20 July 1983

Dr. Frank B. Cross
University of Kansas
Museum & Natural History
Lawrence, Kansas 66045

Dear Frank:

Mr. David Miller, a graduate student studying the fisheries of the Arkansas River, also read your *Ms*. The following are our comments:

1) What is your record for *Phoxinus eos* in the Arkansas R. of Colorado? We know of no record for this species in the Arkansas River Basin. Ellis (1914) and Beckman (1952) reported this species only from the Platte drainage in Colorado.

Mr. Miller found an isolated population of *P. erythrogaster* near Pueblo, Colorado (Arkansas River drainage) in 1981. This was the first reported occurrence of this species in Colorado. All existing evidence (range analysis and glacial evidence) suggests this population is a glacial relict. Corroborating evidence is the occurrence of *P. erythrogaster* in the Canadian River drainage of New Mexico (Koster 1957). Koster kindly sent a ms. written in 1962. In this manuscript he provides fairly convincing evidence that *P. erythrogaster*, *Semotilus atromaculatus* and *Culaea inconstans* are native to the upper Canadian basin in New Mexico.

We agree that *Phoxinus* spp. are archaic in their western distribution and that they had more extensive southern distributions at some time, probably glacial.

2) I assume your consideration of *S. atromaculatus* as native to the Upper Arkansas is based on fossil evidence (C. Lavett Smith, 1954). However, according to recent accounts (Cross and Collins 1975; Miller and Robinson 1973), it is not extant in the Upper Arkansas. However, in 1979 Mr. Miller found a population of *S. atromaculatus* in the Monument Creek drainage just north of Colorado Springs. While the possibility exists that this population is introduced, it probably is a glacial relict native to the Arkansas River drainage of Colorado. Monument Creek provides optimal habitat for creek chub which is lacking throughout most of the Upper Arkansas. Corroborating evidence is provided in Koster (1962 ms.). The creek chub of Monument Creek is likely a glacial relict of a more southern and westward distribution rather than the result of stream capture from the Platte.

3) Mr. Miller also found *Notropis dorsalis* in the Monument Creek drainage north of Colorado Springs. This population is referrable to *N. dorsalis piptolepis*. Initially we thought that this species may have gained access to the Arkansas basin similar to N. topeka (Pflieger 1971). We now consider this highly unlikely. It is also unlikely the result of stream capture. Evidence suggests that this species is introduced (R. R. Miller agrees). If introduced, then this might also

suggest that *S. atromaculatus* is also introduced. However, the evidence for native occurrence of *S. atromaculatus* is much stronger.

4) Koster noted an interesting record for *Hiodon alosoides* in the Arkansas River drainage of Colorado. The specimens are from an archaeological dig at old Fort Bent (near La Junta, Colorado). Most fish bones from this site were of *Ictalurus* with a left hyomondibular, 2 vertebra and 3 fragments of the left preopercle from *Hiodon alosoides*. The fish bones date from before 1870. This is not convincing evidence that *Hiodon* is indigenous to the Fort Bent area. Travellers stopped at Fort Bent. Perhaps smoked or salted mooneyes were among their supplies.

5) Mr. Miller found several isolated populations of *Culaea inconstans* in the Arkansas River drainage of Colorado. We are undecided as to the status of this species. If Koster (1962 ms.) is correct and this species is native to upper Canadaian, then it is interesting that it is mostly found in the foothills region often in association with *Etheostoma cragini*.

reasonable to assume native in Ark. It is

6) An interesting parallel to the distribution of *Phoxinus erythrogaster*, *Senotilus atromaculatus* and *Culaea inconstans* in NE New Mexico is shown by the distribution of the green snake, *Ophodrys vernalis*, the lined snake, *Trapiduclonium lineatum* and the western chorus frog *Pseudacris triseriata* (Conant 1958). These herps not only have their disjunct populations in the same three New Mexico counties as the fishes, but have the main portions of their ranges in the same regions occupied by the three fish species. An indication that some "generalized tracts" are involved.

7) The walleye may have been native to South Platte in Colorado, but became extinct before 1900. Old literature from 1880's decries the rampant poaching and great slaughter of "walleyes" (for ex., at confluence with Poudre R. near Greeley). I can't think of any species that might have been confused with walleye. By late nineteenth centure, irrigation depletion and pollution probably eliminated the walleye.

Thanks for opportunity to review ms. If further information turns up I'll send it on to you.

Sincerely,

Robert J. Behnke
Associate Professor
Fishery Biology

Dr. Frank B. Cross
University of Kansas, Museum of Natural Hist~~ory Ha~~
Lawrence, Kansas 66045

Re: ~~Cross et al~~ (ms)

Dear Frank: Mr. David Miller, a graduate student studying ~~the~~ fishes of the Arkansas River ~~also~~ read your MS. The following are our comments.

①. What is your record for *Phoxinus eos* in the Arkansas R. of Colorado? ~~To my knowledge~~ we know of no record ~~exists~~ for this species in the Arkansas River Basin. Ellis (1914) and Beckman (1952) reported this species ~~from~~ only from the Platte drainage in Colorado.

Mr. Miller ~~I~~ found an isolated population of *P. erythrogaster* near ~~in~~ Pueblo, Colorado (Arkansas River drainage) in 1981. This was the first reported occurrence of this species in Colorado. All existing evidence (range analysis and glacial evidence) suggests this population is a glacial relict. Corroborating evidence ~~comes from~~ is the ~~population~~ occurrence of *P. erythrogaster* in the Canadian River drainage of New Mexico (Koster 1957). ~~I have an unpublished manuscript of~~ Koster, kindly sent a MS written in ~~from~~ 1962. In this manuscript he provides fairly convincing evidence that *P. erythrogaster*, *Semotilus atromaculatus* and *Culaea inconstans* are native to the upper Canadian Basin in New Mexico.

We agree ~~with you~~ that *Phoxinus* spp. are archaic in their western ~~portion~~ distribution and that they had ~~more~~ extensive southern distributions at some time, probably glacial.

②. I assume your consideration of *S. atromaculatus* as native to the Upper Arkansas is based on fossil evidence (C. Lavett Smith, 1954). ~~because~~ However, according to recent accounts (Cross and Collins 1975; Miller and Robinson, 1973), it is not extant in the Upper Arkansas. However, in 1979 ~~I found~~ Mr. Miller found a population of S. atromaculatus in the ~~Monument~~ Monument Creek drainage just north of Colorado Springs. While the possibility exists that this population is introduced, ~~I believe that~~ it probably is a glacial relict native to the Arkansas River drainage of Colorado. ~~Upper This stream system~~ Monument Creek provides optimal habitat for ~~this species~~ creek chub which is lacking throughout most of the Upper Arkansas. Corroborating evidence ~~was from the~~ is provided in Koster (1962 MS). ~~manuscript.~~ ~~I~~ The creek chub of Monument Creek is do not consider this population to have resulted via stream captures along the Rocky Mountain ~~chain, but rather~~ likely a glacial relict ~~remnant~~ of a more southern and westward distribution, rather than the result of stream capture from the Platte.

③ ~~I have~~ Mr. Miller also found Notropis dorsalis in the Monument Creek drainage north of Colorado Springs. This population is referrable to N. dorsalis piptolepis. ~~While I~~ Initially we ~~hoped~~ thought that this species may have gained access to the Arkansas basin similar to N. topeka (Pflieger 1970). ~~I may~~ We now consider this highly unlikely. ~~I also consider~~ It is also unlikely the result of stream capture. ~~along the Rocky mountain chain~~. Evidence suggests that this species is introduced (R.R. Miller agrees). ~~with me on this~~. If ~~it is~~ introduced, then this might also suggest that S. atromaculatus is also introduced. However, the evidence for native occurrence of S. atromaculatus is much stronger. ~~for it being native~~.

④, Koster noted ~~informs me of~~ an interesting record for <u>Hiodon</u> <u>alosoides</u> in the Arkansas River drainage of Colorado. The specimens are from an archaeological dig at old Fort Bent (near La Junta, Colorado). Most fish bones from this site were of <u>Ictalurus</u> with a left hyomandibular, 2 vertebra and 3 fragments of the left preopercle from <u>Hiodon</u> <u>alosoides</u>. The fish bones date from before 1870, ~~which is before warm water stocking began in Colorado; this is not meant to imply~~ This is not convincing evidence that <u>Hiodon</u> is <u>indigenous</u> to the Fort Bent area. ~~Then~~ Travellers ~~from farther east,~~ stopped at Fort Bent. Perhaps smoked or salted mooneyes were among their supplies. ~~If it was indigenous then the known range is extended westward.~~

⑤ Mr. Miller ~~I have~~ found several isolated populations of <u>Culaea</u> <u>inconstans</u> in the Arkansas River drainage of Colorado. We are ~~I am~~ undecided as to the status of this species. If Koster (1962 MS) is correct and this species is native to upper Canadian, then it is a reasonable ~~extension~~ to consider it also native to the Arkansas drainage in Colorado. It is interesting that it is mostly found in the foothills region often in association with <u>Etheostoma</u> <u>cragini</u>. ~~On the record, I favor an undetermined status but off the record I am inclined to believe it is native to the Arkansas Drainage in Colorado.~~

⑥. An interesting parallel to the distribution of Phoxinus erythrogaster, Semotilus atromaculatus ~~and~~ Culaea inconstans in NE New Mexico is shown by the distribution of the green snake, Ophodrys vernalis, the lined snake, Trapidoclonium lineatum and the western chorus frog Pseudacris Triseriata (Conant 1958). These herps ~~terrestrial~~ ~~cold-bloods~~ not only have their disjunct populations in the same three New Mexico counties as the fishes, but have the main portions of their ranges in the same regions occupied by the three fish species. An indication that some ~~While I am not a proponent of vicariance biogeography, this evidence suggests~~ "generalized ~~tracts"~~. tracts" ~~tracks~~ are involved.

7. The walleye may ~~be~~ have been native to South Platte in Colorado, but became extinct before 1900. Old literature from 1880's ~~mention~~ decries the rampant poaching and great slaughter of "walleyes" (for ex., ~~near~~ at confluence with Poudre R. near Greeley). I can't think of any species that might have been confused with walleye. By late nineteenth century, irrigation depletion and pollution probably eliminated the walleye.

Thanks for opportunity to review MS. If further information turns up I'll send it on to you.

Sincerely,

Robert Behnke

THE UNIVERSITY OF KANSAS · LAWRENCE, KANSAS · 66045
MUSEUM OF NATURAL HISTORY

5 July 1983

Dr. Robert Behnke
Department of Fish and Wildlife
Colorado State University
Fort Collins, Colorado 80523

Dear Bob:

I very much appreciated your offer to check parts of our distributional summaries for the zoogeography symposium volume, particularly with respect to streams that have headwaters in the Rocky Mountains. Thus I'm enclosing a copy of the chapter for whatever corrections and suggestions you have time and inclination to make. I've isolated the distributional table on the top of the stack, and highlighted the columns that I'd like most for you to check -- the "Rocky Mountain" region or physiographic province and the streams that enter it. The column entries (N, U, I, etc.) are explained in the heading; the uncertainty with respect to "U" entries means we are uncertain whether the species occurs naturally or as the result of introduction, not the occurrence itself.

Following the lengthy table of individual species distributions by stream and habitat is a one-page table (Table 5) that represents the comparative faunal analyses. Any change in the former table (species distributions) will affect the latter (faunal similarities) of course. We'll make such changes based on the corrections you enter on Table 4, the individual species distributions.

Beyond checking our basic distributional data, we'll welcome any suggestions you have with respect to the general text if you wish to review that as well. I'm really glad to have seen you in Tallahassee, and pleased that you are willing to look at this chapter of the zoogeography tome. It is not in "final" form. Other reviewers have called some problems to our attention, and we've discovered a few ourselves. Right now we are compiling a list of needed changes, so far all minor, toward a revision in August. Wiley and Hocutt have demanded final copy by September 1, so we don't have a lot of time.

Thanks again for any help you can provide.

Sincerely,

Frank Cross.

Frank B. Cross
Curator of Fishes

P.S. – You'll discover that our distributional table is not in full agreement with species maps in the atlas – We did pick up several additional records not known to those who compiled the maps. Although I'm guessing the principal problems you'll find will be omissions, you might also mark any listed occurrences that you question, and I'll let you know our basis for them – FBC.

# FISHES IN THE WESTERN MISSISSIPPI DRAINAGE

Frank B. Cross, Richard L. Mayden, and J. D. Stewart

## INTRODUCTION

The "western Mississippi drainage" as used here includes the Missouri, Arkansas, and Red river basins, and western tributaries of the Mississippi River from the mouth of Missouri River to the Red River. We divide these basins into 18 drainage units (Fig. 1), and tabulate the fauna of the Mississippi mainstream as a nineteenth unit. The great areal expanse of the western Mississippi drainage includes parts of five physiographic provinces, the Coastal Plain, Interior Highlands, Central Lowlands, Great Plains, and Rocky Mountains (Fig. 2). The basins in combination drain areas at elevations exceeding 4000 m to near sea-level, and have a mean annual precipitation from less than 30 to about 150 cm. Much of the region was once an epicontinental sea (chapter XX), accounting for its largely tabular bedrock and land-surface. Only minor portions of the region were glaciated, but the earliest ice sheets markedly rearranged drainage patterns; some streams having Arctic outlets were redirected to the Gulf of Mexico.

