbell, 1953 (abund.; Black R.). Funk and Campbell, 1953 (abund.; Black R. local.). Witt and Marzolf, 1954 (nesting; mouth Little Niangua R.; Lake Ozark). Fisher, 1962:428 (Missouri R. local.).

Longear: Purkett, 1958b:15,37 (growth; Missouri streams). Fry, 1962 (harv.; tailwater Lake Taneycomo).

Distribution and habitat.—The longear sunfish is the most abundant centrarchid over most of the southern half of Missouri (Map 148). The northern and northwestern limits of its distribution correspond closely to the boundary of the Ozark Uplands. North of the Missouri River it occurs only in short, direct tributaries of the Missouri River from Calloway County eastward. *Lepomis megalotis* inhabits clear, permanent-flowing streams having bottoms mostly of sand, gravel, or rubble. The habitats where it occurs often have considerable aquatic vegetation, but this is not essential. Longears are found in small headwater creeks and moderately large rivers, but are most abundant in streams of medium size. *Lepomis megalotis* also thrives in large Ozark reservoirs. Like most sunfishes, the longear avoids strong current, being found most commonly in pools, protected inlets, and overflow waters.

Variation and zoogeography.—*Lepomis megalotis* exhibits considerable variability in coloration and in the development and angle of the opercular flap in different stream systems. Breeding males from the Neosho system, Osage system, and small, direct tributaries of the Missouri River in central Missouri have a broad, reddish stripe on the nape, whereas those from elsewhere in the state lack a nuchal stripe. Throughout most of Missouri the opercular flap is horizontal or is directed upward, but in populations from the upper White River system the flap is decurved. In some populations the flap is strongly expanded posteriorly, while in others it is nearly uniform in width. Individual variation in all these characters is evident within populations. A different subspecies (*L. m. peltastes* Cope) has been recognized in the Great Lakes and northern Mississippi systems, but until variation in this species has been thoroughly investigated, allocation of Missouri populations to subspecies seems unwise.

The strong regional differentiation of *L. megalotis* in the Ozark Uplands suggests that it has long resided there. Probably it has inhabited that region continuously since preglacial time.

Lepomis macrochirus Rafinesque—bluegill

Lepomis pallidus: Jordan and Meek, 1885:14 (Missouri R. at St. Joseph). Garman, 1890:139 (Mississippi R. near Quincy, Ill.). Meek, 1891:119,123 (Big Dry Fork near St. James; Little Dry Fork near Rolla; Gasconade R. and Little Piney Cr. near Arlington; Big Piney R. at Cabool; Osage Fork 6 mi. SE Marshfield). Evermann and Kendall, 1895:471 (spring branch at Neosho). Forbes and Richardson, 1920:map LXXVIII (Mississippi R. local.).

Lepomis macrochirus: Meek, 1891:122,123 (Osage Fork 6 mi. SE Marshfield; Lick Fork at Mansfield). Borges, 1950 (vert. distr.; Niangua Arm, Lake Ozark). Patriarche, 1953 (abund.; growth; Lake Wappapello). Patriarche and Campbell, 1958 (abund.; growth; Clearwater Res.). Fisher, 1962:428 (Missouri R. local.). Burress, 1962 (abund.; Bull Shoals Res.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.). Cross, 1967:263 (Missouri R. local. mapped).

Lepomis macrochirus macrochirus: Barnickol and Starrett, 1951:318 (abund.; Mississippi R. local.). Martin and Campbell, 1953 (abund.; Black R.). Funk and Campbell, 1953 (abund.; Black R. local.).

Bluegill: Purkett, 1958b:16,38,43 (growth; length-weight relat.; Missouri streams). Fry, 1962 (harvest, tailwaters of Table Rock, Taneycomo, and Clearwater res.).

Distribution and habitat.—The bluegill is nearly statewide in distribution (Map 149), but it is rare in the northwestern part of the prairie region and in the central Ozarks. In natural waters, it reaches its greatest abundance in oxbows along the major rivers, and in streams of the Ozark border. *Lepomis macrochirus* is the most abundant centrarchid in many impoundments. The distribution of the bluegill is strikingly similar to that of the largemouth bass, reflecting similarities in their requirements. The bluegill is intolerant of continuous high turbidity and siltation, and thrives best in warm, clear waters having considerable aquatic vegetation.

Zoogeography.—The present distribution of the bluegill provides few clues concerning its preglacial distribution. Perhaps it has had a widespread distribution in the eastern United States east of the Great Plains since late-Tertiary time and has occurred in all or most of the ancestral drainages that now form the Mississippi River system.

Ambloplites rupestris (Rafinesque)—rock bass

Ambloplites rupestris: Call, 1887:78 (West Fork Black R., Reynolds Co.; Spring Valley Cr. and Jacks Fork, Shannon Co.). Meek, 1891:119,130 (Meramec R. near St. James; North Fork White R. S Cabool; James R. near Springfield). Martin and Campbell, 1953 (abund.; hab.; Black R.). Funk and Campbell, 1953 (abund.; Black R. local.). Funk, 1957 (mov.; Missouri streams).

Rock bass: Purkett, 1958b:17,39,43 (growth; length-weight relat.; Missouri streams). Fry, 1962 (harv.; Taneycomo Res. tailwater).

Distribution and habitat.—The rock bass is widespread in the Ozarks, where it is one of the most abundant centrarchids (Map 150). Some ditches of the lowlands have small populations of rock bass, but it does not occur widely in that area. North of the Missouri River it is known only from Lost Creek in Warren County. George Morris, long-time employee of the Missouri Department of Conservation, informed me that the rock bass was not present in the Niangua River until its introduction in the 1930's. There are no early records for this fish in the Missouri River system, so the rock bass may not be native to the Osage or Gasconade systems. At present the rock bass has only a limited distribution in the Osage system, not including all the streams that appear suitable for it. In Missouri the rock bass is primarily a stream fish; it constitutes only a minor element in the fauna of large Ozark reservoirs. Unlike some other centrarchids, it occurs only rarely in overflow pools away from the stream channel. Permanent flow, low turbidity, abundant cover, and silt-free bottoms characterize its habitat. In Ozark streams it lives near boulders, logs, or dense beds of water willow (*Justicia americana*), where there is a slight to moderate current. In the lowlands it is found in the clearer ditches where flow is strong, and dense beds of submergent aquatic vegetation exist.

Variation and zoogeography.—Two subspecies of *A. rupestris* are recognized. These are: *A. rupestris ariommus* Viosca of the lower Mississippi Valley and adjacent Gulf coastal drainages, and *A. r. rupestris* (Rafinesque), occupying the remainder of the Mississippi Valley and the Great Lakes system. Intergrades occur in southeastern Missouri (Bailey and Hubbs, 1949:12). Rock bass from the upper White River system differ strikingly in color pattern from those elsewhere in Missouri, and perhaps represent an as yet undescribed subspecies. Occurrence of a northern and a southern subspecies suggests former isolation of stocks. Perhaps ancestral stock of *A. r. rupestris* were localized in the preglacial Laurentian system, at a time when *A. r. ariommus* had a more widespread distribution in the Mississippi Valley. Drainage diversions and climatic fluctuations accompanying glaciation may have resulted in southward displacement of *A. r. rupestris*, and formation of a zone of secondary intergradation.

Pomoxis nigromaculatus (Lesueur)—black crappie

Pomoxis sparoides: Forbes and Richardson, 1920:map LXXI (Mississippi R. local.).

Pomoxis nigromaculatus: Barnickol and Starrett, 1951:315-319 (abund.; Mississippi R. local.). Martin and Campbell, 1953 (abund.; Black R.). Funk and Campbell, 1953 (abund.; Black R. local.). Patriarche, 1953 (abund.; Lake Wappapello). Patriarche and Campbell, 1958 (abund.; Clearwater Res.). Fisher, 1962:428 (Missouri R. local.). Burress, 1962 (abund.; harv.; Bull Shoals Res.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.).

Black crappie: Purkett, 1958b:18,40 (growth; Missouri streams). Hanson, 1962 (abund.; harv.; Bull Shoals Res.).

Distribution and habitat.—The black crappie is widespread but sporadic in distribution in Missouri (Map 151). It is most prevalent in the large reservoirs of the Ozarks, navigation pools of the upper Mississippi River, and natural lakes and borrow pits of the lowlands. The black crappie is less abundant than the white crappie at most localities. Metcalf (1966:158) and Cross (1967:278) presented evidence suggesting that the black crappie was introduced into Kansas. Early collectors failed to report this fish anywhere in Missouri, except from the Mississippi River, but it is likely that the native distribution of the black crappie included most of the state. *Pomoxis nigromaculatus* is less tolerant of turbidity and siltation than the more adaptable white crappie. Clear water, absence of noticeable current, and abundant cover in the form of submerged timber or aquatic vegetation are the principal requirements of the black crappie.

Zoogeography.—The present distribution and habitat requirements of the two crappies suggest an eastern origin for the black crappie, probably in the preglacial Mississippi, Laurentian or southeastern Gulf and Atlantic coastal drainages.

Pomoxis annularis Rafinesque—white crappie

Pomoxys brevicauda: Gill, 1865:64-65 (orig. descr.; type local. North Grand R., Livingston Co.).

Pomoxys annularis: Jordan and Meek, 1885:14,16 (Missouri R. at St. Joseph; Flat Cr. near Sedalia and/or Blackwater R. at Brownsville). Call, 1887:80 (Bear Cr., Boone Co.).