The fish fauna of the region is well known. Much of it became known before settlement by European man significantly affected the biota. That information stems chiefly from government surveys to establish routes for travel from eastern settlements to the Southwest and the Pacific coast. Notable 19th century reports of the ichthyofauna are those of Girard (1856, 1858), Cope (1864, 1865, 1871), Jordan and Meek (1885), Jordan and Gilbert (1886), Jordan (1891), Meek (1892, 1894, 1896), Woolman (1896), and the cumulative report on the Missouri River fauna by Evermann and Cox (1896). More recently, distributional information on fishes has been compiled for most states of the region: Louisiana (Douglas 1974); Arkansas (Buchanan 1973); Missouri (Pflieger 1971, 1975); Iowa (Harlan and Speaker 1956); Oklahoma (Miller and Robison 1973); Kansas (Cross 1967); Nebraska (Morris, Morris and Witt 1974); South Dakota (Bailey and Allum 1962); North Dakota (Reigh and Owen 1979; Owen, Elsen, and Russell 1981); New Mexico (Koster 1957); Colorado (Beckman 1952); Wyoming (Baxter and Simon 1970); and Montana (Brown 1971). These sources as well as miscellaneous other literature were used in this analysis, together with the recent *Atlas of North American Freshwater Fishes* (Lee, Gilbert, Hocutt, *et*. *al*. 1980). Previous zoogeographic studies of parts of the region, notably those by Metcalf (1966) and Pflieger (1971), were especially useful.

A relatively rich paleontological record also exists for fishes in this region; perhaps its geographic, temporal, and taxonomic scope exceeds that for any region in North America except the intermontane west. The fossils range in age from Ordovician (500 mybp) to Pleistocene and consist repeatedly of both freshwater and marine faunas. This chapter deals only with Cenozoic freshwater faunas (Tables 1 and 2). Pre-Cenozoic freshwater faunas include a number of taxa, of which only sturgeons, paddlefish, amiids and gars persist in Cenozoic faunas and recent river systems of this region.

## DRAINAGE HISTORY

### *Geologic background.*

The Plains region experienced at least three cycles of marine transgression and regression during the Cretaceous Era, being repeatedly inundated and drained from the west by epicontinental seas. This resulted in the deposition of extensive layers of sandstones, shales, and carbonate rocks. It is generally thought that the final regression of this seaway predates or coincides with the Laramide Orogeny which produced the Rocky Mountains; however, an area of Paleocene marine sediments is known from Saskatchewan, Manitoba, and North Dakota. Whether this vestigial sea was connected to the Arctic Ocean or the Gulf Embayment has not been unequivocally established.

The final retreat of the seaways left a nearly planar surface on which the Paleogene sediments of Montana, Wyoming, Nebraska, Colorado, and the Dakotas formed. Almost nothing is known of the Paleogene drainages. Very few of these Paleogene deposits produce significant ichthyofaunas. Of some interest, however, is an Oligocene lake deposit in Florissant, CO, which has produced an abundant biota of plants and insects, as well as a few fishes [*e.g.*, *Amia* (Boreske 1974), *Ictalurus* (Lundberg 1975), *Amyzon* (Cope 1884), and *Trichophanes* (Rosen and Patterson 1969)].

By way of clarification, it must be understood that the terms, "Miocene, Pliocene, and Pleistocene," as currently understood and as used in this paper, are at variance with traditional usage in ichthyological literature. Time periods, provincial land mammal ages, and traditional glacial terminology are incorporated in Table 3. Thus, much of the Plains sediments traditionally designated as Pliocene are included in Miocene times. Pliocene deposition is thought to have begun between 5.5 million years before present (mybp) (Haq 1977) and 5.0 mybp (Berggren, and vanCouvering 1974), and ended between 2.5 mybp (Boellstorff 1977, 1978) and 1.6 mybp (Haq, Berggren, and vanCouvering 1977). Sediments which were deposited after the Ogallala Group and which bear fossils of the Rexroadian subdivision of the Blancan land mammal age (Schultz, Martin, Tanner *et al*. 1978) are now designated Pliocene. The term Pleistocene refers to sediments younger than 2.5 mybp.

Moreover, as recent authors (Bowen, 1978; Boellstorff 1978) have pointed out, interpretation of the glacial history of North America within the framework of four major glacial cycles conflicts with observable data, and is not concordant with our present understanding of European glacial history, the primary source for the traditional view. The pre-Wisconsinan glacial stage terms have generally been applied only conceptually. Studies of the type area of the Nebraskan and Kansan tills indicate that the type Nebraskan till of Shimek (1909) is bracketed by fission track dates on volcanic ashes of 1.2 mybp and 0.7 mybp (Boellstorff 1978). The seven tills which Boellstorff (1978) documented in this area accord with the seven tills detected in Nebraska by Reed and Dreeszen (1965). In addition, it is generally conceded that neither the "Illinoian" nor Wisconsinan glaciations were severe enough to deposit tills in Nebraska.

These facts are discordant with the traditional four glaciation framework not only because there are at least twice as many tills as available glaciations, but also because the earliest tills indicate glaciation commencing in the Late Pliocene. This need not be disturbing when one remembers that the Pliocene epoch was defined before and independent of Agassiz's scheme of European glaciation.

The absurdity of the conceptual vs. the strict application of these pre-Wisconsinan stage terms may be illustrated by the Broadwater-Lisco faunas of Hooker County, NE. Hibbard (1970) lists these faunas as belonging to the Aftonian interglacial, that is, post-Nebraskan. In reality, they are at least 2.8 my old and must therefore be considered of Late Pliocene age, while the type Nebraskan till is no older than 1.2 mybp (Table 3) (Boellstorff 1978).

Of much greater utility as sequential reference markers are the North American land mammal ages, because these are defined biostratigraphically and because mammalian fossils, unlike glacial tills, are frequently found with pertinent fossil ichthyofaunas. For convenience, this paper will consider the Mio-Pliocene boundary as approximating the break between Hemphillian and Blancan Land Mammal Ages. The boundary between Early Blancan (Rexroadian) and Late Blancan (Senecan) faunas will approximate the Plio-Pleistocene boundary.

Miocene sediments are common to Colorado, South Dakota, and all states southward. Little sedimentary evidence is available elsewhere for Miocene drainage patterns in the western Mississippi region. Clearly, the source area for the Miocene alluvium of the Plains was the eastern slopes of the Rocky Mountains, which had undergone renewed uplift shortly before. Most of the sediments of the Ogallala Group in Nebraska, Kansas, Oklahoma, and Texas therefore appear to have been deposited from west to east. Sediments of this age are, however, rarely encountered in eastern Nebraska, eastern Kansas, or any of Oklahoma beyond the panhandle (Frye 1970, Seni 1980). Whether this is from erosion or non-deposition is uncertain. Ogallala sediments, where present, form nearly continuous sheets of sand and gravel across ancestral drainages and constitute the primary aquifer in the western Plains. The Ogallala reaches depths of 90m in Kansas and exceeds 150m in parts of Nebraska.

## Pre-glacial (Mio-Pliocene) Drainage Patterns

Drainage patterns supposed to have been ancestral to the Missouri, Arkansas, and Red rivers have been described in an ichthyological context by Metcalf (1966), Pflieger (1971) and others, and are summarized elsewhere in this volume (see especially chapter XX, fig. XX). Metcalf (1966) recognized three major preglacial components of the regional drainage: the southward flowing Teays/Mississippi, a northern Arctic ("Hudson Bay") component, and a Preglacial Plains Stream System that flowed southward largely independent of the preglacial Mississippi. Two of the elements, the Teays/Mississippi and the Arctic, have been authenticated by geologic and faunal evidence, although the westward extent of the Miocene Mississippi drainage is not precisely known. Owen *et al*. ( 1981:6) indicated that areas within the present Missouri River drainage from the Moreau and Cheyenne rivers northwestward formerly drained northward as the Arctic component (Fig. 3~~a~~A-1). The ancestral Bad, White, and Niobrara flowed southeastward to the Mississippi via the Iowa River; this drainage, as mapped by Owen *et al*. ( 1981:6), extended westward through central South Dakota (Fig. 3~~a~~A-2). Southward from the ancestral Iowa River, tributaries to the Mississippi were thought by

Metcalf (1966) and Pflieger (1971) to have a much more limited westward extent than today. The largest tributary was the ancestral Grand River, originating at a longitude of about 98o in southeastern Nebraska. Southeastward, the Grand was joined by the Kansas River, originating at approximately the same longitude (Fig. 3~~a~~A-3). Southward from the Grand/Kansas river, the western Mississippi drainage was virtually confined to the Ozark-Ouachita plateaus.

Metcalf (1966) believed that areas south of the ancestral Iowa River, and west of the ancestral Grand River and Ozark-Ouachita plateaus, drained southward into or beyond the present Red River. That system, the Preglacial Plains Stream System, incorporated most of the region now drained by the Platte, Arkansas, and Red river basins. Metcalf's conclusions concerning the Plains drainage were derived mainly from evidence presented by Lugn (1935) and Lueninghoener (1947) (Nebraska portion), Frye and Leonard (1952) (Kansas), and Quinn (1957) (Arkansas). There is no known geological evidence of a preglacial Plains stream in Oklahoma. The major geologic evidence for the central portion of this system concerns the path of the western-derived Ogallala sands and gravels. Two arguments permit the deduction that no east-flowing rivers crossed the Flint Hills of Kansas in the Miocene. First, Tertiary gravels composed of rounded locally-derived chert are found as high terraces in the Flint Hills, but never on the crests (Frye and Leonard 1952). Second, the only sediments of western (Rocky Mountain) origin in the lower Kansas River Valley, the only drainage which today cuts through the Flint Hills, appear only after "Kansan" deposition (Davis 1951). Thus, the only outlet for Miocene drainages from western Kansas must have been to the southeast into Oklahoma.

Metcalf (1966) cited evidence that the Preglacial Plains Stream, or its glacial equivalent which he called the Ancestral Plains Stream, transgressed the present Red River valley near the site of Dallas, TX, and continued southward toward the Gulf. If so, it may have received additional southern tributaries that extended westward beyond the present Pecos River (see Koster 1957).

While Metcalf's (1966) arguments are persuasive, the geologic evidence for an extensive Preglacial Plains Stream System is ambiguous. Horberg and Anderson (1956) concluded that the Platte drained to the Mississippi preglacially, an interpretation acknowledged by Metcalf. Subsequently, pre-Oligocene patterns in western Nebraska were mapped by DeGraw (1969) and Stout, DeGraw, Tanner, _et_. _al_. (1971) (Fig. 3A-4). These drainages consisted of several eastward flowing streams south of the Iowa River system. Headwaters of these streams were located in the same region as the present Platte and Niobrara river systems but transgressed many of the present divides. The eastward extent of their map lies in the headwater regions of the present Loup River system. While these streams might there have turned southward to become Metcalf's Preglacial Plains Stream, a "Nebraskan" paleovalley extending from southwestern Wyoming through western Nebraska, and veering northward toward the early Iowa River system (Stanley and Wayne 1972, discussed below) indicates that the drainages mapped by DeGraw (1969) were part of the pre-glacial Iowa River system. Alternatively, some of the streams may have entered the preglacial Grand-Kansas River system described below.

Dreeszen and Burchett (1971) discussed buried channels of the Grand/Kansas River system, which they thought varied in age from Cretaceous to early Pleistocene. As mapped by those authors, the complex channels extended eastward from southeastern Nebraska and northeastern Kansas to discharge into the Mississippi River approximately along the present lower course of the Missouri River. The authors stated additionally that two buried valleys in southeastern Nebraska

> "have been traced westward more than halfway across the state and, presumably, are a part of the Rocky Mountain drainage system. For example, the most southerly of these buried valleys (at various times mistakenly referred to as the 'Ancestral Republican River') extends upgradient into Kansas near Chester, Nebraska, and back into Nebraska near Superior. For 15 miles westward from Superior this 'buried' valley is coincident with the present Republican River valley and then branches. One branch has been mapped to the northwest and the other is approximately coincident with the present Republican River valley."

If these buried valleys represent preglacial drainages, they restrict the southward-flowing preglacial Plains Stream system to a region south of the present Republican River valley. Paleontological data can be brought to bear on the age of these valleys. Eshelman (1975) has recorded an extensive Late Blancan (Senecan) fauna from localities in the "ancestral Republican River" paleovalley four to seven miles south of the Nebraska border in Republic County, KS. These localities correspond exactly with the Kansas loop of the valley described by Dreeszen and Burchett (1971). Correlation with glacial events is not a simple task in unglaciated regions. Eshelman (1975) concluded that the White Rock fauna was deposited in late pre-Nebraskan times (conceptually applied, meaning near the Pliocene-Pleistocene boundary). However, Skinner (1972) considered the Long Pine Gravels of Nebraska to be fluvioglacial in origin; these gravels contain a fauna extremely similar to the White Rock fauna (M. Voorhies, pers. com.). If glacial, it would probably correspond to the earliest till (2.2mybp) of Boellstorff (1978), which is much earlier than the type Nebraskan till. At the very latest, this drainage would have removed Nebraska from the Plains drainage in glacial times, and may have done so preglacially. In northwestern Kansas, Bayne and Fent (1963) asserted that the Solomon (a tributary of the Kansas River) was probably through-flowing to the Mississippi throughout the Pleistocene. However, their evidence seems to be refuted by the conclusions of Frye and Leonard (1952) and Davis (1951), cited previously. In light of the extensive Neogene and Pleistocene drainage shifts in this region, it is significant that Bennett (1983) reports that Prairie Dog Creek, Bow Creek, and the North Fork of the Solomon River in Norton and Phillips Counties, KS, have occupied essentially their present drainages since at least Clarendonian times. An interpretation of the works cited is consolidated into Fig. 3.

### Glacial Drainage Patterns

Whatever the northern extent of the Preglacial Plains Stream System, the advent of glacial ice in the Plains region deflected northward- and eastward-flowing drainages to the south, and also contributed glacial runoff. In the classic conception of the North American glacial history, the first of these cycles has been termed the Nebraskan glaciation. This event united all drainage units of the Plains as far southward as the Grand/Kansas stream. Geologic investigations supporting such a southern deflection along the "Nebraskan" glacial margin have been reported by Stanley and Wayne (1972). Anorthosite-bearing gravels, evidently derived from a source in southwestern Wyoming, constitute three channels through Nebraska. The oldest of these runs to the northern Nebraska border, veers sharply southward adjacent to a "Nebraskan" till, and exits into the northwestern corner of Missouri (Fig. 3B-1). Presumably, this drainage would have passed into the ancestral Iowa River preglacially (Fig. 3A-2). Bennett (1979, fig. 4) placed the Broadwater-Lisco, Sand Draw, and Seneca faunas (Blancan) in this paleovalley. The last fauna may be of earliest Pleistocene age, but the first two are certainly older than the 2.5mybp upper boundary of the Pliocene. The ancestral Republican valley of Dreeszen and Burchett (1971) flowed into the Grand River at this time (Fig. 3A-3). The "Kansan" glacial maximum diverted the drainage systems of the Plains still farther south, at least temporarily, through the McPherson channel in central Kansas (Fig. 3C) (Frye and Leonard 1952). Thus, the *pleistocene* "Ancestral Plains stream" of Metcalf (1966) must have existed (Fig. 3C), whether or not it had a preglacial precursor. Zoogeographically, the "Kansan"-stage of drainage development is important in that it mixed the faunas of all northern plains streams, whether north- (Arctic), south- (Plains), or east- (Iowa/Grand) flowing preglacially.

Western Plains faunas may have been mixed southward to the Gulf of Mexico. Transgression of the present Red River Valley by the Plains stream is a possibility (Metcalf 1966; Fig. 3B-2, this paper). Metcalf (1966) cited, as evidence for southward extension of the Plains stream, high-level pre-Kansan quartzite cobble terraces *of northern origin* near Dallas, TX (Slaughter, Crook, Harris, *et al*. 1962) (presently a headwater region of the Trinity River system). Nevertheless, Metcalf (1966) accepted Frye and Leonard's (1963:10-11) conclusion that the Red River had already established its present valley at this time. We doubt that either the age (Wisconsinan, *fide* Dalquest 1965) or the location of the fossils and terraces discussed by Frye and Leonard provide conclusive evidence as to preglacial or early glacial drainage patterns in the critical area north of Dallas. A Pleistocene Plains stream utilizing the present Trinity valley enroute to the Gulf is suggested also by expansive Pleistocene terraces in the headwater region of the Trinity River (Geological Atlas of Texas, Sherman Sheet, Walter Scott Adkins Memorial Edition, 1967) and by late Pleistocene fish faunas near Dallas (Uyeno and Miller 1962) composed mostly of large river, lowland species. This fauna implies that a much larger river existed in the area during the Pleistocene than exists there today.

In southwestern Kansas, a post-Miocene - pre-Illinoian southward flowing river system crossing the present Arkansas and Cimarron rivers was mapped by Frye and Leonard (1952), Metcalf (1966) and later, based on bedrock data by McGovern (1971). Metcalf suggested that this system was a western tributary of the Plains Stream System and joined it in northcentral Oklahoma.

As the most southerly lobe of the "Kansan" glacier began its retreat, flow through the Kansas River outlet was restored, establishing the Missouri River basin approximately in its present form. The Smoky Hill River, a former tributary to the Arkansas, was transferred to the Kansas (Missouri) system by Wisconsinan time.

58?

Quinn (1957) proposed that a minor stream south of the glaciated region transgressed the Interior Highlands to capture part of the Plains drainage, establishing the present Arkansas River system.

The Mississippi/Teays ultimately vacated its valley west of Crowley's Ridge along the eastern flank of the Interior Highlands, in southeastern Missouri and northeastern Arkansas, to discharge through the ancestral Ohio River valley.

Drainage patterns within the Interior Highlands were not directly affected by glaciation, and have maintained their basic configuration since the Paleozoic (Pflieger 1971). The character of streams in the Highland region has changed greatly over time, however, as the Ozark dome was alternately elevated and degraded (Bretz 1965).

## ZOOGEOGRAPHY

### Preglacial Fossil Fishes

Paleontological evidence of the preglacial fish fauna is extensive for the Plains region from Nebraska southward, but published fossil records are few or absent from the northernmost plains and Rocky

Mountains (Arctic component of the present Missouri Basin), the Interior Highlands region, and the Coastal Plain segment of the present western Mississippi drainage.

The pertinent fossil localities and their approximate ages are summarized in Table 1 and Fig. 4. The following extant fishes or their ancestral stock evidently inhabited the central and southern Plains prior to the Pliocene: *Atractosteus spatula*, *Amia calva*, *Esox sp.*, *Ictiobus bubalus*, *Ictalurus furcatus*, *Ictalurus natalis*, *Ictalurus punctatus*, *Ictalurus nebulosus* and/or *Ictalurus melas*, *Pylodictis olivaris*, *Lepomis gulosus*, *Micropterus punctulatus*, *Menidia* sp. and *Aplodinotus grunniens*. Also present is an extinct species referred to *Notropis*. However, the systematics of living *Notropis* are poorly established and there is no basis for relating it to any living taxon. Likewise, an extinct species of *Pomoxis* is described from this period, and it may be ancestral to either or both living taxa. Of the fishes listed, the fossil record of *Aplodinotus* continues into the early Blancan of this region, *Ictiobus bubalus* to the Irvingtonian, *Esox* to the Rancholabrean. *Ictalurus punctatus* and *I. melas* or its probable ancestor (*I. sawrockensis*) have a generally continuous fossil record to the present day in this area.

Many of these fishes are characteristic of "big river" and lentic habitats. That result may mean only that depositional processes are most likely to preserve fossils in such habitats, and that the skeletal parts of large riverine or lacustrine species are most likely to be discovered and identified. Nevertheless, the records indicate large rivers and lakes, probably warm and containing macrophytes, occurred widely on the Miocene Plains. Noteworthy are the many records of extinct species of *Amia* in the Paleogene of Colorado, Nebraska, and the Dakotas, and especially records of *Amia calva* in the Miocene of Kansas and Nebraska. *Amia* apparenly disappeared in these areas by the onset of glaciation and would not be expected under present stream-conditions. Similarly, records of *Esox*, *A. spatula*, and *Micropterus* extend much farther into the plains in preglacial epochs than they do now, as native fishes.

The following extant taxa make their first appearance in the Plains region in the pre-glacial portion of the Pliocene (faunas of the Rexroadian subdivision of the Blancan and mammal age; see Table ): *Hiodon alosoides*, *Notropis stramineus*, *Pimephales promelas*, *Semotilus atromaculatus*, *Ictiobus cyprinellus*, *Ambloplites rupestris*, *Lepomis cyanellus*, *Lepomis humilis*, and *Morone chrysops*. The records of *Semotilus* and *Pimephales* continue into the Irvingtonian, and those of *L. cyanellus* and *L. humilis* into the Rancholabrean of this region.

## *Hypothesized Preglacial Stream Faunas*

*Ancestral Upper Missouri Basin (Arctic component)*.-- Lacking fossil evidence from the area drained by the Hudson Bay streams, Bailey and Allum (1962) proposed that the following extant fishes, or their progenitors, occupied the Arctic drainage preglacially: *Semotilus margarita* (ssp. *nachtriebi*), *Phoxinus neogaeus*, *Phoxinus eos*, *Couesius plumbeus*, *Catostomus catostomus*, and *Catostomus platyrhynchus*. Bailey and Allum doubted that other members of the present Missouri River fauna would have survived the rigors of glaciation in the northwesternmost part of the basin; thus, by implication, they attributed other extant species to more southerly sources and/or later entry into the Missouri basin.

McPhail and Lindsey (1970) believed that a more extensive fauna survived in the preglacial Arctic drainage. They assumed that organisms in the extensive Hudson Bay drainage were forced south by an early glacial advance until they occupied only that southwestern portion of the drainage that was free of ice. This refugium was "The source from which central Canada was repopulated." McPhail and Lindsey (1970) suggested that *Hybopsis gracilis* and *Hiodon alosoides* originated in the ancestral Hudson Bay Drainage. In this context, the record of *Hiodon* cf. *alosoides* in the pre-glacial Pliocene of Nebraska is noteworthy (Smith and Lundberg 1972).

Metcalf (1966) listed numerous fishes thought to occupy the ancestral Hudson Bay drainage and/or the ancestral Iowa River drainage: *Scaphirhynchus albus*, *H. alosoides*, *Hybopsis gracilis*, *H. gelida*, *H. meeki*, *Rhinichthys cataractae*, *Notropis atherinoides*, *N. heterolepis*, *P. promelas*, *Moxostoma macrolepidotum*, *Catostomus commersoni*, *Lota lota*, *Percopsis omiscomaycus*, and *Culaea inconstans*. Pflieger (1971) concurred with most of Metcalf's assumptions, except for *N. atherinoides* and *N. heterolepis* which he thought more likely to have entered the Missouri system from the Mississippi/Teays and the Laurentian system, respectively. Pflieger (1971) added seven species to the list of possible inhabitants of the preglacial Arctic drainage: *Ichthyomyzon unicuspis*, *Lepisosteus platostomus*, *Notropis dorsalis* (ssp. *piptolepis*), *Hybognathus hankinsoni*, *Hybognathus argyritis*, *Noturus* *flavus*, and *Stizostedion canadense*.

*Preglacial Plains Stream and/or Western Mississippi Basin*.-- Species represented by pre-Pliocene fossils, listed in an introductory paragraph to this subsection, probably ocupied either the south-flowing Plains Stream System of Metcalf (fig. :chpt ), or extensive western tributaries of the Mississippi/Teays (Fig. 3A, especially the Grand River system). Metcalf listed these additional species as probable inhabitants of his Preglacial Plains Stream System: *Hybopsis aestivalis* (especially ssp. *tetranemus*), *H. gracilis* (ssp. *gulonella*), *Phenacobius mirabilis*, *Notropis lutrensis*, *N. topeka*, *N. stramineus* (ssp. *missuriensis*), *Hybognathus placitus*, *Carpiodes carpio*, *Fundulus kansae* (=*zebrinus*), *F. sciadicus*, and *Etheostoma spectabile* (ssp. *pulchellum*). He concluded further that *N. atherinoides*, *N. blennius*, *Campostoma anomalum*, *Carpiodes cyprinus*, and *Catostomus commersoni* occupied both the Plains stream and other basins.

Pflieger (1971) accepted the evidence for an independent, south-flowing Plains drainage, and generally agreed with Metcalf's conclusions as to its faunal significance. Notable modifications are Pflieger's belief that *Notropis topeka* originated in the ancestral Iowa River, that *Carpiodes carpio* inhabited the Mississippi as well as southwestern drainages, and that *Fundulus sciadicus* evolved in the ancestral Iowa or Grand River drainage rather than in the Plains stream.

Bailey and Allum (1962) proposed that many of the species which Metcalf (1966) attributed to the Plains Stream were acquired instead from the Mississippi drainage during and following integration of the Missouri River Basin by glacial action, or by postglacial stream captures.

### Glacial redistribution of the Fish Fauna

The earliest glacial cycle blocked Arctic drainage outlets, diverting them and their faunas first into the Iowa River system, then into the ancestral Grand/Kansas River system. The southernmost extension of glacial ice (during the Kansan glaciation, as conceptually applied) temporarily diverted flow into the Arkansas system (Fig. 3c), which may have continued southward as the "Ancestral Plains Stream", before receding to leave the Missouri River Basin in essentially its present form. Simultaneously, species inhabiting the ancestral Laurentian and Mississippi/Teays systems would have been displaced southward beyond the glacial front. Therefore opportunities for mingling of the faunas of virtually all preglacial drainages occurred from the earliest glacial stages.

At the onset of glaciation in the Late Pliocene (Fig. 4; Senecan subdivision of the Blancan Land Mammal Age), these taxa appear in the Plains region: *Anguilla rostrata*, *Notropis cornutus*, *Nocomis biguttatus*, and a species of the *Noturus furiosus* group. Of these, only *Nocomis* has a later fossil record in this region, continuing into Irvingtonian faunas.

In the Early Pleistocene (faunas of the Irvingtonian land mammal age), the first occurrences of several taxa are recorded: *Esox masquinongy*, *Campostoma anomalum*, *Hybognathus placitus*, *Hybopsis gracilis*, *Notemigonus crysoleucas*, *Notropis rubellus*, *Rhinichthys* sp., *Catostomus commersoni*, *Ictiobus niger*, *Moxostoma duquesnei*, *M. carinatum*, *Noturus* cf. *placidus*, *Perca flavescens*, *Lepomis megalotis*

and *Micropterus salmoides*. In this area *Esox*, *Hybopsis gracilis*, 779
*Notemigonus*, *Catostomus commersoni*, *Moxostoma duquesnei*, *Micropterus* 784
*salmoides* and *Perca* continue into the Rancholabrean faunas. Taxa which 786
first occur in the Rancholabrean faunas in this region include 790
*Hybognathus hankinsoni*, *Notropis nubilus*, *Catostomus platyrhinchus*, 793
*Noturus gyrinus*, *Lepomis microlophus*, *L. macrochirus*, *Etheostoma exile*, 795
and *Percina copelandi*. 798

Several extant fishes are represented by fossil records not fully 802
congruent with their present ranges, and the adjustments may be 803
attributable to glacial events. *Amia calva* was extirpated from the 804
northern Plains, as mentioned previously, perhaps as a glacial effect; 807
so was *A. spatula*. *Pylodictis olivaris*, however, was widespread in 808
preglacial faunas and inhabits most of the region today, but is not 811
represented in any glacial fossil assemblages in the central or northern 812
Plains, although it persisted in Pliocene-Pleistocene associations in 813
Texas. *Esox masquinongy* and *Perca flavescens* occurred in Irvingtonian 814
(Illinoian of some authors) faunas in southwestern Kansas and 820
northwestern Oklahoma far southwest of their current native ranges 821
(Smith 1954; 1958; Smith 1963), and *P. flavescens* and *Stizostedion* 823
*vitreum* were found in an Irvingtonian fauna in nearby McPherson County 828
KS (Semken 1966). None of these species persisted into Holocene faunas 830
in that area, although *P. flavescens* and *S. vitreum* maintain populations 831
there now, following their introductions into impoundments. *Notropis* 837
*nubilus*, *Hybognathus hankinsoni*, *E. masquinongy*, and *P. flavescens* 840
occupied the southwestern Kansas fossil site at a slightly later date. 844
The site is well south of the nearest extant populations of *H*. 845

*hankinsoni*, and well west of the nearest extant populations of *N. nubilus*. *Semotilus atromaculatus* and *Catostomus commersoni* also are represented in fossil associations in Meade County, KS, and Butler County, OK. Their occurrence may be significant in that both species are now absent from the Prairie region south of the Kansas River basin, although the ranges of both extend farther southward in the Interior Highlands and Rocky Mountains. Perhaps they reached the southern Rockies by having had continuous ranges across the southern Plains under glacial conditions, rather than by a route involving stream captures along the Rocky Mountain chain.