Pomoxis annularis: Borges, 1950 (vert. distr.; Niangua Arm, Lake Ozark). Barnickol and Starrett, 1951:315-319 (abund.; Mississippi R. local.). Martin and Campbell, 1953 (abund.; Black R.). Funk and Campbell, 1953 (abund.; Black R. local.). Patriarche, 1953 (abund.; growth; Lake Wappapello). Funk, 1957 (mov.; Missouri streams). Purkett, 1958a:127 (growth; Salt R.). Patriarche and Campbell, 1958:244-245 (abund.; growth; Clearwater Res.). Burress, 1962 (abund.; Bull Shoals Res.). Fisher, 1962:428 (Missouri R. local.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.). Cross, 1967:274 (Missouri R. local. mapped).

White crappie: Purkett, 1958b:19,41,43 (growth; length-weight relat.; Missouri streams). Hanson, 1962 (abund.; harv.; Bull Shoals Res.).

Distribution and habitat.—The white crappie is nearly statewide in distribution, but it is rare or absent in many streams of the central Ozarks and northwestern part of the prairie region (Map 152).

It is most abundant in impoundments and the navigation pools of the upper Mississippi River. The habitat of this fish is much like that of the black crappie, except that *P. annularis* is more tolerant of turbidity and siltation, and is less closely associated with dense cover.

Zoogeography.—The distributional relationships and habitat preferences of the two crappies suggest a more western origin for *P. annularis*. However, fossil remains from Middle Pliocene beds of Logan County, Kansas seem to be closer to *P. nigromaculatus* than to *P. annularis* (C. L. Smith, 1962:514).

Centrarchus macropterus (Lacépède)—flier

Centrarchus macropterus: Barnickol and Starrett, 1951:318 (abund.; Mississippi R. local.).

Distribution and habitat.—The flier is confined to the lowlands, where it is uncommon and sporadic in distribution (Map 153). Its preferred habitat is clear, heavily vegetated waters without noticeable current. The swamps which formerly were present in the lowlands probably provided a more desirable habitat than the ditches, and it is likely that the flier is now less abundant than it was before settlement.

Zoogeography.—Centrarchus macropterus may have occupied the lower Mississippi Valley continuously since preglacial time or invaded from the eastern Gulf Coast by way of temporary stream connections formed during the Pleistocene.

Elassoma zonatum Jordan—banded pygmy sunfish

Distribution and habitat.—The pygmy sunfish is strictly a lowland species (Map 154). It is sporadic in occurrence but is sometimes abundant. Like the flier, it inhabits quiet, clear waters with thick growths of aquatic vegetation, and was probably more abundant before the lowland swamps were ditched and drained.

Zoogeography.—The present distribution of this fish suggests an origin in the lowlands of the Mississippi Valley or Gulf coastal drainages to the east. The presence of related species (*E. evergladei* Jordan and *E. okefenokee* Böhlke) in Georgia and Florida indicates that stocks of this group have long inhabited lowlands of the eastern United States.

Percidae

Stizostedion vitreum (Mitchill)—walleye

Stizostedion vitreum vitreum: Borges, 1950 (vert. distr.; Niangua Arm, Lake Ozark). Barnickol and Starrett, 1951:314-315 (abund.; Mississippi R. local.). Martin and Campbell, 1953 (abund.; Black R.). Funk and Campbell, 1953 (abund.; Black R. local.). Fisher, 1962:428 (Missouri R. local.).

Walleye: Purkett, 1958b:32 (growth; Missouri streams). Fry, 1962 (harv.; Table Rock, Taneycomo and Clearwater res. tailwaters).

Distribution and habitat.—The walleye occurs at least occasionally in nearly all large streams of the state (Map 155). It is most abundant in navigation pools of the upper Mississippi River and large streams and reservoirs of the Ozarks. An extensive spawning run occurs each spring out of Lake of the Ozarks into the upper Osage River. In the Missouri and lower Mississippi rivers the walleye is far less abundant than the sauger, but replaces that species in tributary streams. The walleye inhabits reservoirs and the deeper pools of streams. Its requirements are much like those of the sauger, except that the walleye is less tolerant of continuous high turbidity, and is more successful than the sauger in impounded waters.

Zoogeography.—This species may have been localized preglacially in northern drainages, entering the Mississippi Valley by way of stream connections that developed with glaciation. The occurrence of *S. vitreum* in late-Illinoian fossil deposits of central Kansas (Semkin, 1966:137) documents its presence in the Mississippi Valley by mid-Pleistocene time.

Stizostedion canadense (Smith)—sauger

Stizostedion canadense: Jordan and Meek, 1885:14 (Missouri R. at St. Joseph). Barnickol and Starrett, 1951:314-315 (abund.; Mississippi R. local.). Martin and Campbell, 1953 (abund.; Black R.). Funk and Campbell, 1953 (abund.; Black R. local.). Fisher, 1962:428 (Missouri R. local.). Cross, 1967:285 (Missouri R. local. mapped).

Distribution and habitat.—The sauger is more restricted in distribution than the walleye, being confined almost entirely to large, free-flowing streams (Map 156). The sauger is the more abundant of the two species in the Missouri and Mississippi rivers; elsewhere in Missouri the walleye generally predominates. The requirements of the sauger are much like those of the walleye, except that it is more tolerant of turbidity, and exhibits a greater predilection for strong current.

Zoogeography.—This wide-ranging northern species may have invaded the Mississippi Valley from more northern drainages during Pleistocene time. Its predilection for large, turbid rivers suggests an origin in the western part of the ancestral Hudson Bay system.

Perca flavescens (Mitchill)—yellow perch

Distribution and habitat.—I know of only one specimen of the yellow perch from natural waters in Missouri (Map 157). This specimen was taken by a fisherman in mid-April, 1962, from the Salt River east of New London in Ralls County. No specimens were taken by Barnickol and Starrett (1951) or Fisher (1962) in their extensive surveys of the Mississippi and Missouri rivers, and none has been captured by biologists of the Missouri Department of Conservation during long-term surveys of the fish populations in Salt River and other north Missouri streams. It therefore seems certain that no self-sustaining populations of this species occur in natural waters of Missouri, and occurrence here is limited to occasional stragglers from farther north. I have unverified reports of small self-sustaining populations in some artificial lakes in north Missouri where this species was stocked. Extensive attempts were made to establish the yellow perch in natural waters throughout Missouri in the 1930's and before by the Missouri Fish and Game Commission. These attempts are summarized in the annual report of that organization for 1933 (p. 48) with the statement: "Still another foreigner which was formerly introduced in Missouri without appreciable results is the yellow perch. More than three million have been planted in our state in the last five years without success."

Zoogeography.—Occurrence of this northern species in Pleistocene (Illinoian?) fossil deposits from the Oklahoma panhandle (C. L. Smith, 1954:288) documents its occurrence in the Mississippi Valley by mid-Pleistocene time, and suggests a more widespread southern distribution in the past. The disjunct populations in the Apalachicola, Choctawatchee, and Mobile Bay drainages of Alabama and Florida probably represent native occurrence (Smith-Vaniz, 1968:108), providing further evidence for a formerly more widespread southern distribution.

Percina cymatotaenia (Gilbert and Meek)—bluestripe darter

Etheostoma (Hadropterus) cymatotaenia: Gilbert and Meek *in* Gilbert, 1888: 51-52 (orig. descr.; types from Niangua R. and Osage Fork of Gasconade R. near Marshfield, and Sac. R. near Greenfield). Meek, 1891:123-125 (Osage Fork 6 mi. SE Marshfield; Little Piney Cr. at Newburg; Maries R. near Dixon).

Percina cymatotaenia: Bailey and Gosline, 1955:table 1, p. 35 (vert. counts; Missouri local.). Collette, 1965:575-576 (char.; Gasconade R.).

Distribution and habitat.—The bluestripe darter is confined to the Osage and Gasconade systems (May 158), where it is rare. It

may have been more abundant and widely distributed before 1900 than it is today. At the time of its original description it was reported by Gilbert (1888:51) as "abundant in the Niangua, Osage Fork and Sac river systems." Subsequently it has not been collected in the Sac. The bluestripe darter inhabits clear, medium-sized streams having permanent flow and bottoms that are mostly free of silt. Except when spawning, it is found in quiet pools and backwaters, often in accumulations of dead leaves and sticks.

Zoogeography.—*Percina cymatotaenia* occurs disjunctly in the Ozark Uplands and in uplands of western Kentucky. Absence of any apparent differentiation between eastern and western populations suggests that the range disjunction is recent, possibly dating no farther back than the Wisconsin glacial period. Perhaps the Wisconsin ice advance resulted in the fragmentation of a continuous distribution that existed during the preceding interglacial period; alternatively the lowering of sea level and formation of steep-sided valleys within the Mississippi Embayment during glaciation may have created stream conditions that permitted dispersal from one upland area to the other by way of the Ohio and Mississippi rivers.

Percina maculata (Girard)—blackside darter

Percina maculata: Hanson and Campbell, 1963 (linear distr.; Perche Cr.).

Distribution and habitat.—The blackside darter has two centers of occurrence in Missouri (Map 159). One of these is in the ditches and streams of the lowlands; the other is in the prairie and Ozark border streams of central and northeastern Missouri. Five specimens of *P. maculata* (MCZ 24539) were collected by P. R. Hoy in Grand River near Chillicothe in 1854, suggesting a more widespread distribution for this species in western Missouri before 1900. This darter inhabits small to medium sized streams having low or moderate gradients and permanent flow. It tolerates moderate turbidity if there is enough current to keep the bottom mostly free of silt. The blackside darter is usually found on gravel riffles in a slight current, or in short, gravelly pools where pools and riffles alternate in rapid succession.

Zoogeography.—The present distribution of *P. maculata* suggests that it is autochthonous to the Mississippi Valley.