*Phoxinus* spp. in the western Mississippi basin probably are archaic, despite the absence of fossil evidence to that effect. Their modern distributions imply that each had more extensive southern distributions at some previous time, presumably glacial; Figure 5 shows the present distributions of two of the three species. continental divide, *Catostomus platyrhinchus* is presently confined to headwaters of the Missouri River system, but is represented at a Rancholabrean site in northwestern Kansas (unpublished data of J. D. Stewart and G. R. Smith), indicating that it was more widely distributed southward at a late glacial stage (*ca*. 12,000 yr bp).

The modern distribution of *Fundulus sciadicus* suggests southeastward displacement of that species from a place of origin in the central plains into the northern and western parts of the Interior Highlands, where relic populations persist (Fig. 5). The Ozarkian populations might have been established as early as Kansan glaciation via the newly integrated Missouri River basin or the Ancestral Plains

Stream.

Glacial events must have caused important distributional adjustments in the eastern part of the region, though evidence from fossil occurrences is lacking. Isolated populations of *Percopsis omiscomaycus* in northwestern Missouri and southwestern Iowa presumably are glacial relics. The distribution of *N. nubilus* is strangely disjunct in the Ozark Upland and the upper Mississippi basin, including the unglaciated "Driftless Area" (Burr and Page, chapter XX). Pflieger (1971) suggested a formerly widespread distribution for this species in the Central Lowland province, which was vacated while glaciated and not subsequently reinvaded because streams on the glacial till-mantled land-surface do not afford suitable habitat. Evidence of southwestward displacement of *N. nubilus* during the Illinoian glacial advance was cited previously.

In the unglaciated southeastern part of the western Mississippi basin, ice advances probably had the following effects. First, the advances concentrated species by compression of their ranges for some distance below the glacial front, contributing to the high diversity in the faunas of the Interior Highlands (as well as in the Cumberland Plateau to the east. Second, glaciation facilitated exchange of upland species across the Mississippi Embayment, at times when sea level was as much as 100 meters below its present level; then, presumably, the Mississippi channel was deeply incised to a lower base-level, and its tributaries were more steeply inclined in their lower courses. Third, ice advances facilitated transport of Interior Highland species via the Mississippi and lower Arkansas rivers to the several distinct drainage units they now inhabit within the Highlands province. Retreat of the ice sheets may have isolated many species of Highland streams from one another by alluvial deposition in the lower stream courses east and west of the Mississippi valley as it again became aggraded. Finally, the eastward translocation of the Mississippi mainstream from its former course against the Highland ridge isolated populations of upland species inhabiting the St. Francis and White River systems, by addition of extensive areas of Coastal Plain to their lower courses. That addition markedly increased the species diversity in those small river systems as well, by enlargement of their drainages to include lowland faunas. Some species whose present distributions may exemplify effects of such Pleistocene events are mapped here (Figs. 5 and 7) and in chapter XXXX.

## *Minor Stream Connections*

Range extensions of some species within this zoogeographic region may be attributed to interchanges between headwater tributaries of distinct drainages. A number of hypothesized stream captures are presented below to explain range extensions of western Mississippi fishes. They have been proposed on the basis of geological, genetic or faunal distribution data.

*Belle Fourche-Little Missouri rivers*. Capture of the little Missouri headwaters by the Belle Fourche "is classic in its simplicity," (Bailey and Allum 1962) in that the abrupt southwest bend of the Belle Fourche was an old section of the Little Missouri. The presence of *Catostomus catostomus*, *C. platyrhynchus*, *Couesius plumbeus* and *Rhinichthys cataractae* in the Belle Fourche may support such an interpretation.

*White (South Dakota)-Niobrara. Capture by the White River of* a 28
former tributary to the Niobrara River is implied by topographic maps 29
of Todd and Bennett Counties, SD, and Cherry Co., NB. Occurrences of 30
*Notropis dorsalis* and *Fundulus sciadicus* in that part of the White River 32
drainage support this interpretation (Mayden, unpublished data). 36

*Big Sioux-Minnesota rivers; Little Sioux-Des Moines rivers.* The 40
middle Missouri River drainages contain a number of species which Bailey 41
and Allum (1962) thought entered this part of the Missouri basin from 42
the upper Mississippi River system, namely the Minnesota and Des Moines 43
rivers. Some headwaters of these drainages are or were connected during 44
periods of flooding. Bailey and Allum suggested that low divides 47
between drainages, and lakes of glacial moraines in eastern South Dakota 48
and northwest Iowa, provided means of dispersal for species adapted for 50
such habitats. They listed species that may have used such connections 51
to gain access to the Little Sioux, Vermillion and James rivers. They 53
also suggested that these connections allowed *Notropis topeka* to gain 55
access to the Des Moines basin where it probably occurred sympatrically 58
with its presumed closest relative, *N. anogenus* (Bailey 1959). 59

*White-Gasconade rivers.* Physiographic evidence for the connection 66
of these rivers was presented by Bretz (1965). Supportive data was 67
given by Miller (1968) for the movement of the White River subspecies 69
of the greenside darter, *Etheostoma blennioides newmani*, into the 70
Gasconade where it intergrades with *E. b. pholidotum*. An isolated 74
population of *Ichthyomyzon gagei* in the Gasconade may also support such 77
a connection (Pflieger 1971). 80

*St*. *Francis*-*Black*-*White* *rivers*. Stream captures involving 84
tributaries to these drainages have been discussed by McKeown, Hocutt, 85
Howard *et* *al*. (1982). It seems doubtful that faunal transfers 86
resulting from these connectives can be distinguished from transfers 89
facilitated by the former location of the Mississippi mainstream west 90
of Crowley's ridge. 92

*Arkansas* (*Spring* *River*)-*Osage* *rivers*. The connection of these 95
rivers is based on scanty geological data, the proximity of their 96
headwaters (Metcalf 1966; Pflieger 1971) and faunal data. Frye and 97
Leonard (1952, fig. xx) indicated that the headwaters of the present 99
Neosho River discharged eastward into the Osage system in the early 100
Pleistocene. Taxa supporting such an exchange include *Fundulus* 101
*sciadicus*, *Etheostoma* *chlorosomum*, *E*. *gracile*, *E*. *microperca*, *E*. 104
*punctulatum*, *Notropis* *spilopterus*, *N*. *pilsbryi* and *N*. *zonatus* (Gibbs 106
1957; Pflieger 1971; Buth and Mayden 1981). An electrophoretic analysis 112
of the last two species by Buth and Mayden (1981), considered to be 113
sister species of the Ozarks (Gilbert 1964; Buth 1979), revealed that 115
small quantities of the primitive *Gpi* A 100 allele (found in *N*. *pilsbryi* 116
and other *Luxilus*) were mixed with the derived *Gpi* A 125 in *N*. *zonatus* 123
populations from the Sac and Pomme de Terre drainages. *Ambloplites* 133
*rupestris* is considered an introduction in the Arkansas and Lower 136
Missouri systems, but coupled with its close relative *A*. *constellatus* 138
(Cashner and Suttkus 1977), the present distribution is congruent with 142
that of other Ozarkian species. Fossil evidence from Kansas and an 143
early Kansas River report (Snow 1875) indicate that Neosho and Missouri 145
River populations of *A*. *rupestris* may be natural. 146

_Neosho-White rivers_. Branson (1963, 1967) and Branson, Triplett, 153
and Hartman (1969) hypothesized that the Neosho captured the Spring and 154
Elk rivers from the White River. A number of Ozark fishes of the lower 155
Missouri and White rivers have populations in eastern tributaries of the 157
Neosho Basin; but, several other fishes endemic to these streams should 158
also have been transferred but apparently were not. Wiseman (1976), 160
Wiseman, Echelle, and Echelle (1978) and Buth and Mayden (1981) found 161
no genetic evidence in studies of _Etheostoma spectabile_ and _Notropis_ 162
_zonatus-N. pilsbryi_ to indicate former connections between the Neosho 168
and White rivers. 169

_White-Illinois rivers_. Burr, Cashner, and Pflieger (1979) recently 173
reported _Notropis ozarcanus_ and _Campostoma oligolepis_ from the Illinois 175
River system of the Arkansas drainage. Both were previously known from 181
all Ozark drainages except the Arkansas. Knapp (1964) reported a 182
specimen of _Etheostoma caeruleum_ from the Illinois River drainage. 184
These records have been considered introductions, but are included here 188
as possible evidence for stream piracy (Branson 1967). 189

_Arkansas-Red rivers_. No geological data are available for this 193
connection except geographic proximity of tributaries. The 195
distributions of several species imply a former connection between these 196
drainages near the western edge of the Interior Highlands province, and 197
to some degree between the Red and Ouachita rivers: *_Nocomis asper_, 198
*_Notropis ortenburgeri_, _N. pilsbryi_, *_N. rubellus_, *_Pimephales tenellus_, 201
_Noturus exilis_ (Robison and Winters 1978), *_Fundulus catenatus_, 203
*_Etheostoma nigrum_, *_E. microperca_, *_Percina copelandi_, _P. phoxocephala_, 206
and _P. caprodes fulvataenia_. Those species shared with the Ouachita are 209

indicated by an asterisk. Alternatively, the present distributions of 212
these species may reflect glacial displacement into widespread southern 214
ranges, followed by isolation in highland tributaries of each drainage. 216
Some species in the Red and Ouachita rivers have their closest relatives 218
in the White and Middle Arkansas systems: *E. radiosum* with *E. whipplei*; 219
*E. pallididorsum* with *E. cragini* and *E. punctulatum*; *P.* sp. (cf. 227
*nasuta*) with *P. phoxocephala* and *P. nasuta*; *Noturus taylori* with *N.* 236
*eleutherus* and *N. placidus* (Page 1974, 1981; LeGrande 1981). 245

*Red-Brazos rivers*. Stricklin (1961) documented capture by the Red 252
River of drainage that formerly entered the Brazos. Distributions of 253
three species indicate such a connection in the past. *Notropis* 255
*oxyrhynchus*, *N. potteri*, and *Percina macrolepida* may have entered the 258
Red River by this route. 262

*Ouachita-Caddo-Little Missouri rivers*. Robison and Harris (1978) 265
presented evidence that exchanges occurred between these rivers in 266
reporting new Ouachita records of two species previously considered to 268
be Caddo River endemics, *Noturus taylori* and *Etheostoma pallididorsum*. 269
It would not be expected that both entered as bait, and neither species 276
seems likely to have dispersed through existing connectives because of 277
unfavorable habitats in the lower portions of the Ouachita drainage. 278

## FAUNAL COMPOSITION 2

### Present Composition of the Regional Fauna 5

The North American freshwater fish fauna consists of approximately 8
950 species north of the Isthmus of Tehuantepec, Mexico (Gilbert 1976) 9

or about 775 species from the United States and Canada (Lee *et al*. 10
1980). The extant fauna of the western Mississippi drainages includes 14
at least 264 species in 84 genera and 33 families (Table ~~1~~ 4), slightly 16
more than one-third of the fauna of the United States and Canada. 17
Thirty-one of these species were introduced into the region or represent 18
waif dispersal. Therefore, the number of resident native families is 19
27 and native species 232, or 88% of the extant fauna of this region. 20
Two species (1%), *Anguilla rostrata* and *Alosa alabamae*, are diadromous 21
and 34 (15%) are endemic to one or more river systems of the western 28
Mississippi drainage. 29

Most of the 27 (11%) introduced species were released intentionally 31
in lakes. Waifs include four marine species that were found in the 32
Mississippi River floodplain as far north as Alton, Illinois (Thomerson, 33
Thorson and Hemp~~a~~el 1977): *Carcharhinus leucas*, *Strongylura marina*, 35
*Syngnathus scovelli*, and *Mugil cephalus* (Douglas, 1974; Lee *et al*., 37
1980). Because of the uninformative zoogeographic nature of the 44
accidental, introduced, and diadromous species they are omitted from the 45
comparative analysis of drainage units. 46

In order, among native fishes the Cyprinidae, Percidae, 49
Catostomidae, and Ictaluridae are the most diverse; collectively they 50
make up about 70% of the fauna. The Cyprinidae and Percidae contribute 51
more than 50% of the indigenous species. Polyodontidae, Amiidae, 52
Anguillidae, Umbridae, Aphredoderidae, Percopsidae, Gadidae, 53
Gasterosteidae, and Sciaenidae are each represented by one extant 54
species. 55

Within the western Mississippi River system at least six drainage divides allow meaningful comparisons of species diversity in relatively distinct basin units: the Red, Arkansas, White, St. Francis, Meramec, and Missouri rivers. As pointed out by many authors (Kuehne 1962; Sheldon 1968; Lotrich 1973; Harrel, Davis and Doris 1967; Cashner and Brown 1977), species diversity in a watershed is dependent on its size, along with other factors. In conjunction with size of the system, historical factors and habitat diversity influence species diversity. A history of frequent drainage fracturing allowing isolation that may lead to speciation, or a history of frequent species acquisition from adjacent drainages, can lead to great diversity in a relatively old and stable system.

Among the six natural drainage units, size of basin and native species diversity (Table ~~4~~5) are not highly correlated. The Missouri River, the largest basin, has only 138 native species, whereas the much smaller Red (including Ouachita River) and White rivers have 152 and 150 species, respectively. The small St. Francis basin contains 139 species, the Arkansas (second largest i~~s~~n the region) 141 species, and the Meramec 96 native species. However, examination of the total diversity in each basin-- including introduced, waif, and diadromous species (Table ~~3~~4) -- does show a positive relationship between size of watershed and number of species. The Missouri River system has the highest total diversity with 173 species, Red River 171, Arkansas 170, White 165, St. Francis 150 and Meramec 108.

The two largest systems, Missouri and Arkansas rivers, have the highest percentage of introduced species with 19% and 13% respectively.

In the White and St. Francis rivers only 9% and 7% of the extant fauna consists of "non-native" species. The larger river systems have higher frequencies of introduction and lower percentages of native species than the smaller systems, leading to an apparent correlation between size of drainage and species diversity.

### Phenetic relationships of drainage units.

For zoogeographic analysis the six natural drainage basins have been divided into 19 drainage units (Fig. 1). Except for the Mississippi River unit (19) these divisions are based on natural drainage divides and/or changes in the regional physiography and faunas. Figure 6 summarizes the faunal affinities among these drainage units, based on percent of shared taxa as recorded in Table ~~4~~ 5. The phenogram simplifies interpretations of the basic distributional pattern of fishes in the western Mississippi basin as a whole. Rather than forming groups strictly representative of discrete basins, groupings of overall similarity among the 18 drainage units tend to be more concordant with physiographic features, although intrabasin similarities are apparent. Three basic phenetic groupings can be extracted: 1) the Missouri River fauna, 2) a southern plains fauna, and 3) a southeastern Interior Highlands fauna.

The Missouri River fauna forms a discrete cluster, except that its lowermost segment shows greater affinity with the Highland fauna because a number of its tributaries drain the northern Ozarks. Within the Missouri basin two groupings are apparent: the three northernmost units, and a cluster of 4 central units of the Plains and Central Lowlands--each showing decreasing similarity as one moves downstream through the system.

The second major grouping, the southern Plains, links the western faunas of the Red and Arkansas river basins. These units are faunally similar because most of their taxa occur widely in the Plains physiographic region. External similarities of this cluster are with both the Missouri River and Highlands clusters (*i.e.*, occupy an intermediate position in the phenogram) because of low species diversity in the southern plains drainage units, and the ubiqitous nature of a high percentage of its fauna. The slightly greater overall similarity with the Highland region is logical because the lower portions of the Arkansas and Red rivers drain the Interior Highland province.

Within the Highlands cluster two well differentiated phenetic groupings emerge, 1) drainages of the Ouachita and Ozark uplands and 2) drainages peripheral to these formations. In group 1, the White and St. Francis rivers form a distinctive faunal unit characteristic of the Ozark uplands, whereas the Ouachita and Lower Red rivers characterize the Ouachita Mountain Unit. The Lower Arkansas unit clusters with the Red-Ouachita units, probably because it includes larger southern (Ouachita) than northern (Ozark) tributaries as this unit is delineated for the analysis. The close association of the two Interior Highland subregions, and the lesser degree of similarity between these drainages and the peripheral drainage units (middle Arkansas, lower Missouri, and Meramec rivers) is partly a function of taxa unique to the Ozark and Ouachita mountains, and partly due to absence in the two Highland areas of some taxa that are widespread in the Central Lowlands.

### *Analysis of the individual drainage units*

Among the 18 drainage units (Fig. 1), the White River unit is most outstanding with respect to diversity and endemism. The 150 native species include five that are endemic: *Noturus flavater*, *Ambloplites constellatus*, *Etheostoma euzonum*, *E. juliae*, and *E. moorei*. Relationships of these with their congeners are reasonably well understood. *N. flavater* appears to be an early derivative of the *N. furiosus* species group; its other members occur south and east of the White River in the Ohio, Tennessee, Ouachita, Gulf, and East-coast drainages (LeGrande 1981). *Etheostoma juliae* is an early isolate of the subgenus *Nothonotus*, which also includes species in the Tennessee and Ohio river systems, and one species known from the Mobile Bay area. *E. euzonum* and its sister species *E. tetrazonum* of the lower Missouri unit, like *E. juliae*, are most closely related to a group of species inhabiting the Ohio River system. *Ambloplites constellatus* has sister-species relationship (Cashner and Suttkus 1977) with the wide-ranging eastern species *A. rupestris*, native to the Meramec in this region. The distributionally restricted *E. moorei* is not considered to be closely related to its geographically nearest relative, *E. juliae*, but is closely allied to *E. rubrum* (Page 1981), which inhabits an adventitious eastern tributary of the Mississippi River in southern Mississippi.

In addition to the above endemic species, two subspecies of the orangethroat darter, *E. spectabile fragi* and *E. s. uniporum* (Distler 1968; Wiseman *et at* 1978), an undescribed subspecies of *E. caeruleum* (Knapp 1964), an undescribed species of *Cottus*, and a distinctive form of *Nocomis biguttatus* (Lachner and Jenkins 1971) are endemic to portions of the White River drainage. The extinct *Lagochila lacera* is known west of the Mississippi only from the White River; other records of it are from the Ohio and Tennessee river systems.

The White River shares the greatest number of species with the St. Francis (130), Ouachita (116), and lower Red (109) rivers, and has the highest similarity index values with the same systems and the lower and middle Arkansas (Table ~~4~~ 5). The number of species shared and percent of similarity with the geographically adjacent Osage and Gasconade rivers of the lower Missouri drainage are not as great as with the drainages cited. Three factors appear to have influenced the great diversity of the White River fauna and its similarity to faunas in the above streams: the high degree of endemism; the occurrence of several species having disjunct distributions in the Cumberland Plateau and the Interior Highlands; and the subtantial proportions of both Highlands and Coastal Plain habitats in its watershed. The fauna includes species characteristic of high-gradient, clear streams and of large base-level rivers. Because many species occur in most or all drainage units that enter the Highlands province, high similarity coefficients among these drainages (White with St. Francis, Ouachita, lower Red, and to a lesser extent the Middle Arkansas unit) would be expected. In some cases such distribution has resulted in differentiation of an ancestral species into two or more descendant species endemic to one or more of the above drainages.

The second most diverse drainage, with 139 species, is the St. Francis-Little River unit. No species are endemic to these rivers.

Among species endemic in this zoogeographic region, however, eight occur 276
in these rivers and are shared with the White, Lower Missouri, Lower 277
Arkansas, or Ouachita rivers, all of which drain portions of the 278
Interior Highlands. The great diversity of the St. Francis-Little River 279
fauna may be due to their highland origin and lowland discharge, and to 281
their proximity to the White River unit. Of the 139 species, 130 are 282
shared with the White system, giving these two drainages a 90% 283
similarity value, higher than for any other pair of drainages except 285
some adjacent units in the upper Missouri system. Historic reasons for 286
this similarity are discussed in the sub-section on Drainage History, 287
concerning eastward movement of the Mississippi mainstream. 289

The Ouachita and Lower Red rivers are equally diverse with 133 292
native species in each; 118 are shared, giving a similarity value of 89. 293
*Noturus lachneri*, *N. taylori*, *Percina* sp. (cf. *nasuta*) and *Etheostoma* 296
*pallididorsum*) are endemic to headwaters of the Ouachita, and *Percina* 302
*pantherina* is endemic to the Little River of the Red River drainage. 305
*Notropis ortenburgeri*, *N. perpallidus*, *N.* sp. (cf *fumeus*) (Snelson 309
1973), *Etheostoma radiosum radiosum* and *E. r. paludosus* are either 313
restricted to or are found primarily in the Ouachita Mountains including 319
the Lower Red and Ouachita drainages. *Notropis bairdi* is endemic to the 320
Red River system, primarily its western part (but see sub-section on 324
Introductions concerning its recent establishment elsewhere). Several 325
other species have southern relic populations in the Red River drainage: 326
*Nocomis asper*, *Notropis pilsbryi*, *N. rubellus*, *Etheostoma microperca*, 329
*E. nigrum*, *E. radiosum cyanorum*, and *Percina caprodes fulvitaenia* (Moore 332
and Rigney 1952; Gilbert 1964; Lachner and Jenkins 1971; Burr 1978; 336

Morris and Page 1981).

Higher diversity in the Lower Red River than in the lower portions of the Arkansas and Missouri rivers (Table 4) results partly from uniqueness of the Ouachita regional fauna, but also from inclusion of species characteristic of Gulf coastal drainages. Coastal Plain species in the Red River fauna include *Hybognathus hayi*, *Notropis chalybaeus*, *N. hubbsi*, *N. maculatus*, *N. texanus*, *Moxostoma poecilurum*, *Erimyzon sucetta*, *Noturus phaeus*, *Fundulus blairae*, *F. chrysotus*, *Etheostoma histrio*, *E. parvipinne*, and *Menidia beryllina*. Other species shared with southwestern Gulf drainages include *Notropis atrocaudalis*, *N. potteri*, *N. sabinae*, *Etheostoma collettei*, and *Perci~~m~~na macrolepida*.

The next most diverse group of drainage units includes the Lower Arkansas (117 species), Lower Missouri (114), and Middle Arkansas (111). Although the numbers of species are similar in these drainages, their similarity indices are not especially high. The lower and middle Arkansas, as expected, have the highest number of shared species and similarity index (80%). The lower Arkansas and Missouri have similar numbers of species but show a significantly lower number of shared taxa (73) and lower similarity (63%). The Middle Arkansas and Lower Missouri show a greater number of shared taxa (85) and similarity (76%) than do the Lower Missouri and Lower Arkansas. This increase in similarity is due mainly to taxa shared between the Osage River drainage (Lower Missouri unit) and the Neosho (Grand) River drainage, both inhabited by prairie taxa and by Interior Highlands taxa shared also between the Neosho, White, Gasconade, and Osage rivers.

Endemic species are fairly well represented in these drainages 380
except for the Lower Arkansas which has none. The Lower Missouri has 381
three endemic species, are darters inhabiting southern tributaries in 382
the Osage and Gasconade rivers. Etheostoma nianguae is endemic to the 384
Osage River; its closest relative, E. sagitta, is in the upper 387
Cumberland and Kentucky rivers of Kentucky and Tennessee. Percina 390
cymatotaenia, whose sister species P. (Odonto~~ce~~ph~~a~~ol~~u~~is) sp. is also in 393
the headwaters of the Kentucky and Green rivers in Kentucky, is endemic 397
to the Osage and Gasconade (Page 1974). Etheostoma tetrazonum is 398
endemic to the Osage, Gasconade, and Meramec rivers. Its closest 401
relative, E. euzonum, is in the White River drainage; their closest 402
relative is E. variatum of the Ohio River system (Page 1981) (Fig. 5). 405

Only Noturus placidus and Etheostoma spectabile squamosum are 410
endemic to the Middle Arkansas unit (Neosho River, principally). 416
Nocomis asper occurs mainly in the Middle Arkansas, but also has small, 418
presumably native populations in the Red and Ouachita basins (Douglas 419
and Harris 1977). Notropis girardi and Etheostoma cragini are endemic 420
to the Middle and Upper Arkansas drainage units. The closest relatives 427
of the former, N. bairdi and N. buccula, are in the Red and Brazos 428
rivers, respectively; E. cragini's nearest relatives are E. 434
pallididorsum in the Ouachita and E. punctulatum in the Neosho, White, 439
and Osage rivers. 443

The Meramec River, a rather large adventitious tributary of the 445
Mississippi just south of the mouth of the Missouri River, has 96 native 446
species, three of which are endemic to this zoogeographic region but 447
none of which are confined to the Meramec. Consistent with its location 448

in the Interior Highlands, the Meramec shares many species with the White (78), Lower Missouri (78), St. Francis (76), and Middle Arkansas (69). The percent similarity of species is, however, slightly different than expected from the number of shared taxa. The highest similarity is with the lower Missouri (77%), because of northern Ozarkian species shared, and primarily because several Coastal species present in the White and St. Francis do not range so far north as the Lower Missouri and Meramec rivers.

The drainage units compared thus far lie partly or wholly within the Interior Highlands and Coastal Plain provinces, with the exception of the Middle Arkansas and Lower Missouri units which have Highland and Central Lowland components. The remaining units (Upper Red, Upper Arkansas and the several western subdivisions of the Missouri system) lack eastern Highland and Coastal Plain components. Like the western portions of the Arkansas and Red rivers, which have low diversity compared to their eastern portions, the Missouri River units show a westward decrease in faunal diversity, such that the two uppermost units (Upper Missouri and Yellowstone) have exceptionally low native species diversity (36 and 35 taxa); low numbers of taxa shared with external drainages (10 to 17); and low percent similarity with other drainages (17 to 38%).

In the Missouri basin, diversity declines abruptly between the lower unit (114 species) and the Chariton-Nishnabotna unit and Kansas River (each with 66 species), representing a loss of 48 species. Diversity increases to 76 species in the Platte-Niobrara unit, which gains its relative richness from two sources: acquisition of some northern and western species that persist as relics in mountainous headwaters and in lakes of the Sand Hills in northwestern Nebraska; and westward dispersal of some eastern species, from the upper Mississippi basin, via connectives with the Sioux and James rivers. The Sioux and James units retain species-diversity equal to the Kansas River and Chariton-Nishnabotana (66 native fishes), despite loss of some taxa characteristic of the lower part of the Missouri basin. That loss is compensated by species acquired from the upper Mississippi, as cited elsewhere (see Bailey and Allum 1962). Diversity decreases again to 50 species, a loss of 16 taxa, in the next drainage unit, which includes the Missouri mainstream and its western tributaries from the White (SD) through the Little Missouri rivers. The Upper Missouri and Yellowstone rivers have the least number of species with 36 and 35, respectively, but have some species typical of the Rocky Mountain Region not found elsewhere in the drainage.