Percina sciera (Swain)—dusky darter

Distribution and habitat.—The dusky darter is one of the commonest darters in the lowlands, and it penetrates into the Ozarks for a considerable distance along the larger streams (Map

160). *Percina sciera* is characteristic of clear, low-gradient streams and ditches that have continuous strong flow and silt-free sand or gravel bottoms. It is usually found on sluggish gravel-bottomed riffles, but also occurs in quiet backwaters in accumulations of leaves, sticks and other organic debris.

Zoogeography.—The present distribution of *P. sciera* suggests an origin in the southern Mississippi Valley or adjacent Gulf coastal drainages to the west. Clark Hubbs (1954) discussed variation and nomenclature in this species and described *P. s. apristis* from the Guadalupe River in Texas; Missouri specimens are referable to *P. s. sciera.* Suttkus and Ramsey (1967:138) suggested that the closely related *Percina aurolineata* evolved from a stock of *P. sciera* that invaded the upper Alabama system from the Tennessee system.

Percina phoxocephala (Nelson)—slenderhead darter

Hadropterus phoxocephalus: Jordan and Meek, 1885:17 (Grand R. at Clinton).

Percina phoxocephala: Bailey and Gosline, 1955:table 1, p. 36 (vert. counts.; Salt R., Ralls Co.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.).

Distribution and habitat.—The slenderhead darter occurs along the Ozark border from Spring River in Jasper County northeastward into the upper Mississippi River and its tributaries (Map 161). Within this area it is one of the commonest darters in large streams. *Percina phoxocephala* inhabits medium-sized creeks to large rivers that have moderately clear water and permanent flow. It is usually found on gravelly or rocky riffles in moderate to swift current. It avoids silty or turbid streams, and those with extremely high gradients and continuously cool water.

Zoogeography.—The presence of *P. phoxocephala* in the middle part of the Arkansas system suggests either that it formerly ranged more widely in the lower Mississippi Valley, or that it entered the Arkansas system by way of former connections between the Arkansas and Missouri systems. Either explanation seems plausible. There are documented stream connections between the Arkansas and Missouri systems in Kansas one or more times during the Pleistocene (Frye and Leonard, 1952:180-199). Also, it seems likely that changes in climate and stream environments in the lower Mississippi Valley would have created conditions favorable to the dispersal of upland fishes by way of the lower Mississippi and Arkansas rivers during the Pleistocene ice advances. The present distribution of *P. phoxocephala* in the central Mississippi Valley suggests that it would have been in a position to take advantage of such conditions.

Percina nasuta (Bailey)—longnose darter

Distribution and habitat.—The longnose darter is known in Missouri only from the section of White River now covered by Table Rock Reservoir (Map 162). It has not been collected since impoundment, and may no longer occur in Missouri. This darter inhabits clear, upland streams with permanent flow and well defined riffles and pools. Bailey (1941:7) reported its habitat as quiet backwaters having silt bottoms and an abundance of aquatic vegetation.

Zoogeography.—Percina nasuta is endemic to the White and Arkansas systems of the Ozark and Ouachita uplands. Although closely related to *P. phoxocephala,* its nearest relative seems to be *P. oxyrhyncha* (Hubbs and Raney), a species known only from the Cheat and New river systems of West Virginia and Virginia. Possibly *P. nasuta* and *P. oxyrhyncha* were derived independently from *P. phoxocephala* stock. More likely they represent the remnants of a common stock that had a wide preglacial distribution in the Teays-Mississippi system. The range disjunction that initiated speciation probably dates from an early ice advance of the Pleistocene. Perhaps the ice sheets so modified the glaciated territories as to make them unsuitable for the common ancestral stock. It is also possible that failure of this stock to reoccupy much of its former range resulted from invasion of those areas by *P. phoxocephala* from more northern or western drainages, but there is no evidence that *P. phoxocephala* ever had a more northern or western distribution than it has today.

After this report went to press, Dr. Jamie E. Thomerson called my attention to two juvenile *P. nasuta* which he and his students obtained from the St. Francis River approximately ¼ mile upstream from the mouth of Leatherwood Creek (T31N, R5E, S10), Madison County, Missouri on 2 August 1969. These specimens represent a significant range extension for *P. nasuta,* and confirm that this species is still present in Missouri waters.

I had previously examined two adult specimens supposedly collected in the St. Francis system but doubted the authenticity of the record. These specimens were in a collection labeled "Lake Wappapello, 1953" (exact locality and collector unknown) at the fisheries research laboratory of the Missouri Department of Conservation. Since Department biologists at that time were sampling the White River where *P. nasuta* was known to occur, I suspected a mixing of collections.

Percina caprodes (Rafinesque)—logperch

Etheostoma caprodes: Meek, 1891:123,130 (Osage Fork 6 mi. SE Marshfield; Lick Fork at Mansfield; James R. near Springfield). Evermann and Kendall, 1895:471 (Indian Cr. near Neosho).

Percina caprodes: Patriarche and Campbell, 1958 (abund.; Clearwater Res.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.).

Percina caprodes carbonaria: Martin and Campbell, 1953 (abund.; Black R.). Funk and Campbell, 1953 (abund.; Black R. local.). Collette, 1965:577-578 (breeding tub.; Lamine R.).

Distribution and habitat.—The logperch is widespread in the Ozarks and northern Ozark border (Map 163), where it is one of the most common darters. It occurred in a few collections from the lowland ditches in the early 1940's, but it was not collected there during a survey made in 1964. *Percina caprodes* inhabits a variety of stream types, but it does not penetrate into headwater creeks unless they maintain large, permanent pools, and it avoids streams that are continuously turbid, excessively silty, or that lack well defined gravel or rubble riffles. It is most often found in the deeper and more sluggish sections of riffles, but it also occurs in pools if the bottom is mostly free of silt.

Variation and zoogeography.—The southern logperch, *P. c. carbonaria* (Baird and Girard) occupies most of the range of this species in Missouri, but specimens from the Mississippi River as far downstream as Lincoln County seem to be intergrades between this form and the northern logperch, *P. c. semifasciata* (DeKay). The suspected intergradation is indicated by a more or less intermediate color pattern and nearly or quite naked nape. Surprisingly, specimens from tributaries of the upper Mississippi (Salt and Cuivre rivers), where the logperch is rare, seem to be typical *P. c. carbonaria.* The nominate subspecies, *P. c. caprodes* (Rafinesque) occurs in the Ohio system and southern parts of the Great Lakes basin. The distributional relationships of the three forms suggest that *P. c. carbonaria* has long inhabited the central Mississippi Valley. Probably *P. c. semifasciata* inhabited the preglacial Laurentian or Hudson Bay systems, and was brought into contact with the other subspecies as a result of drainage derangements that accompanied glaciation. *Percina c. caprodes* probably inhabited the preglacial Ohio or Teays.

Percina evides (Jordan and Gilbert)—gilt darter

(?) *Etheostoma aspro:* Meek, 1891:123 (Gasconade R. and Little Piney Cr. near Arlington).

Hadropterus evides: Martin and Campbell, 1953 (abund.; Black R.).

Distribution and habitat.—The gilt darter is common and widespread in the eastern and southern Ozarks (Map 164). It has occurred in only a single collection from the Osage River system, and it is not present in the Neosho system. *Percina evides* inhabits clear, medium-sized to large streams with clean, silt-free bottoms and continuous strong flow. It is most often found in the gravelly sections of riffles and pools, in a slight or moderate current.

Zoogeography.—*Percina evides* is probably autochthonous to the Teays-Mississippi system. Perhaps the disjunctions in its present range result from failure to reoccupy parts of its former range after becoming localized in the Driftless Area and the Ozark and Appalachian uplands during the Wisconsin ice advance. Fragmentation of its range could alternatively have resulted from the extirpation of intervening populations by man's activities. Gerking (1945:87) noted a recent decline in abundance of the gilt darter in Indiana, and no specimens have been taken in Iowa since the 1890's (Harlan and Speaker, 1956:148).

Percina shumardi (Girard)—river darter

Distribution and habitat.—The river darter is the most abundant darter in the Mississippi River and is common in many of the larger ditches and streams of the lowlands (Map 165). It is almost invariably found in deep chutes and riffles where the current is swift and the bottom is composed of coarse gravel or rubble. It seems more tolerant of continuous high turbidity than most darters, as indicated by its occurrence in the lower Mississippi River.

Zoogeography.—The distributional relationships of this fish and the related *P. uranidea* suggest a northern origin for the river darter, in the Teays, upper Mississippi, or Laurentian systems.

Percina uranidea (Jordan and Gilbert)—stargazing darter

Percina uranidea: Bailey and Gosline, 1955:table 37 (vert. counts; Little R. Floodway, New Madrid Co.; ditch 1 mi. E Anniston, Mississippi Co.). Smith, 1965:12 (Scott Co.).

Distribution and habitat.—The stargazing darter is confined to the lowlands, where its distribution and abundance are much like those of the related river darter (Map 166). Although the two species seem similar in their requirements, both are seldom abundant at the same locality. Possibly they compete intensively, and tend to exclude each other microgeographically.

Zoogeography.—The distribution of *P. uranidea* suggests that it is autochthonous to the Mississippi Valley.

Percina copelandi (Jordan)—channel darter

Etheostoma copelandi: Meek, 1891:127 (scarce; Shoal Cr. and/or Hickory Cr. near Neosho). Evermann and Kendall, 1895:471 (Shoal Cr. near Neosho).

Distribution and habitat.—The channel darter is common in the larger streams of the Neosho system (Map 167), where it occurs on sluggish riffles or in pools having enough current to create silt-free rocky or gravelly bottoms.