The overall decrease in species diversity in the Missouri River system from the Lower Missouri to the Yellowstone River is 79. Of the 35-36 species in the two uppermost units (Yellowstone and Upper Missouri rivers), 23 and 24 are shared with the Lower Missouri for a faunal similarity of 42-45%. Faunal similarities of the Upper Missouri and the Yellowstone rivers are mainly with each other (93%) and with the adjacent White-Little Missouri and Platte-Niobrara units (70-80%); similarity with other Missouri drainage units is 55% or less. External to the Missouri basin their highest similarities are with the Upper Arkansas (38%), Middle Arkansas (34%), and Canadian (32%) units. Significant portions of the Missouri and Arkansas basins drain the Rocky

Mountains and the Great Plains, and share species typical of each province. The Upper Red River fails to reach the Rockies, and has but 26% faunal similarity with the Upper Missouri and Yellowstone units.

The few species shared between the upper Missouri drainages and drainages outside the Missouri system include mostly large river species like *Scaphirhynchus platyrhynchus*, *Polyodon spathula*, *Lepisosteus platostomus*, *Hiodon alosoides*, *Hybopsis gracilis*, *Hybognathus placitus*, *Notropis atherinoides*, *Carpiodes carpio*, *Cycleptus elongatus*, *Ictiobus bubalus*, *I. cyprinellus*, *Ictalurus punctatus*, *Stizostedion canadense* and *Aplodinotus grunniens*. Species not typical of large turbid rivers that are shared with other drainages are those whose ranges extend southward through Rocky Mountain headwaters: *Salmo clarki*, *Rhinichthys cataractae*, *Catostomus catostomus* and *C. commersoni*.

No fishes are endemic to the Upper Missouri and Yellowstone units although a few species are confined to the Missouri system and the Mississippi River below the mouth of the Missouri. These include *Scaphirhynchus albus*, *Hybognathus argyritis*, *Hybopsis gelida*, and *H. meeki*, all typical of large, turbid rivers with sandy substrates. Several northern or western species are found only in the upper portions of the Missouri system within our zoogeographic region. These include *Salmo clarki*, *Prosopium williamsoni*, *Couesius plumbeus*, *Rhinichthys cataractae*, *Hybognathus hankinsoni*, *Notropis hudsonius*, *Phoxinus eos*, *P. neogaeus*, *Semotilus margarita*, *Lota lota*, *Fundulus diaphanus*, *Culaea inconstans*, and *Etheostoma exile*.

Some inhabitants of the Lower Missouri basin whose westward distributions terminate in that drainage unit are *Acipenser fulvescens*, *Amia calva*, *Notropis boops*, *N. chrysocephalus*, *N. volucellus*, *Moxostoma anisurum*, *M. duquesnei*, *Fundulus notatus*, *F. olivaceus*, *Labidesthes sicculus*, *Etheostoma blennioides*, *E. caeruleum*, *E. flabellare*, *E. zonale*, and the two species of *Cottus*. Species whose northwestward distributions end in the Sioux or James units include *Lepisosteus osseus*, *Phoxinus erythrogaster*, *Hybopsis aestivalis*, *Notropis blennius*, *N. heterolepis*, *Pimephales notatus*, *Carpiodes cyprinus*, *Ictiobus niger*, *Moxostoma carinatum*, *M. erythrurum*, *Percopsis omiscomaycus*, *Percina caprodes*, *P. maculata*, and *Etheostoma nigrum*.

The Upper Red and Upper Arkansas rivers, like the Missouri, lose faunal diversity from east to west. The reduction in the Red River is from 133 species in the lower unit to 56 in the upper; 81 species are lost, but 4 (*Notropis oxyrhynchus*, *Pimephales promelas*, *Cyprinodon rubrofluviatilis*, and *Fundulus zebrinus*) are gained. Along the Arkansas, diversity varies from 117 in the lower unit to 111 in the middle unit and 64 in the upper. Taxa shared between the lower and middle units number 91, so 26 taxa are lost, but others are gained along the western Ozark-prairie border. Between the middle and upper units the difference of 47 species is accounted for by loss of 51 species and addition of 4 (*Salmo clarki*, *Rhinichthys cataractae*, *Hybopsis gracilis*, and *Fundulus zebrinus*). A few species are added to the west in both of these systems and in the Missouri, but the great majority of species are lost and not replaced.

## Ecological Aspects of Fish Distribution

The ranges of most species in the Missouri, Arkansas, and Red River systems conform less well with drainage boundaries than with

physiographic boundaries, essentially ecological units. Thus many 7
species inhabit parts of several drainages, while few species occur 8
throughout any single river system. Some species (like *Semotilus* 9
*atromaculatus* and *Catostomus commersoni*) are abundant in eastern 13
streams, absent from the southern plains, but reappear in the 17
headwaters of tributaries that extend to western highlands. Their 18
distributions imply that access to all streams of the region was not 20
restricted by physical barriers to dispersal. The present distributions 21
of *Phoxinus eos* and *P. erythrogaster* (Fig. 7), *Hybopsis meeki* and 22
*Fundulus zebrinus* (Fig. 8), and several fishes represented in Fig. 5 33
similar~~ity~~ly imply ecological restriction of ranges that transcend 34
drainage divides. 35

The major trend throughout the region is ~~i~~impoverishment of the 38
fauna westward and northward. Diversity is limited progressively by 38
variable flow, high turbidity, extreme temperature, and low habitat 39
diversity. If species having only marginal or sporadic occurrence are 40
excluded from the analysis, similarity index values between the faunas 42
of the five physiographic provinces are low, exceeding 50% only in the 43
Central Lowlands/Great Plains combination. Values for the Coastal 44
Plain/Interior Highlands (13%) and Interior Highlands/Central Lowlands 45
(23%) are strikingly low despite the physical proximity of these 46
provinces. 47

These relationships have also been pointed out by Smith and Fisher 49
(1970) and Stevenson, Schnell, and Black (1974) who found a high level 50
of ecological control of faunal composition using multivariate analysis 51
of entire faunas against sets of environmental variables. The result 52

appeared to be a complex of environmental (ultimately climatic) controls, stream size, and drainage constraints on dispersal.

The precision with which the fish communities conform to ecological boundaries was illustrated by Pflieger (1971), who analyzed distributional patterns by assigning each species to one "faunal group", and plotting the group-distributions based on the frequency of occurrence of all member species at localities throughout Missouri. Two of the resulting maps are reproduced here (Fig. 9). All localities of capture for 83 species are represented in the two maps.

On a local basis, Hall (1952) compared the faunas of small eastern and western tributaries of Grand River in northeastern Oklahoma. In the area where Hall's collections were made the Grand River mainstream conveniently delimits the interior Highlands and Central Lowlands provinces. Forty-three species inhabited the eastern tributaries and 21 the western tributaries. Twenty-three species were confined to the eastern tributaries and eight additional species were taken in those streams and in Grand River, but not in the western tributaries. Four species were found exclusively in the western tributaries, five other species in those streams plus the mainstream. Thus only 12 species were shared by the opposing tributaries, yielding a similarity index of 42.5%, a value lower than most values obtained in the interbasin comparisons (Table ~~4~~5). Most species represented in Hall's (1953) study have extensive geographic ranges. Differences in habitat clearly explain their pronounced segregation in the opposing tributaries. Differences apparent from Hall's description of the streams include local relief, land-use, substrate type, turbidity, summer temperatures, and extent of aquatic vegetation. 89

Similar but less extreme local segregation of faunas is apparent in 92
areas surveyed recently by Reigh and Owen (1979) in the Missouri basin 93
of western North Dakota. The Heart and Little Missouri rivers contain 94
39 and 24 species, respectively; 22 are shared, yielding a similarity 95
index of 74%. Dominant species in the two streams differ markedly, 96
however. *Hybopsis gracilis* and *Hybognathus* spp. (*argyritis* and 97
*placitus*) comprised 79% of the fishes captured in the Little Missouri 108
but less than 2% of those in the Heart. *Notropis lutrensis* and *N*. 110
*stramineus* comprised 48% of the fish collected in Heart River but less 115
than 2% in the Little Missouri. Seven centrarchids were found in the 117
Heart River, but only one, *Lepomis cyanellus*, in the Little Missouri. 119
Reigh and Owen (1979) described the Heart River, with its tributaries, 122
as having "some of the finest aquatic habitat in southwestern North 123
Dakotas," due in part to impoundments that trap silt, along with springs 125
and beaver dams that provide pool areas and flow during dry periods. 126
The authors described the Little Missouri River as having extreme 127
fluctuation in flow (0 to 1,840 m3/sec), high silt loads, and an 128
unstable stream bed devoid of vegetation. Several of the species 129
prevalent in the Little Missouri fauna, but rare or absent in Heart 131
River, are characteristic of the original prairie fish-community. In 132
addition to the three species cited above, these included *Hiodon* 133
*alosoides*, *Hybopsis gelida*, *Lota lota*, and *Stizostedion canadense*. 136
Populations of these species have declined alarmingly over much of their 140
ranges in recent decades, perhaps excepting *Hiodon* and *Stizostedion* 141
which occupy impoundments. 147

### Faunal Diversity as a Function of Physiographic Province.

The Interior Highlands is the smallest of five physiographic provinces represented here, yet it has the richest fauna, with 150 native species, or 65% of the total fauna; 27 of its species are endemic to the western Mississippi basins (Tables ~~3~~ 4 and ~~4~~ 5). The high species diversity in this province is likely due to its long history of drainage stability since the Paleozoic, generally high amount of precipitation (100cm/year), and constant base-flows supplied by some of the largest springs in North America. These factors sustain clear waters and diverse habitats that were not disrupted by glaciation or inland seas. Similarities with other provinces are relatively low, the largest index values being with the Central Lowlands (64%) and Coastal Plain (56%), as expected geographically. The Coastal Plain province, south and east of the Highlands, has 122 species (53% of total fauna). The Highlands and Coastal Plains share substantially fewer species (75) than are shared by the Highlands and Central Lowlands (92), adjoining the Highlands to the north and west.

Diversity of the Central Lowlands is second greatest in this region, with 139 native species. Its fauna is largely a conglomerate of species found also in the Great Plains, Interior Highlands, and Coastal Plain provinces. Of the 13 western Mississippi endemic species that inhabit this province, only *Notropis bairdi* and *Noturus placidus* can be considered endemic to the Central Lowlands province specifically. The remaining 11 have their centers of distribution in one of the two adjacent regions (*Notropis pilsbryi*, *N. ortenburgeri*, *Nocomis asper*, *Etheostoma radiosum*); are large-river species (*Scaphirhynchus albus*, *Hybognathus argyritis*, *Hybopsis gelida*); or are equally shared with other provinces (*Notropis girardi*, *Pimephales tenellus*, *Fundulus sciadicus*, *Etheostoma cragini*).

The affinities of the Central Lowlands lie mainly with the Highlands based on shared species (92), but its similarity index is greatest with the Great Plains (72%). The Plains fauna consists, with the exception of five species, of a subset of the Central Lowlands species that tolerate the harsh environmental conditions on the Great Plains. Similarity values of the Lowlands with the Coastal Plain (83 species in common) and with the Interior Highlands are equal (64%) but less than that with the Great Plains. As expected, the prevalent species shared with the Highlands generally are upland species. Central Lowland - Coastal Plain shared species include those typical of large rivers or low-gradient and homogeneous habitats.

The Great Plains, probably the largest physiographic province in this region, has 77 native species (86 including introductions). Nearly all native species occur also in the Central Lowlands, giving these two provinces the highest similarity coefficient (72%) of any pair of provinces in the region. The Great Plains fauna is least similar to the Coastal Plain (39%) and Highlands (41%).

The most depauperate of the physiographic provinces is the Rocky Mountains, with 18 native species (30 including introductions). Fourteen of its native species are shared with the Plains, 10 with the Central Lowlands, only 6 with the Interior Highlands, and 3 with the Coastal Plain. The highest and lowest similarity index values (48% and 10%) are with the Great Plains and Coastal Plain, respectively. No species is endemic to the Rocky Mountain portion of the Mississippi drainage. Species unique to this province, within our region, include the salmonids *Prosopium williamsoni*, *Salmo clarki*, and *Thymallus arcticus*; all occur also in western or northern drainage basins external to the Mississippi system. The faunas of northern and southern drainages in the Rocky Mountain province are dissimilar. Only five species inhabit mountain streams of both the Missouri and Arkansas basins: *Salmo clarki*, *Rhinichthys cataractae*, *Hybopsis gracilis* (more characteristic of the larger Plains streams), *Catosomus commersoni*, and *C. catostomus*. Arkansas River populations of the last species may be introduced.

Comparison of similarity values between drainage units and physiographic provinces yields some noteworthy results (Table ~~4~~5). The Lower Arkansas and Lower Red rivers have high similarity coefficients with the Coastal Plain province, as do the White and St. Francis rivers; all these drainage units occupy the Coastal Plain, in part, but have headwaters in the Interior Highlands, accounting for their relatively high faunal richness. The Lower Missouri and Meramec rivers, both in proximity to the Mississippi floodplain, do not have high faunal similarity (40-50%) with the Coastal Plain. Similarity of the Interior Highlands fauna with that of various drainage units is substantially below 50%, except for drainages included within the Highlands, indicating the distinctiveness of its fauna. Drainage similarity with the Central Lowlands province is rather uniform across all drainage units, except for low values in the upper Missouri River units. That result is due partly to the fact that the Central Lowlands transect most of the drainage units, but due also to the high number of species shared by this province and all others; thus the Central Lowlands fauna is only moderately distinctive.