Zoogeography.—Populations of the channel darter in the middle Arkansas and Red river systems and in the Mobile Bay drainage of Alabama are broadly disjunct from the main part of the range of this northeastern species. Probably these populations are glacial relicts, dating from southward displacement during one of the Pleistocene ice advances. Dispersal into the Arkansas and Red systems most likely was by way of the lower Mississippi Valley, although utilization of temporary connections between the middle Missouri (Kansas River) and upper Arkansas systems cannot be ruled out.

Ammocrypta asprella (Jordan)—crystal darter

Ammocrypta asprella: Smith, 1965:12 (St. Louis Co.).

Distribution and habitat.—The crystal darter is common in lower Black and St. Francis rivers and the larger lowland ditches (Map 168). It is rare in the lower Meramec and Gasconade rivers. *Ammocrypta asprella* inhabits open stretches of large, clear streams with low or moderate gradients. It is usually found in a slight current, on a bottom of sand or small gravel.

Zoogeography.—This distinctive darter is probably autochthonous to the Mississippi Valley.

Ammocrypta clara Jordan and Meek—western sand darter

Ammocrypta clara: Bailey and Gosline, 1955:table 1, p. 38 (vert. counts; Salt R., Pike Co.; Mississippi R., Lincoln Co.). Linder, 1959 (char.; compar.; Missouri local. mapped). Collette, 1965:583 (breeding tub.; Salt R.).

Distribution and habitat.—The western sand darter is nowhere abundant in Missouri, but it occurs most commonly in the upper Mississippi River and in lowland ditches of the southeast (Map 169). In the lowlands it is less common than the scaly sand darter. *Ammocrypta clara* is invariably found on a bottom composed of fine, silt-free sand. It avoids strong currents, occupying the quiet margins of the channel and shallow backwaters.

Zoogeography.—This species is replaced east of the Mississippi River by the closely related *A. pellucida* (Baird). The distributional relationship of these two fishes suggests an origin for *A. pellucida* in the preglacial Teays or the Laurentian system, at a time when ancestral stocks of *A. clara* occupied the western or lower parts of the Mississippi Valley.

Ammocrypta vivax Hay—scaly sand darter

Ammocrypta vivax: Martin and Campbell, 1953 (abund.; Black R.). Bailey and Gosline, 1955:table 1, p. 38 (vert. counts; Black R., Butler Co.). Smith, 1965:12 (Cape Girardeau Co.).

Distribution and habitat.—The scaly sand darter is confined to the lowland ditches and lower sections of large Ozark streams entering the lowlands (Map 170). It is not abundant, but occurs more commonly in the lowlands than the western sand darter. The habitats of the two are much alike.

Zoogeography.—The present distribution of this species suggests that it is autochthonous to the lower Mississippi Valley. It is replaced in eastern Gulf coastal drainages by the closely related *A. beani* Jordan.

Etheostoma nigrum Rafinesque—johnny darter

Bolesoma brevipinne: Cope, 1871:440 (St. Joseph).
Poecilichthys beani: Jordan, 1885:479 (orig. descr.; type local. Tabo Cr. near Lexington).

Bolesoma olmstedi maculatum: Jordan and Meek, 1885:12,16,17 (Hundred and Two R. at Maryville; Flat Cr. near Sedalia and/or Blackwater R. at Brownsville; Grand R. at Clinton and/or Tebo Cr. at Calhoun).

Bolesoma olmstedi ozarkanum: Call, 1887:78,79 (nomen nudum; Jacks Fork, Shannon Co.; Big Cr., Texas Co.; Bear Cr., Boone Co.).

Etheostoma nigrum: Meek, 1891:119,123,125,131 (Meramec R. and Big Dry Fork near St. James; Lick Fork near Mansfield; Niangua R. near Marshfield; Maries R. near Dixon; North Fork White R. S Cabool). Evermann and Kendall, 1895:471 (Indian Cr. near Neosho). Hanson and Campbell, 1963 (linear distr.; Perche Cr.).

Distribution and habitat.—The johnny darter is one of the common Missouri darters, occurring over most of the state except for the lowlands and the central Ozarks (Map 171). It is most common in the prairie and Ozark border streams of central and northeastern Missouri. Westward in the prairie region it becomes progressively more scarce and spotty in distribution. *Etheostoma nigrum* occurs in streams of all sizes but is more abundant in creeks than in rivers. It is more tolerant of turbidity than most darters, but avoids streams that are excessively turbid and silty, and those with high gradients or continuous strong flow of cool water. Unlike most darters, it inhabits the quieter areas of streams rather than riffles. It is usually found over a sand, gravel, or rubble bot-

tom. Perhaps the johnny darter is excluded from the lowlands by competition from the related bluntnose and speckled darters.

Variation and zoogeography.—The johnny darter varies in squamation of the nape, cheek, and breast in Missouri. Specimens from the Neosho system and streams of the southeastern Ozarks have these areas largely scaled, as is typical of *E. n. eulepis* (Hubbs and Greene). Specimens from some streams of west-central Missouri, especially the Lamine system, have less complete squamation, and could be interpreted as intergrades between *eulepis* and *nigrum*. Elsewhere in Missouri, populations with squamation typical of the latter subspecies occur.

Greene (1935:179) postulated a glacial refugium for *E. n. eulepis* in the Driftless Area. If populations in southern Missouri are properly referable to that subspecies, it also occupied a refugium in or near the Ozark Uplands, and became isolated in these areas by intervening populations of the typical subspecies. There is little evidence for determining the place of origin for either form. A related species (*E. olmstedi* Storer) occurs on the Atlantic slope.

Etheostoma chlorosomum (Hay)—bluntnose darter

Etheostoma chlorosomum: Martin and Campbell, 1953 (abund.; Black R.).

Distribution and habitat.—The bluntnose darter inhabits lowland streams and ditches of the southeast and small prairie creeks of northeastern Missouri (Map 172). It is otherwise known in the state only from one locality in the Osage system and another in the North Fork of Spring River. It seems to have declined in abundance since the 1940's, especially in northeastern Missouri. *Etheostoma chlorosomum* occupies sluggish streams and ditches draining lowlands and level, undissected uplands. It is found in pools and backwaters without noticeable current, where the bottom is composed of sand or organic debris. Increased siltation has probably been a factor in the decline of this fish in the intensively cultivated prairies of northeastern Missouri.

Zoogeography.—The present distribution of the bluntnose darter suggests that it is autochthonous to the Mississippi Valley. The presence of an isolated population in the upper Osage system could have resulted from either: (1) dispersal from the Arkansas system by way of a former stream connection, (2) range adjustments during and subsequent to the warm, moist Climatic Optimum involving westward dispersal into the lower Missouri system, or (3) extirpation of populations elsewhere in the lower Missouri system as a result of man's activities within historic time.

Etheostoma stigmaeum (Jordan)—speckled darter

Etheostoma stigmaeum: Bailey and Gosline, 1955: table 1, p. 38 (vert. counts; Black R., Butler Co.). Smith, 1965:12 (Cape Girardeau Co.).

Distribution and habitat.—The speckled darter has two distribution centers in the state (Map 173). One is in the lowlands and adjacent sections of the Ozarks; the other is in the southwestern Ozarks. The habitat of *E. stigmaeum* is much like that of the johnny and bluntnose darters, except that the speckled darter occurs more often in clear, high-gradient streams. It occupies sluggish riffles when spawning, but is otherwise confined to quiet pools and backwaters with sandy or rocky bottoms.

Zoogeography.—*Etheostoma stigmaeum* has probably long occupied the lower Mississippi Valley or adjacent Gulf coastal drainages. Its nearest relatives occur in the Tennessee River system.

Etheostoma tetrazonum (Hubbs and Black)—Missouri saddled darter

Etheostoma uranidea: Meek, 1891:123 (Gasconade R. at Arlington; Little Piney Cr. at Newburg).

Poecilichthys variatus: Hubbs and Trautman, 1932:33 (Niangua R. near Marshfield).

Poecilichthys tetrazonus: Hubbs and Black, 1940:11-14, fig. 1 (orig. descr.; type local. Big Niangua R. at mouth of Greasy Cr., 6 mi. SE Buffalo, Dallas Co.).

Distribution and habitat.—The Missouri saddled darter is endemic to Missouri, occurring in streams draining the northern slope of the Ozarks from the Moreau and Osage systems east to the Meramec (Map 174). In this area it is one of the most abundant darters. *Etheostoma tetrazonum* inhabits clear, high-gradient streams with continuous strong flow. It is most often found in the swifter riffles over a coarse gravel or rubble bottom.

Zoogeography.—*Etheostoma tetrazonum* is represented in the upper Ohio River system by the closely related *E. variatum* (Kirtland). Morphological differences between the two are not great, and they could be considered allopatric subspecies rather than distinct species. Both occur along the glacial border without penetrating far into glaciated regions. Probably their common ancestral stock had a widespread preglacial distribution from the upper Teays system westward to the lower Missouri system, perhaps including also the preglacial Iowa and upper Mississippi systems. Absence of *E. variatum* from the Wabash, Green, and Tennessee systems indicates that this ancestral stock was not present in the preglacial Ohio or Tennessee systems, and did not utilize the lower

Ohio River in its dispersal. Probably this stock had its range split by an early ice advance of the Pleistocene, followed by differentiation of *E. variatum* and *E. tetrazonum* in the Appalachian and Ozark uplands respectively.

Etheostoma euzonum (Hubbs and Black)—Arkansas saddled darter

Poecilichthys euzonus erizonus: Hubbs and Black, 1940:17-23 (orig. descr.; types from Current R.).

Etheostoma euzonum euzonum: Bailey and Gosline, 1955:table 1, p. 39 (vert. counts; Little North Fork, Ozark Co.).

Etheostoma euzonum erizonum: Bailey and Gosline, 1955:table 1, p. 39 (vert. counts; Current R., Carter Co.).

Etheostoma euzonum: Collette, 1965:589-590 (breeding tub.; White and Current rivers).

Distribution and habitat.—The Arkansas saddled darter occurs on the southern slope of the Ozark Uplands, from the upper White east to the Current River (Map 175). It replaces the closely related Missouri saddled darter in streams of that region, and the habitat of the two is not recognizably different.

Variation and zoogeography.—The Arkansas saddled darter is endemic to the White River system of Missouri and Arkansas. It is quite distinct from *E. tetrazonum* and *E. variatum,* suggesting an early separation from the stock ancestral to the latter two species. Probably stocks of *E. euzonum* have inhabited the southern Ozarks continuously since late-Tertiary time.

Two subspecies have been recognized (Hubbs and Black, 1940): *E. e. euzonum* (Hubbs and Black), in the White River system upstream from Batesville, Arkansas, and *E. e. erizonum* (Hubbs and Black) in Current River farther east. Intergrades occur in White River below Batesville and in the lower Black River. The two subspecies differ in squamation and color pattern.

Etheostoma histrio Jordan and Gilbert—harlequin darter

Etheostoma histrio: Bailey and Gosline, 1955: table 1, p. 39 (vert. counts; Black R., Butler Co.; Floodway ditches 4 mi. E Kennett, Dunklin Co.). Tsai, 1968:fig. 1 (Missouri local. mapped).

Distribution and habitat.—The harlequin darter is known only from the lowlands (Map 176). It is one of the rarest Missouri fishes and seems to be less common and widely distributed now than in the early 1940's. *Etheostoma histrio* is primarily an inhabitant of moderately large, lowland streams. In Missouri it has been found in quiet water among finely divided tree roots or in beds of organic debris. Elsewhere it has been reported most often from swift, gravelly riffles (Tsai, 1968).

Zoogeography.—The present distribution of this fish suggests an origin in the lower Mississippi or Alabama river systems. Related species occur in the Tennessee River system and coastal drainages eastward of the range of *E. histrio.*

Etheostoma zonale (Cope)—banded darter

Etheostoma zonale arcansanum: Jordan and Gilbert, 1886:5 (orig. descr.; types in part from Spring R. near Carthage and James R. near Springfield). Martin and Campbell, 1953 (abund.; Black R.).

Etheostoma zonale: Meek, 1891:119,131 (Meramec R. near St. James; James R. near Springfield). Evermann and Kendall, 1895:471 (Indian Cr. near Neosho).

Distribution and habitat.—In Missouri the banded darter is confined to the Ozarks where it is one of the most abundant and widespread darters (Map 177). It inhabits clear, high-gradient streams having permanent strong flow. Adults are most often found on swift riffles over a gravel or rubble bottom, but the young commonly occur in quiet water around aquatic vegetation or accumulations of organic debris.

Zoogeography.—The range of the banded darter consists of three disjunct segments, centering in the Ozark Uplands, Appalachian Uplands, and the Driftless Area. Possibly this species survived the last ice advance in all three of these areas, and failed to reoccupy fully the glaciated regions. The Ozark isolate is sometimes accorded subspecific status as *E. z. arcansanum* Jordan and Gilbert.

Etheostoma blennioides Rafinesque—greenside darter

Diplesion blennioides: Call, 1887:78 (Jacks Fork and Sinking Cr., Shannon Co.; West Fork of Black R., Reynolds Co.).

Etheostoma blennioides: Meek, 1891:119,123,125,130 (Meramec R. and Big Dry Fork near St. James; Little Dry Fork near Rolla; Lick Fork near Mansfield; Osage Fork 6 mi. SE Marshfield; Little Piney Cr. and Gasconade R. near Arlington; Maries R. near Dixon; Sac R. and James R. near Springfield; North Fork White R. S Cabool). Evermann and Kendall, 1895:471 (Indian Cr. near Neosho). Martin and Campbell, 1953 (abund.; Black R.). Patriarche and Campbell, 1958 (abund.; Clearwater Res.). Miller, 1968 (char.; syn.; subspecies; Missouri local. mapped).

Distribution and habitat.—The greenside darter is confined to the Ozarks, where it is similar in distribution and abundance to the banded darter (Map 178). No two Missouri fishes are more closely associated than the greenside and banded darters; there seems to be no significant difference in their habitat preferences in Missouri.

Variation and zoogeography.—R. V. Miller (1968) recognized two subspecies of the greenside darter in Misssouri. *Etheostoma b. newmani* (Agassiz) occurs in streams draining the southern slope of the Ozark Upands, whereas *E. b. pholidotum* Miller occurs

in the Osage, Gasconade, and Meramec systems, as well as direct tributaries of the Mississippi River south of the Meramec. Intergrades between the two occur in the upper Gasconade system, presumably as a result of stream capture involving headwaters of the Current or White rivers. According to Miller, *E. b. pholidotum* evolved within its present area of occurrence in the Ozark Uplands. He recognized a "Missouri race" which has long been present in eastern Missouri. During one of the interglacial periods preceding the Wisconsin, this race crossed the Missouri River and gave rise to a "Wabash-Great Lakes race." *Etheostoma b. newmani* evolved in the Tennessee and Cumberland systems. In late-Tertiary time the "Tennessee River race" of *E. b. newmani* dispersed westward, where it gave rise to an "Arkansas race," which now occupies the Arkansas, Ouachita, Saline, and Little Red systems. The "Cumberland River race" moved westward at a later date and evolved into subraces in the St. Francis, Black, and White systems. Perhaps the successive waves of dispersal into the southern Ozarks postulated by Miller were associated with the Pleistocene ice advances, when erosional cycles associated with lowering of sea levels may have created conditions favorable to the alternate dispersal and isolation of upland fishes east and west of the Mississippi Embayment.

Etheostoma nianguae Gilbert and Meek—Niangua darter

Etheostoma niangue: Gilbert and Meek *in* Gilbert, 1888:52-53 (orig. descr.; type local. Niangua R. near Marshfield). Meek, 1891:125 (Niangua R. near Marshfield). Bailey and Gosline, 1955:table 1, p. 41 (vert. counts; Barren Fork, Miller Co.). Kuhne and Bailey, 1961 (char.; Missouri local. compiled and mapped). Collette, 1965:595-596, fig. 6 (breeding tub.; Big Tavern Cr., Miller Co.).

Poecilichthys nianguae: Bailey, 1948:79 (char.; range).

Distribution and habitat.—This distinctive darter is known only from a few tributaries of the Osage River (Map 179), most commonly in the Maries River and Big Tavern Creek. There seem to have been no noticeable changes in the abundance or distribution of this rare and highly localized fish since the early 1940's. Its status before that is unknown, but there is no indication that it was more widespread or abundant before 1900 than it is today. *Etheostoma nianguae* inhabits clear, high-gradient streams with permanent flow. Except when spawning, it is found along the margins of pools having clean gravel or rubble bottoms, often near water willow or other aquatic plants. During spring, when spawning occurs, the adults are found on riffles.

Zoogeography.—The Niangua darter is closely related to the arrow darter, *E. sagitta* (Jordan and Swain), which is confined to

the upper Cumberland and Kentucky systems east of the Mississippi Embayment. The ancestor of these two forms may have had a wide preglacial or interglacial distribution in the central Mississippi Valley, in which case divergence of *E. nianguae* and *E. sagitta* probably resulted from fragmentation of a continuous range by an early ice advance of the Pleistocene. Alternatively, the ancestral stock could have been localized preglacially east or west of the Mississippi River, and dispersed across the Mississippi during one of the ice advances of the Pleistocene. *E. sagitta* occurs in the headwaters of both the Cumberland River, a tributary of the preglacial Ohio or Tennessee, and the Kentucky River, a tributary of the preglacial Teays. Kuehne and Bailey (1961) presented evidence that this species entered the Kentucky system by stream capture. This suggests that the common *nianguae-sagitta* ancestral stock did not inhabit the preglacial Teays system, and enjoyed a continuous east-west distribution at some time in the past by way of the lower Ohio and Mississippi rivers.

Etheostoma whipplei (Girard)—redfin darter

Etheostoma whipplei: Evermann and Kendall, 1895:471 (char.; Indian Cr. near Neosho). (?) Meek, 1891:131 (North Fork White R. S Cabool).

Poecilichthys whipplii whipplii: Hubbs and Black, 1941:14-15, map 1 (syn.; char.; Missouri local. mapped).

Distribution and habitat.—This darter is rare in Missouri, and is known definitely only from the Neosho system (Map 180). Meek (1891) reported it from the North Fork of White River, but his record may have been based on a misidentification. Recent efforts to find the redfin darter in southwestern Missouri have been unsuccessful, and it may no longer be present in the state. According to Cross (1967:309), *E. whipplei* inhabits the gravelly riffles of streams with moderate or low gradients.

Zoogeography.—The closest relatives of *E. whipplei are E. radiosum* (Hubbs and Black) of the Red River system, and *E. artesiae* (Hay) occurring disjunctly in southern tributaries of Red River and in Gulf coastal streams east of the Mississippi River (Moore and Rigney, 1952). The marked regional differentiation of this complex indicates that it has long occupied the lower Mississippi and adjacent Gulf drainages. Perhaps *E. whipplei* was derived from stocks that were localized in the ancestral lower Arkansas or White river systems, followed by dispersal into the upper Arkansas system when the lower Arkansas breached the Ozark-Ouachita divide. It is also possible that the isolation of stocks that gave rise to *E. whipplei* in the Arkansas and *E. radiosum* in the Red is

more recent, dating from diversion of upper Arkansas drainage from the Red into the lower Arkansas during the Pleistocene. If this explanation is correct, the common *whipplei-radiosum* stock had a preglacial distribution that included the ancestral drainage of the central and southern plains.