Other Habitat Associations.

Of the 230 native non-diadromous species in the region, 166 (72% occupy small rivers, 122 (52%) inhabit creeks, 91 (39%) inhabit lakes, and 84 (36%) inhabit large rivers (Table ~~2~~5). ~~inhabit creeks, 91 (39%) inhabit lakes, and 84 (36%) inhabit large rivers (Table 2)~~. Three (1%) are upland karst topography, cave-dwelling species (Amblyopsidae) (Table 4). Species inhabiting both small rivers and creeks number 89 (38%), whereas those in both large rivers and creeks number only 12 (5%). Big and small river, small river and lake, and lake and creek combinations have the next highest numbers of shared species with 60, 57, and 47 respectively. Seventy-six percent (26) of the western Mississippi endemics are typical of small rivers and 52% (18) inhabit creeks. Lakes and big rivers contain two and four endemic species, respectively.

The small-river habitat is faunally rich partly because of its inter-mediacy between large-river and creek habitats. Small rivers are a mixing zone analogous to the Central Lowlands province with respect to species diversity. Many species are characteristic of small rivers, but many lake, creek, and big-river taxa are also found in the small-river situation. The big-river fauna, although low in number of species, is fairly distinctive, characterized by wide-ranging species. The lake habitat is the least common natural habitat in this region, except in the Rocky Mountain and Coastal Plain provinces, because most of the region is unglaciated. The rarity of lakes accounts for the low diversity of typically lake species.

## Introductions

At least 27 species have been introduced in the region, and 40 additional species now inhabit parts of the western Mississippi basin to which they are not indigenous. Most introductions involved sport fish and forage fish stocked in impoundments, or bait-minnows transported from other regions. Exotics introduced include 9 salmonids, *Osmerus mordax*, *Astyanax mexicanus*, *Esox masquinongy*, 7 cyprinids, *Ictalurus catus*, 3 poeciliids, *Morone americana*, *Morone saxatilis*, *Lepomis auritus*, and *Lepomis gibbosus*. Species transplanted into basins or sub-basins other than those where they occurred naturally include *Amia calva*, *Dorosoma petenense*, *Thymallus arcticus*, *Umbra limi*, *Esox lucius*, 10 cyprinids, *Moxostoma macrolepidotum*, 3 ictalurids, 3 cyprinodontids, *Gambusia affinis*, *Menidia beryllina*, 13 centrarchids, and 3 percids.

Extraneous fishes were released in the region during early phases of settlement, often before the native fauna was catalogued adequately (Snow 1875). In Kansas, for example, 13 species were introduced before 1885 (Graham 1885). Cashner (1980) concluded that all populations of *Ambloplites rupestris* in the Arkansas and Missouri River systems resulted from early introductions. *Cyprinus carpio* was introduced widely in 1880, primarily as a pondfish. The carp now occurs in all drainage units (Table ~~3~~4), and comprises more than half the commercial catch of food-fishes from the Missouri River (Funk and Robinson 1974). *Ctenopharyngodon idella* was introduced in 1963 into experimental ponds in Arkansas and soon thereafter into impoundments in that state as a means of vegetation control. It escaped almost immediately and dispersed throughout the Missouri-Mississippi mainstream (Pflieger 1978). The grass carp is now being distributed in Kansas by more than 20 private vendors who have stocked it in thousands of ponds, mostly since 1975.

*Stizostedion vitreum* has been stocked in reservoirs throughout the region and reproduces in many of them, dramatically expanding its range to the southwestern limits of the Mississippi basin within the past 30 years. Over a longer period the range of *Micropterus salmoides* has expanded from the easternmost parts of the Dakotas, Nebraska, and Kansas westward to the limits of the basin. Other centrarchids, notably *Lepomis macrochirus*, *L. microlophus*, and *Pomoxis nigromaculatus* have undergone similar westward range extension. Other sport fishes widely introduced are *Morone chrysops*, *M. saxatilis*, *Esox lucius*, *Salmo gairdneri*, and *S. trutta*; only *M. chrysops* has established substantial wild populations in streams, but sustained releases of the others insure their persistence in most states of the region. Numerous salmonids (Table ~~2~~ 4) have been introduced into rivers and reservoirs of the upper Missouri system, principally Lake Sakakawea, ND, in 1976 and 1977 (Reigh and Owen 1979).

Fish-management agencies have tended increasingly to introduce "forage" species as well as game fishes into reservoirs. *Osmerus mordax* was released in Lake Sakakawea in 1976, where it increased explosively and dispersed downstream into other reservoirs and the unimpounded Missouri. *Osmerus* has been collected also in the Mississippi mainstream in Illinois and Kentucky (Burr and Mayden 1980), ~~and~~ Louisiana (Suttkus and Conner

Tennessee and Arkansas (Buchanan, Carter, Henry and Shirley 1982)

1980), and may originate from Lake Michigan as well as from upper Missouri River stocks. *Dorosoma cepedianum*, *D. petenense*, and *M. beryllina* have been introduced into many impoundments in the southern Plains, often in conjunction with *Morone*. Several minnows, notably *Notemigonus crysoleucas*, *Pimephales promelas*, and *P. notatus*, have gained access to areas where they once were absent, apparently due to frequent releases. *Pimephales vigilax* became etablished in the lower Kansas River in 1976, spread throughout the mainstream, and by 1981 was the fourth most abundant cyprinid in that river; it did not occur naturally in the Missouri River system. *Notropis bairdi* appeared in the Cimarron River (Arkansas system) in the 1970's and rapidly replaced its cognate species, *N. girardi*, in that river. *Gambusia affinis* apparently entered Kansas via the State Fish Hatchery near Pratt in about 1940. It occurred in most streams south of 39° latitude by 1970, and became established in the Kansas River system by 1970.

## *Changes in the Fauna Due to Recent Habitat Alterations*

Modifications of habitats for fishes, including pollution, siltation, and impoundment of streams, have had important effects on the regional fauna. Excessive consumption of water in the Great Plains, principally for irrigation, has become an especially serious decimating factor in the past decade. Grain crops have been produced in some segments of the Arkansas River channel, legally a navigable stream. However, the cumulative effects of impoundments-farm ponds, fishing lakes, and mainstream reservoirs-probably have had the most significant impact on the fauna. Most of the western Mississippi Basin, apart from the Interior Highlands and Coastal Plain, has less surface water than its residents demand. Precipitation varies erratically, and the region has few natural lakes. The thousands of impoundments constructed for convenient water supply have vastly increased lentic habitats for fishes, stimulated the introductions discussed above, and altered the flow regimes, sediment loads, and microbiota of streams throughout the region. Control of stream-flow by impoundment has facilitated further modifications of rivers for navigational purposes and expanded development of adjacent floodplains. Therefore, streams over much of the region have become narrower, less turbid, and less subject to wide fluctuations in discharge and temperature than in their original condition. The principal result has been increased diversity of the prairie fauna. Concurrently, several fishes native to Plains rivers and adapted to shallow sandy streams with widely fluctuating flows, high turbidity, and extreme summer temperatures, have declined. *Hybopsis gracilis*, *H. gelida*, *H. meeki*, *Hybognathus placitus*, and *H. argyritis* are examples of formerly abundant, widespread species that are affected adversely. Their populations have yielded dominance to pelagic planktivores such as *Dorosoma cepedianum* and *Notropis lutrensis*, to sight-feeding carnivores such as centrarchids and *Morone*, and to salmonids where stream-temperatures have been depressed by hypolimnetic discharge from reservoirs.

Several species of the Interior Highlands have been jeopardized, mainly by impoundment and channelization, although the ecological effects of impoundment may differ importantly in the Highlands and Plains. The most vulnerable Highland species have extremely limited geographic ranges, and many are dependent on riffle habitats.

## Figure Legends

Fig. 1. The western Mississippi River basin with drainage units circumscribed. 1. Ouachita. 2. Lower Red. 3. Upper Red. 4. Lower Arkansas. 5. Middle Arkansas. 6. Canadian. 7. Upper Arkansas. 8. White. 9. St. Francis. 10. Meramec. 11. Lower Missouri. 12. Chariton- Nishnabotna. 13. Kansas. 14. Platte-Niobrara. 15. Sioux-James. 16. White-Little Missouri. 17. Yellowstone. 18. Upper Missouri. 19. Mainstream Mississippi.

Fig. 2. Physiographic provinces in the region. Coastal Plain=CP, Interior Highlands=IH, Central Lowlands=CL, Great Plains=GP and Rocky Mountains=RM.

Fig. 3. Reconstructions of preglacial and glacial drainages in central North America. A) Preglacial Grand ~~(stippled)~~, Iowa and Arctic drainages. Grand River ~~modified by~~ from Dreeszen and Burchett (1971), Iowa and Arctic drainages from Pflieger (1971) Owen (1981), and DeGraw (1969). B) Nebraskan drainages based on Frye and Leonard (1952), Stanley and Wayne (1972) and interpretations by the authors. C) Kansan drainages based on Frye and Leonard (1952), Metcalf (1966) and interpretation by the authors. Stippled area at top of figure represents extent of Kansan Glacier.

Fig. 4. Post-Barstovian and preglacial fossil fish localities in the western Mississippi drainages (●): 1 Wolf Creek local fauna; 2. WaKeeney local fauna; 3. Logan County Diatomite; 4. Laverne local fauna; 5. Santee local fauna; 6. Airport

30 as ● or ▲? (see map).

locality; 7. Saw Rock local fauna; 8. Rexroad local fauna; 9. 31
Bender local fauna; 10. Broadwater-Lisco local fauna; 11. Sand 32
Draw local fauna; 29. Roger Mills Co., OK; 30. Kilgore, local 33
fauna. Glacial Pliocene and Pleistocene fossil fish 34
localities in the western Mississippi drainage (▲): 12. Seneca 35
(not numbered on map)
local fauna; 13. Plainville local fauna; 14. White Rock local 36
fauna; 15. Sappa local fauna; 16. Wathena local fauna; 17. 37
Angus local fauna; 18. Rezabek local fauna; 19. Sandahl local 37
fauna; 20. Kanopolis local fauna; 21. Butler Spring local 38
fauna; 22. Berends local fauna; 23. Doby Springs local fauna; 39
24. Mt. Scott local fauna; 25. Duck Creek local fauna; 26. Ree 40
Heights local fauna; 27. Litchfield local fauna; 28. Hill City 41
local fauna; 31. Good Creek local fauna; 32. Clear Creek local 41
fauna; 33. Trinity River local fauna; 34. Ben Franklin local 42
fauna. 43

Fig. 5. Present ranges of several fishes having disjunct 45
distributions in the Ozark region and elsewhere, superimposed 45
on major drainage elements of the preglacial Mississippi 46
basin. Presumably the relatively stable, unglaciated Highland 47
streams served as refugia for these species during glacial 48
epochs. 49

Fig. 6. Phenogram depicting percent similarity of fish faunas in 51
18 drainage units of the western Mississippi River basin. 51
Similarity values are from Table ~~4~~. 52

Fig. 7. Present distributions of *Phoxinus eos* (cross hatching and 55
circles) and *P. erythrogaster* (stippling and squares). Ranges 58

of both species have receded northward and eastward from areas occupied during glacial maxima, leaving relic populations in habitats that remained suitable. The range of <u>Phoxinus neogaeus</u> is similarly disjunct.

Fig. 8. Present distributions of <u>Hybopsis meeki</u> (Missouri mainstream) and <u>Fundulus zebrinus</u> (stippled area plus isolated dot). Other species adapted to Plains rivers have similar distributions, notably <u>Scaphirhynchus albus</u>, <u>Hybopsis gracilis</u>, <u>H. gelida</u>, <u>Hybognathus placitus</u>, and <u>H. argyritis</u>.

Fig. 9. Two of seven ~~primary~~ faunal groupings of Missouri fishes/ From Pflieger (1971).

Table 1. Preglacial Tertiary fossil records. Numbers directly below localities correspond to Fig. 4. ~~Other~~ numbers refer to the following sources: 1. Bennett, 1979; 2. Bjork, 1967; 3. Boreske, 1974; 4. Cope, 1874; 5. Cope, 1875; 6. Cope 1884; 7. Corner, 1982; 8. Einsohn, 1971; 9. Eshelman, 1975; 10. Estes and Tihen, 1964; 11. Green, 1956; 12. 13. Hibbard, 1936; 14. Hubbs, 1942; 15. Lundberg, 1975; 16. Martin, ms.; 17. Neff, 1975; 18. Ossian, 1973; 19. Robertson, 1943; 20. Semken, 1966; 21. Schultz, 1965; 22. Smith, 1954; 23. Smith, 1958; 24. Smith, 1962; 25. Smith, 1963; 26. Smith and Lundberg, 1972; 27. Stewart, ms; 28. Stewart and Smith, ms.; 29. Voorhies, 1982; 30. Wilson, 1968. 31. Lundberg, 1967; 32. Uyeno, 1963; 33. Uyeno and Miller, 1962.