Etheostoma asprigene (Forbes)—mud darter

Distribution and habitat.—The mud darter is locally common at scattered localities in the lowlands and occurs occasionally in the Mississippi River and the lower parts of some of its major tributaries (Map 181). It inhabits lowland lakes and ponds, and the sluggish riffles and pools of large, low-gradient streams.

Zoogeography.—*Etheostoma asprigene* seems to have originated in lowlands of the lower Mississippi Valley or adjacent Gulf drainages to the west.

Etheostoma juliae Meek—yoke darter

Etheostoma juliae: Meek, 1891:130-131 (orig. descr.; type local. James R. near Springfield). Bailey and Gosline, 1955:41,42,table 1 (vert. counts; James R., Webster Co.; North Fork White R., Ozark Co.).

Distribution and habitat.—The yoke darter is endemic to the White River system of Missouri and Arkansas (Map 182), where it is one of the most abundant darters. It inhabits clear, high-gradient streams with continuous strong flow, occuring only on riffles having swift current and coarse gravel or rubble bottoms.

Zoogeography.—Unlike many Ozark endemics, *E. juliae* seems to have no near-relative in uplands east of the Mississippi River or elsewhere. Probably this distinctive darter has inhabited the southern Ozarks continuously since preglacial time.

Etheostoma punctulatum (Agassiz)—stippled darter

Poecilichthys punctulatus: Agassiz, 1854:304 (orig. descr.; type local. Osage R.).

Etheostoma punctulatum: Call, 1887:79 (trib. Big Cr., Texas Co.). Gilbert, 1888:60-61 (descr.; abund.; small streams, SW Missouri; Sac R. near Greenfield; Niangua R., James R., and Osage Fork near Marshfield). Meek, 1891:123,125 (Jones Cr. near Dixon; Big Piney R. at Cabool; Osage Fork 6 mi. SE Marshfield; Lick Fork near Mansfield; Niangua R. near Marshfield). Bailey and Gosline, 1955:42, table 1 (vert. counts; Shoal Cr., Taney Co.). Collette, 1965:600 (breeding tub.; Osage R.).

Distribution and habitat.—The stippled darter is locally common and widely distributed over the western half of the Ozarks (Map 183). It is very rare in the southeastern Ozarks, where it may be less common than before 1900. *Etheostoma punctulatum* is most often found in small creeks and spring branches having clear water, permanent flow, and silt-free bottoms. Except when spawning, it is found in quiet pools and backwaters, where it hides beneath large rocks or in accumulations of organic debris.

Zoogeography.—The stippled darter is most closely related to *E. cragini* and *E. pallididorsum* Distler and Metcalf, which are endemic to the Arkansas and Caddo (Ouachita) systems, respectively. *Etheostoma punctulatum* is sympatric with *E. cragini* in the Neosho system, but its range otherwise lies north and east of the ranges of those two species. Perhaps *E. punctulatum* evolved in the Ozark Uplands east of the Arkansas River system, and was brought into secondary contact with *E. cragini* by stream capture between the Neosho system and the Osage or White systems. It is also possible that it dispersed westward through the lower Arkansas River after that stream breached the Ozark-Ouachita uplands and captured the upper Arkansas.

Etheostoma cragini Gilbert—Arkansas darter

Etheostoma pagei: Meek, 1894:957 (orig. descr.; type local. spring branch on grounds of U.S. Fish Hatchery at Neosho).

Etheostoma cragini: Bailey and Gosline, 1955:42, table 1 (vert. counts; Shoal Cr., Barry Co.). Collette, 1965:599 (breeding tub.; Shoal Cr., Neosho R.).

Distribution and habitat.—The Arkansas darter is known in Missouri only from the Neosho system of the southwestern Ozarks (Map 184), where it is locally abundant. The habitat of *E. cragini* is much like that described for the stippled darter. The Arkansas darter occupies quiet pools of the smallest spring branches and creeks, where the water is clear and cool, and there is an abundance of watercress or other aquatic vegetation. The Arkansas and stippled darters have never been taken together in Missouri. Where both occur in the same area, the stippled darter tends to occupy somewhat larger streams than the Arkansas darter.

Zoogeography.—*Etheostoma cragini* is endemic to the Arkansas River system, where it probably evolved from the same ancestral stock that gave rise to *E. punctulatum* in the Ozark Uplands to the northeast, and to *E. pallididorsum* in the Caddo (Ouachita) river system to the southeast. Isolation from the stock which gave rise to *E. pallididorsum* may date from the Pleistocene, when the ancestral lower Arkansas River cut through the Ozark-Ouachita Uplands (Quinn, 1958:42) and captured the present upper Arkansas from the ancestral Red River.

Etheostoma caeruleum Storer—rainbow darter

Poecilichthys versicolor: Agassiz, 1854:304 (orig. descr.; paratypes from Osage R.).

Etheostoma caeruleum: Meek, 1891:119,123,125,131 (Little Dry Fork near Rolla; Gasconades R. syst., "Found in all streams"; Osage R. syst., "few specimens . . . taken from each stream"; James R. near Springfield; Bryants Cr. near Mansfield). Martin and Campbell, 1953 (abund.; Black R.). Collette, 1965:597 (breeding tub.; Madison Co.; Gasconade R.).

Poecilichthys caeruleus: Fowler, 1921:399 (Fox Cr., trib. Meramec R.).

Distribution and habitat.—The rainbow darter is one of the most abundant and characteristic darters of the Ozarks, where it occurs in all the principal stream systems except for the Neosho (Map 185). North of the Missouri River this fish is definitely known only from Lost and Charrette creeks in Warren County. Hanson and Campbell (1963) reported *E. caeruleum* from Perche Creek in Boone County, and there are specimens at UMMZ that were supposedly collected in Richland Creek, Calloway County. Neither of these streams now harbors this species, nor do they appear to be suitable for it. I suspect that the Perche Creek record is a misidentification, and the Richland Creek record results from mixing of collections. *Etheostoma caeruleum* inhabits clear, high-gradient streams with permanent strong flow. It is most often found on the swifter riffles, over a coarse gravel or rubble bottom.

Zoogeography.—Knapp (1964) recognized three subspecies of the rainbow darter—one in the White and Black river systems of Missouri and Arkansas, another in the Homochitto River, Mississippi, and the nominate subspecies elsewhere (Map 185). He suggested that *E. caeruleum* originated in the Ozark Uplands. The present distribution of this fish suggests that it survived the Wisconsin ice advance in the Ozark and Appalachian uplands, and perhaps also in the Driftless Area. The disjunct population in the Homochitto drainage of Mississippi indicates a more widespread southern distribution in the past, possibly during Wisconsin time.

Etheostoma spectabile (Agassiz)—orangethroat darter

Poecilichthys spectabilis: Agassiz, 1854:304 (orig. descr.; type local. Osage R.).

Etheostoma variatum spectabile: Jordan and Meek, 1885:16,17 (Flat Cr. near Sedalia and/or Blackwater R. at Brownsville; Grand R. at Clinton and/or Tebo Cr. at Calhoun).

Etheostoma caeruleum spectabile: Call, 1887:79 (West Fork Black R. and Barren Cr., Reynolds Co.; Sinking Cr. and Spring Valley Cr., Shannon Co.; Big Cr., Texas Co.). Meek, 1891:123,127,131 ("found in all streams, but in much larger numbers than *E. caeruleum,*" Gasconade R. syst.; "very abundant," Neosho R. syst.; James R. near Springfield; Bryants Cr. near Mansfield). Evermann and Kendall, 1895:472 (spring branch and Indian Cr. near Neosho).

Etheostoma spectabile: Martin and Campbell, 1953 (abund.; Black R.). Fisher, 1962:428 (Missouri R. trib.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.). Pflieger, 1966:139 (fry in bass nests; Little Saline Cr., Miller Co.).

Etheostoma spectabile spectabile: Bailey and Gosline, 1955:42, table 1 (vert. counts; Bois Brule Cr., Cole Co.). Collette, 1965:600-601 (breeding tub.; Osage R.). Distler, 1968:148-159, map 1 (char.; syn.; distr.).

(?) *Etheostoma caeruleum:* Hanson and Campbell, 1963 (linear distr.; Perche Cr.).

Etheostoma spectabile uniporum: Distler, 1968:159-162, map 1 (orig. descr.; type local. Pigeon Cr., Dent Co.; char.; distr.).

Etheostoma spectabile pulchellum: Distler, 1968:165-173, map 1 (intergrades with *E. s. spectabile;* distr.).

Etheostoma spectabile squamosum: Distler, 1968:173-177, map 1 (orig. descr.; type local. Indian Cr., Newton Co. (char.; syn.; distr.).

Distribution and habitat.—The orangethroat darter is one of the most abundant darters in the Ozarks and northern Ozark border, and occurs at scattered localities westward along the Missouri River to Clay and Jackson counties (Map 186). It is typically an inhabitant of small creeks and spring branches. It tolerates moderate turbidity but is most abundant in clear streams with clean sand and gravel bottoms. *Etheostoma spectabile* avoids streams with continuous strong flow, where it is largely replaced by the closely related *E. caeruleum.* The orangethroat darter is most often found on sluggish riffles, or in pools where there is sufficient current to prevent extensive siltation.

Variation and zoogeography.—The orangethroat darter exhibits extreme geographic variation. Distler (1968) recognized five subspecies and treated the nominate subspecies as a complex of weakly differentiated races. Four subspecies occur in Missouri. Distler suggested that the center of origin for *E. spectabile* is in the Ozark Uplands, because it is there that it shows the greatest amount of racial differentiation. He indicated that a stock of *E. spectabile* dispersed into the Missouri-Platte stream system early in the Pleistocene, where it evolved into *E. s. pulchellum,* dispersing southward over the plains through connectives that existed then and subsequently. Populations of this stock became isolated in streams draining the Springfield Plateau during the extensive pluvial periods of the Pleistocene and evolved into *E. s. squamosum.* Another stock of *E. spectabile* was isolated in Current River and other streams of the Black River system in post-Nebraskan time when the Mississippi River shifted its course eastward from the Ozark Uplands, and gave rise to *E. s. uniporum.* Distler recognized two races of the nominate subspecies in Missouri—the "northern Ozark" race in tributaries of the Missouri River from Osage River eastward, and in streams of the eastern and southeastern Ozarks west to the upper Black River; and the "southern Ozark" race in the upper White River system. The nominate subspecies intergrades with *E. s.*

pulchellum (Girard) in tributaries of the Missouri River westward from the mouth of the Osage River.

Etheostoma flabellare Rafinesque—fantail darter

Etheostoma flabellare: Meek, 1891:123,125,127 (Jones Cr. and Maries R. near Dixon; Little Piney Cr. near Newburg; Osage Fork and Niangua R. near Marshfield; Shoal Cr. and/or Hickory Cr. near Neosho).

Etheostoma flabellare lineolatum: Martin and Campbell, 1953:47 (abund.; Black R.). Bailey and Gosline, 1955:43, table 1 (vert. counts; Hickory Cr., Newton Co.).

Distribution and habitat.—The fantail darter occurs over most of the Ozarks and northeastern extension of the Ozark border (Map 187). It is abundant over most of its Missouri range except for the southern Ozarks. *Etheostoma flabellare* inhabits moderately clear, permanent-flowing streams, where it is most often found on the swifter riffles, over a bottom of gravel or rubble.

Variation and zoogeography.—The fantail darter is represented in Missouri by two, and perhaps by three distinct forms. The nominate subspecies occurs in the upper two thirds of the Current and Black river systems. Populations from the upper White River and its tributaries are not definitely referable to either of the currently recognized subspecies, and perhaps are worthy of separate taxonomic recognition. The remainder of the Missouri range is occupied by the wide-ranging *E. f. lineolatum* (Agassiz), possibly intergrading with the nominate subspecies in lower Current River.

Populations of *E. f. flabellare* in the southeastern Ozarks are isolated from the main range of the subspecies to the north and east. Possibly these disjunct populations are glacial relicts, dating from a westward dispersal across the Mississippi Embayment during the Wisconsin ice advance, when conditions there were more favorable for upland fishes. Perhaps the undescribed White River form resulted from a similar movement during an earlier ice advance. An alternate possibility is that ancestral stocks of the undescribed form and the nominate subspecies were widespread in the preglacial Mississippi River system. Perhaps the ancestral stock of *E. f. lineolatum* then occupied the Neosho River and other upland streams draining the Flint Hills and western slope of the Ozark-Ouachita uplands, because its present distribution and habitat suggest a western or southwestern origin. Diversion of western drainages into the middle Missouri and lower Arkansas systems late in the Pleistocene would have permitted eastward dispersal of *E. f. lineolatum,* and partial replacement of *E .f. flabellare* and its White River counterpart.

Etheostoma gracile (Girard)—slough darter

Etheostoma gracile: Collette, 1962:132-149 (char.; syn.; relat.; Missouri local. compiled and mapped).

Distribution and habitat.—The slough darter is common in the lowlands, and occurs rarely in the southwestern and northeastern Ozark border (Map 188). The distribution and habitat requirements of the slough darter are much like those of the bluntnose darter. Both are confined to sluggish streams and ditches of lowlands and level, undissected uplands. As its name suggests, the slough darter commonly occurs in oxbows and other overflow waters away from the main stream. Increased siltation and the drainage of lowland swamps and sloughs have probably been unfavorable to the slough darter.

Zoogeography.—The present distribution of the slough darter suggests an origin in the lower Mississippi Valley or adjacent Gulf drainages. Eastward in the Alabama and Tombigbee rivers *E. gracile* is replaced by the closely related *E. zoniferum* (Hubbs and Cannon). Occurrence of an isolated population of *E. gracile* in the upper Osage system is subject to the same explanations as similarly isolated populations of *E. chlorosomum* (see account of that species).

Etheostoma proeliare (Hay)—cypress darter

Etheostoma proeliare: Bailey and Gosline, 1955:44, table 1 (vert. counts; floodway ditches 4 mi. E Kennett, Dunklin Co.; drainage ditch 1 mi. E Anniston, Mississippi Co.).

Distribution and habitat. — *Etheostoma proeliare* is the most common darter in the lowlands (Map 189). It is characteristic of clear, heavily vegetated ditches without noticeable current, occurring along the swifter ditches only in quiet, marginal waters.

Zoogeography.—The distributional relationship of this species and the closely related least darter (*E. microperca*) suggests that the cypress darter had a southern origin, probably in the lowlands of the Mississippi Valley or adjacent Gulf drainages.

Etheostoma microperca Jordan and Gilbert—least darter

Etheostoma microperca: Meek, 1891:123 (Jones Cr. near Dixon. Cross, 1967: 323 (Osage Fork Gasconade R., Webster Co.).

Distribution and habitat.—The least darter is widely distributed along the northern and western margin of the Ozarks (Map 190). Because of its specialized requirements, it is sporadic in occurrence, but it is often abundant where it occurs. *Etheostoma microperca* replaces the cypress darter in upland streams; the habitats of the

two are otherwise similar. The least darter is invariably found in clear, quiet, heavily vegetated waters: pools of small creeks with permanent flow, and spring-pools and seeps along the flood plains of larger streams.

Zoogeography.—The distributional relationship of this fish and the cypress darter suggests a northern origin for the least darter; perhaps *E. microperca* was localized preglacially in the Laurentian system, and entered the Mississippi Valley by way of stream connections that developed with glaciation. Ozark populations of the least darter are broadly disjunct from the remainder of the range and perhaps are glacial relicts. The Ozark Uplands probably served as a glacial refugium for this fish during the Pleistocene. The presence of isolated populations in the Neosho system provides further evidence for a former stream connection between the Arkansas and middle Missouri systems.

Sciaenidae

Aplodinotus grunniens Rafinesque—freshwater drum

Amblodon lineatus: Agassiz, 1854:307-308 (orig. descr.; Osage R.).

Amblodon grunniens: Girard, 1858:98 (St. Louis).

Aplodinotus grunniens: Jordan and Meek, 1885:14,16,17 (Missouri R. at St. Joseph; Flat Cr. near Sedalia and/or Blackwater R. at Brownsville; Grand R. at Clinton and/or Tebo Cr. at Calhoun). Garman, 1890:136 (Mississippi R. near Quincy, Ill.). Borges, 1950 (vert. distr.; Niangua Arm, Lake Ozark). Berner, 1951:table 5 (commerc. catch; Missouri and Mississippi R.). Barnickol and Starrett, 1951:311-312 (abund.; Mississippi R. local.). Funk and Campbell, 1953 (abund.; Black R. local.). Patriarche, 1953 (abund.; growth; Lake Wappapello). Funk, 1957 (mov.; Missouri streams). Purkett, 1958a:119-121 (growth; import.; Salt R.). Witt, 1960 (length and weight in relat. to otolith length and weight; Mississippi R. at Hannibal). Fisher, 1962:428 (Missouri R. local.). Burress, 1962 (abund.; harv.; Bull Shoals Res.). Hanson and Campbell, 1963 (linear distr.; Perche Cr.). Cross, 1967:324 (Missouri R. local. mapped).

Freshwater drum: Purkett, 1958b:20,42,43 (growth; length-weight relat.; Missouri streams). Fry, 1962 (harv.; Table Rock, Taneycomo, and Clearwater res. tailwaters).

Distribution and habitat.—The freshwater drum occurs over much of the state (Map 191), but it is most abundant in the Missouri and Mississippi rivers and the downstream sections of their larger tributaries. It is scarce in most Ozark streams, but is rather common in the large reservoirs of that region. This fish is an inhabitant of large lakes, impoundments, and the pools of large streams.

Zoogeography.—The present distribution of this vagile, big-river fish indicates an origin in the preglacial Mississippi system or other Gulf drainages to the west. It is the sole freshwater representative

of a large marine family, and probably was derived from marine stock that invaded freshwater streams in pre-Pleistocene time.

Cottidae

Cottus bairdi Girard—mottled sculpin

(in part ?) *Uranidea richardsoni:* Call, 1887:79 (West Fork of Black R. and tribs., Reynolds Co.; Jacks Fork and tribs., Shannon Co.; Piney R., Texas Co.; Meramec R., Dent Co.).

(in part?) *Cottus bairdi:* Meek, 1891:119,123,125,131 (Meramec Spring and Meramec R. near St. James; Big Piney and Little Piney Cr. near Arlington; Osage Fork and Niangua R. near Marshfield; Jones Cr. and Maries R. near Dixon; Lick Fork and Bryants Cr. near Mansfield; Sac R. and James R. near Springfield). Fowler, 1921:399 (Fox Cr. near St. Louis).

Distribution and habitat.—The mottled sculpin is common and widespread in the Ozarks, occurring in all the principal stream systems except the Neosho (Map 192). North of the Missouri River it is known only from Lost Creek in Warren County. *Cottus bairdi* inhabits clear streams and spring branches with a permanent strong flow of cool water. It is found in riffles as well as pools, usually in association with thick growths of water cress or other cover.

Zoogeography.—Populations of the mottled sculpin in the Ozark Uplands are disjunct from the main range of the species to the north and east. Ozarkian populations are probably glacial relicts. Robins (1954:303) indicated that the *bairdi* group had as its eastern center of dispersal the old Teays system and perhaps other portions of the preglacial upper Mississippi system. Glaciation permitted southwestward dispersal, followed by isolation of Ozarkian populations when the ice sheets again retreated northward. Robins (1954) recognized another species of this group in the Ozark Uplands; this species is still technically undescribed.

Cottus carolinae (Gill)—banded sculpin

Cottus bairdi: Meek, 1891:127 (Hickory and Shoals crs. near Neosho). Evermann and Kendall, 1895:472 (Indian Cr. near Neosho).

Cottus carolinae: Martin and Campbell, 1953 (abund.; Black R.).

Distribution and habitat.—The banded sculpin occurs throughout the Ozarks, and is known from a few localities north of the Missouri River in Lincoln and Pike counties (Map 193). In the Ozarks it is about as common and widely distributed as the mottled sculpin. The requirements of *C. carolinae* are much like those of *C. bairdi,* and the two are often found together. However, the banded sculpin tends to occupy the larger and warmer Ozark streams, the mottled sculpin the smaller creeks and spring branches.

Zoogeography.—The distribution of the banded sculpin suggests that it survived the Wisconsin ice advance in the Ozark and Appalachian uplands, from which it has scarcely penetrated the glaciated regions. According to Robins (1955:302-303), the Tennessee River system was the dispersal center for the *carolinae* group, and glaciation has had little effect on their dispersal and distribution.

SUMMARY AND CONCLUSIONS

In this report, information about the distribution of Missouri fishes is summarized, and the patterns of fish distribution in the state are interpreted in terms of the environmental conditions and historical factors that have determined their development.

The fish fauna of Missouri is diverse; 191 species are listed for the state. From analyses of range limits and the species composition of collections, four fish faunal regions are recognized. Three of these (Ozark, lowland, and prairie) correspond closely to major physiographic subdivisions of Missouri (Ozark Uplands, Southeastern Lowlands, and Osage and Dissected Till plains, respectively). The fourth faunal region (big river) includes the Missouri and Mississippi rivers and the down-stream portions of their major tributaries. The faunal regions are separated by broad ecotones, designated as an "Ozark border" where fishes characteristic of different faunal regions meet and mix in complex fashion. "Lines of best fit" are also designated; these indicate zones of abrupt faunal change within the Ozark border.

Missouri fishes are classified into four primary and three secondary faunal groups. Primary faunal groups include species having their distribution centered in a single faunal region; secondary faunal groups include species that are more widespread. Four rare species are left unclassified. The Ozark faunal group is the largest of the primary faunal assemblages, including 65 species. Thirteen of these are endemic to the Ozark Uplands. Fishes of the Ozark group are confined primarily to regions underlain by limestone bedrock, and inhabit clear streams having permanent flow and a predominance of coarse gravel or rock bottoms. Thirty-eight species are in the lowland faunal group. Lowland species occur in areas of low relief, inhabiting lentic environments and low-gradient streams having clear water and bottoms composed mostly of sand, fine gravel, and organic debris. The prairie faunal group is the smallest of the primary faunal assemblages, including 18

species. Prairie species inhabit streams subject to wide fluctuations of turbidity, temperature, and volume of flow. Thirty species and one subspecies belong to the big river faunal group. The distribution of big river fishes is correlated with gradients in environmental factors (notably turbidity, current velocity, and bottom type) within the Missouri and Mississippi rivers. Certain fishes are nearly equally abundant in two faunal regions. Seven of these belong to the Ozark-lowland faunal group. All are characteristic of the quiet pools of moderately clear, permanent-flowing streams. Six species belong to the Ozark-prairie faunal group. The requirement for coarse gravel or rock bottoms seems to be the principal factor controlling the distribution of fishes in this faunal group. Twenty-three species are placed in a wide-ranging faunal group. All species of this group are characteristic of lentic environments and the quiet pools of streams, but otherwise have broad tolerances for many environmental factors. Fishes of this group disperse readily through big rivers, and most have been favored by man's activities.

Competition seems to be an important factor in controlling the distribution of certain fishes, as indicated by: (1) the complementary distribution patterns of species that seem to have similar requirements, (2) the occurrence of certain species outside of their usual habitat in faunally depauperate areas, and (3) the avoidance of faunally-rich habitats by certain species that otherwise seem to have broad environmental tolerances. Climate is also thought to limit the distribution of fishes in the state, but its effects are largely obscured by gradients in other environmental factors.

Marked variations occur in faunal diversity within Missouri. Stream systems in the prairie faunal region have the fewest species; streams that span the boundaries between faunal regions are faunally rich. Lack of faunal diversity in the prairie faunal region seems to be related to the instability of aquatic environments there.

The character of the Missouri fish fauna has been profoundly affected by changes in physiography, drainage relationships, and climate since the late Tertiary. Meager fossil evidence and what can be deduced concerning environmental condition suggests that the late-Tertiary fish fauna of Missouri was much like that now found on the coastal plain of the southeastern United States. The strong regional differentiation that characterizes the present fauna was probably little developed, although evidence is presented suggesting that certain species were already localized in the Ozark region by the late Tertiary.

Renewed uplift of the Ozark Uplands, withdrawal of the sea

from the Mississippi Embayment, and a shift towards a cooler and less humid climate near the close of the Tertiary resulted in changing environmental conditions in Missouri, and the fish fauna began to take on a more modern character. The intrusion of continental ice sheets into the central United States during the Pleistocene had profound effects on the fish fauna, both within and beyond the glaciated regions. Glaciation was accompanied by the southward displacement of species ranges, and drainage changes that resulted directly or indirectly from glaciation permitted a mixing of faunal elements formerly localized in separate stream systems. Certain Missouri fishes may have been localized preglacially in the Hudson Bay or Laurentian systems north of the Mississippi Valley, dispersing southward as avenues became available. Examples are: silver lamprey, northern brook lamprey, pallid sturgeon, goldeye, northern pike, sturgeon chub, sicklefin chub, northern flathead chub, common shiner, brassy minnow, western silvery minnow, northern redhorse, pumpkinseed, northern logperch, and least darter. All are primarily northern in distribution, and are represented southward by forms that appear to be autochthonous to the Mississippi Valley. Large springs in the Ozark Uplands have sustained ecological conditions favorable to survival of northern species displaced southward during the Pleistocene. Disjunct populations of five fishes (northern brook lamprey, spotfin shiner, channel darter, least darter, and mottled sculpin) in the Ozark Uplands are considered to be glacial relicts.

Alternating cycles of erosion and aggradation in the lower Mississippi Valley as a result of sea level fluctuations during the Pleistocene were accompanied by changing ecological conditions that provided for the alternate dispersal and isolation of fishes in uplands east and west of the Mississippi Embayment. East-west disjuncts whose present distributions may have resulted from this process include: least brook lamprey, telescope shiner, whitetail shiner, bluntface shiner, studfish, southern cavefish, bluestripe darter, greenside darter, and banded darter.

Glaciation was accompanied by restriction of ranges as well as by range extensions. Certain fishes that had a widespread preglacial distribution seem to have given rise to geminate species after becoming localized in uplands east and west of the Mississippi River during an early ice advance of the Pleistocene. Ozarkian species that may have been derived in this manner include: Ozark shiner, Ozark cavefish, longnose darter, Missouri saddled darter, and Niangua darter. Disjunct populations of the Ozark minnow and largescale stoneroller in the Ozark Uplands and the Driftless Area of Wisconsin also may indicate a more widespread preglacial or interglacial distribution.

Certain fishes formerly localized in the preglacial drainage of the central and southern plains (including the Flint Hills and the western slope of the Ozark-Ouachita uplands) have gained access to the central Mississippi Valley when drainage of that region was diverted eastward into the lower Arkansas and Missouri Rivers. Examples are: plains killifish, plains minnow, duskystripe shiner, bluntface shiner, western slim minnow, and Arkansas darter. All members of this group are primarily western in distribution, and most are represented eastward by forms that seem to be autochthonous to the central Mississippi Valley. Other fishes that are primarily northern or eastern in distribution occur disjunctly in the upper Arkansas, and may have dispersed southwestward by way of stream connections between the Arkansas and Missouri systems. Included are: spotfin shiner, blacknose shiner, Topeka shiner, stonecat, plains topminnow, slenderhead darter, channel darter, johnny darter, and least darter. Dispersal of some of these by way of the lower Mississippi and Arkansas rivers cannot be ruled out, although none of them now occur in that area.

Climatic fluctuations since retreat of the Wisconsin ice sheet have resulted in minor adjustments in the ranges of some fishes. Disjunct northern populations of the ironcolor shiner, weed shiner, bantam sunfish, and spotted sunfish are perhaps relicts from the warm, moist Climatic Optimum. Disjunct eastern populations of the bigmouth shiner may be relicts from the warm, dry Xerothermic Interval.

Habitat modifications by man during the last two centuries have resulted in rapid and dramatic changes in the distribution of many fishes. Five species that occurred in the state as recently as 30 years ago may no longer be present. Numerous others are now more restricted in distribution. Several species are more abundant and widespread than formerly. One exotic (carp) introduced in the late 19th century is now a dominant element in the Missouri fish fauna.

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