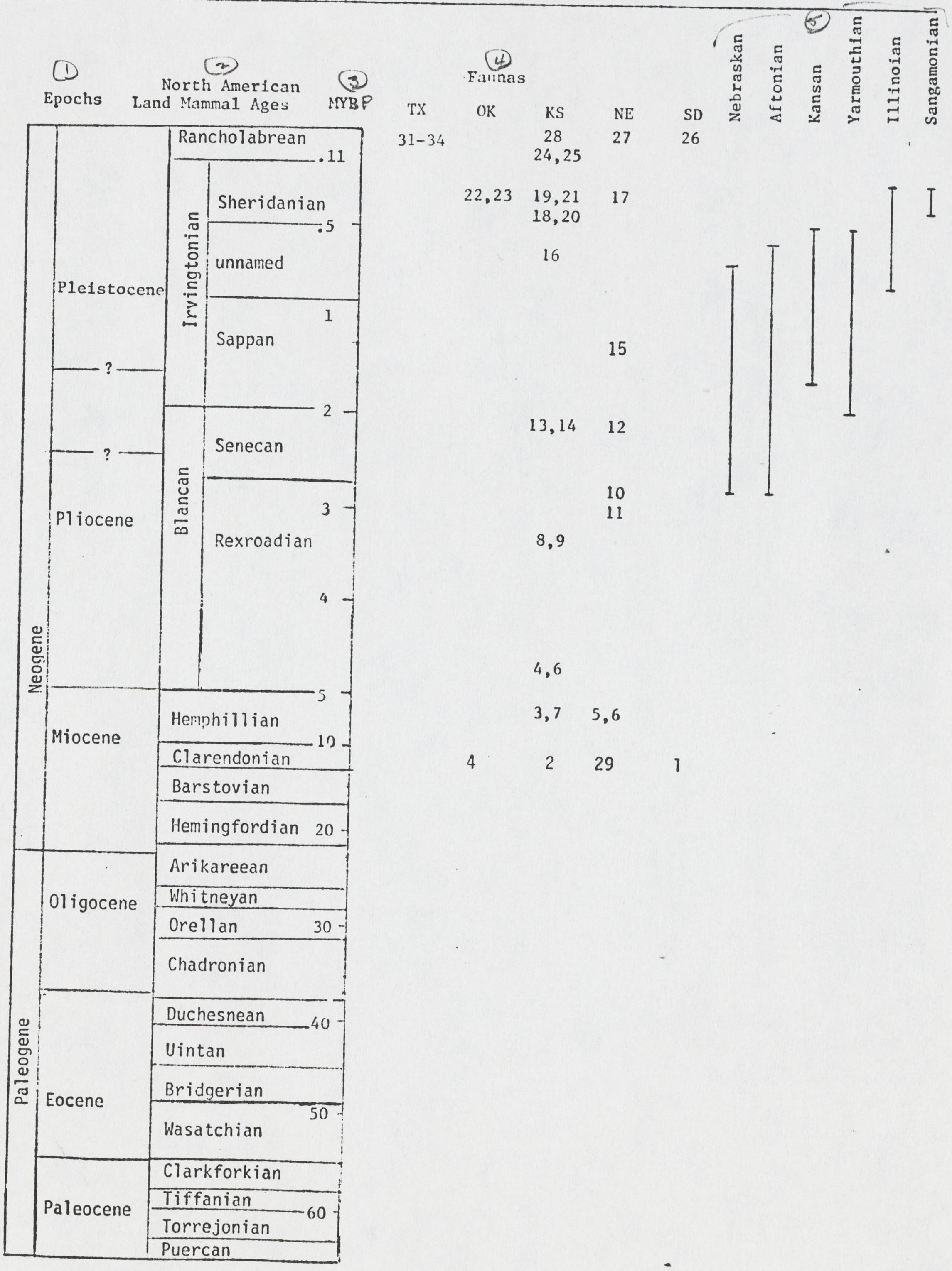
| | Faunas | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| TAXON | Tiffanian of WY | Tiffanian of MT | Wasatchian of ND | Wasatchian of WY | Bridgerian of WY | Duchesnian of SD | Chadronian of SD | Orellan of MT | Orellan of SD | Florissant, Park Co., CO | Hemingfordian of SD | Hemingfordian of NE | Hemingfordian of CO | Barstovian of SD | Barstovian of NE | Wolf Creek, Shannon Co., SD | Clarendonian, NE | Kilgore, Cherry Co., NE | WaKeeney, Trego Co., KS | Laverne, Beaver Co., OK | Roger Mills Co., OK | diatomite, Logan Co., KS | Santee, Knox Co., NE | Airport, Knox Co., NE | Saw Rock, Meade Co., KS | Rexroad, Meade Co., KS | Bender, Meade Co., Ks | Broadwater-Lisco, Morrill Co., NE | Sand Draw, Brown Co., NE |
| | | | | | | | | | | | | | | | | 1 | | 30 | 2 | 4 | 29 | 3 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
| | | Paleocene | | Eocene | | | | | Oligocene | | | | | | | | Miocene | | | | | | | | | | | Pliocene | |
| | | | | | | | | | | 1 | | | | | | 2 | | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |
| Atractosteus spatula | | | | | | | | | | | | | | | 29 | | | | | 24 | | | 29 | | | | | | |
| Lepisosteus platostomus or occulatus | | | | | | | | | | | | | | | | | | | 30 | | | | | | | | | | |
| Lepisosteidae indet. | | | | | | 2 | | | | | | | | | 10/24 | | | | | | | | | | | | | | 26 |
| Amia calva | | | | | | | | | | | | | | | 24 | | | | 30 | | | | | 27 | | | | | |
| Amia fragosa | 3 | 3 | 3 | 3 | 3 | | | | | | | | | | | | | | | | | | | | | | | | |
| Amia scutata | | | | | | | 3 | 3 | 3 | 5 | | | 3 | | | | | | | | | | | | | | | | |
| Amia uintaensis | 3 | 3 | 3 | 3 | 3 | | | | | | | | | | | | | | | | | | | | | | | | |
| Hiodon alosoides | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 26 |
| Esox sp. | | | | | | | | | | | | | | | | | | | | 24 | | | | 27 | | | | | |
| Notropis megalepis | | | | | | | | | | | | | | | | | | | | | | 24 | | | | | | | |
| Notropis stramineus | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | |
| Notropis sp. | | | | | | | | | | | | | | | | | | | 30 | | | | | | | | | | |
| Pimephales promelas | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 26 |
| Semotilus atromaculatus | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | |
| Ictiobus bubalus | | | | | | | | | | | | | | | | | | | | 24 | | | | | | | | | |
| Ictiobus cyprinellus | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 26 |
| Ictiobus sp. | | | | | | | | | | | | | | | | | | | 30 | | | | | | | | | | |
| Amyzon spp. | | | | | | | | | | 6 | | | | | | | | | | | | | | | | | | | |
| Ictalurus echinatus | | | | | | | | | | | | | | | 15 | | 24/15 | | | | | | | | | | | | |
| Ictalurus lambda | | | | | | | | | | | | | | | | | 15 | | 30 | | | | | | | | | | |
| Ictalurus lavetti | | | | | | | | | | | | | | | | | | | 30/15 | | | 24/15 | | | | | | | |
| Ictalurus leidyi | | | | | | | | | | | | 15 | | | 15 | | 15 | | | | | | | | | | | | |
| Ictalurus pectinatus | | | | | | | | | | 4 | | | | | | | | | | | | | | | | | | | |
| Ictalurus punctatus | | | | | | | | | | | 15 | 15 | | | 15 | 11 | 15 | | | | | | | | | | | | |
| Ictalurus sawrockensis | | | | | | | | | | | | | | | | | | | | | | | | | 24 | 26 | 26 | 1 | 26 |
| Pylodictis olivaris | | | | | | | | | | | | | | | 15 | | 15 | | | | | | | | | | | | |
| Fundulus detillai | | | | | | | | | | | | | | | | | | | | | | 24 | | | | | | | |
| Fundulus sternbergi | | | | | | | | | | | | | | | | | | | | | | 19 | | | | | | | |
| Fundulus sp. | | | | | | | | | | | | | | | | | | | | 24 | | | | | | 24 | | | |
| Menidia sp. | | | | | | | | | | | | | | | | | | | | | 14 | | | | | | | | |
| (Aphredoderus) Trichophanes foliarum | | | | | | | | | | 6 | | | | | | | | | | | | | | | | | | | |
| Ambloplites rupestris | | | | | | | | | | | | | | | | | | | | | | | | | | 24 | | | |
| Lepomis cyanellus | | | | | | | | | | | | | | | | | | | | | | | | | | 24 | | | |
| Lepomis humilis | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 26 |
| Lepomis kansasensis | | | | | | | | | | | | | | | | | | | | | | 24 | | | | | | | |
| Lepomis serratus | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 26 |
| Micropterus punctulatus | | | | | | | | | | | | | | | | | | | 30 | | | | | | | | | | |
| Micropterus sp. | | | | | | | | | | | | | | | | | 24 | | | | | | | | | | | | |
| Pomoxis lanei | | | | | | | | | | | | | | | | | | 27 | | | | 13 | | | | | | | |
| Morone chrysops | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 26 |
| Aplodinotus grunniens | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 26 |

Table 2. Glacial fossil records. Numbers directly below localities correspond to numbers in Fig. 4. Other numbers as in ~~preceding~~ Table, 1.

| TAXON | Faunas | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Seneca, Hooker Co., NE 12 | Plainville, Rooks Co., KS 13 | Whiterock, Republic Co., KS 14 | Sappa, Harlan Co., NE 15 | Wathena, Doniphan Co., KS 16 | Angus, Nuckolls Co., NE 17 | Rezabek, Lincoln Co., KS 18 | Sandahl, McPherson Co., KS 19 | Kanopolis, Ellsworth Co., KS 20 | Butler Spring, Meade Co., KS 21 | Berends, Beaver Co., OK 22 | Doby Springs, Harper Co., OK 23 | Mt. Scott, Meade Co., KS 24 | Duck Creek, Ellis Co., KS 25 | Ree Heights, Hand Co., SD 26 | Litchfield, Sherman Co., NE 27 | Hill City, Graham Co., KS 28 | Good Creek, Foard Co., TX 31 | Clear Creek, Denton Co., TX 32 | Trinity River, Dallas Co., TX 33 | Ben Fanklin, Delta Co., TX 34 |
| | Blancan | | | Irvingtonian | | | | | | | | | Rancholabrean | | | | | | | | |
| | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 |
| Atractosteus spatula | | | | | | | | | | | | | | | | | | | | 33 | |
| Lepisosteus osseus | | | | | | | | | 17 | 21 | | | | | | | | | | | |
| Lepisosteus platostomus | | | | | | 16 | 27 | | | 21 | | | 25 | | | | | | | | |
| Lepisosteidae indet. | | | 9 | | | | | 20 | | | 22 | | | | | | | 31 | 32 | 33 | |
| Hiodon lirellus | 1 | | | | | | | | | | | | | | | | | | | | |
| Anguilla rostrata | | 27 | | | | | | | | | | | | | | | | | | | |
| Esox masquinongy | | | | | | | | | | | 22 | | 25 | | | | | | | | |
| Esox sp. | | | | | 27 | | | | | 27 | | | | | | | | | | | |
| Campostoma anomalum | | | | | | | | | | | | | 25 | | | | | 31 | | | |
| Campostoma sp. | | | | | 8 | | | | | | | | | | | | | | | | |
| Hybognathus hanknsoni | | | | | | | | | | | | | 25 | | | | | | | | |
| Hybognathus placitus | | | | 1 | 8 | | | | | | | | | | | | | | | | |
| Hybopsis gracilis | | | | | 8 | | | | | | | 23 | | | | | 28 | | | | |
| Nocomis biguttatus | | | 9 | | 8 | | | | 17 | | | | | | | | | | | | |
| Notropis chrysoleucas | | | | | | | | | | | 22 | | | | | | | | | | 32 |
| Notropis cornutus | 1 | | | | | | | | | | | | | | | | | | | | |
| Notropis nubilus | | | | | | | | | | | | | 25 | | | | | | | | |
| Notropis stramineus | 1 | | | | | | | | | | | | | | | | | | | | |
| Notropis rubellus | | | | | | | | | 17 | | | | | | | | | | | | |
| Notropis sp. | | 27 | | | 8 | | | | | | | | | | | | | | | | |
| Pimephales promelas | | | | | 8 | | | | 17 | | | 23 | | | | | | | | | |
| Pimephales sp. | | 27 | | 1 | | | | | | | | | | | | | | | | | |
| Proballostomus longulus | | | | | | | | | | | | | | | 18 | | | | | | |
| Rhinichthys sp. | | | | 1 | | | | | | | | | | | | | | | | | |
| Semotilus atromaculatus | 1 | | | | | | | | | | 22 | 23 | 25 | | | | | | | | |
| Semotilus sp. | | 27 | | | | | | | | | 22 | | | | | | | | | | |
| Catostomus commersoni | | | | | | 16 | | | | 23 | 22 | 23 | 25 | 27 | | | 28 | | | | |
| Catostomus platyrhinchus | | | | | | | | | | | | | | | | | 28 | | | | |
| Carpiodes carpio | | | | | | | | | | | | | | | | | | 31 | | | |
| Ictiobus bubalus | | | | | | | 27 | | | | | | | | | | | | | | |
| Ictiobus niger | | | | | | | | | 17 | | | | | | | | | | | | |
| Ictiobus sp. | | | | | | | | | | | | | 25 | | | | | | | 33 | |
| Minytrema melanops | | | 9 | | | | | | | | | | | | | | | | | | |
| Moxostoma carinatum | | | | | 8 | | | | | | | | | | | | | | | | |
| Moxostoma duquesnei | | | | | 8 | | | | | | | | | | | | | | | | |
| Ictalurus sawrockensis | 1 | 27 | 9 | | 8 | | | | | | | | | | | | | | | | |
| Ictalurus melas | | | | | | 16 | 27 | | 17 | 23 | 22 | 23 | 25 | | | | | | | | |
| Ictalurus natalis | | | 9 | | | | | | | | | | | | | | | 31 | | | |
| Ictalurus punctatus | | | 9 | | | | | | 17 | 23 | 22 | | 25 | | | | | | | 33 | |
| Ictalurus sp. | | | | | | | | | | | | | | | | | | | | 33 | 32 |
| Noturus gyrinus | | | | | | | | | | | | | | | | 7 | | | | | |
| Noturus hildebrandi | | | | | | | | | | | | | | | 18 | | | | | | |
| Noturus furiosus group | | | 9 | 1 | 16 | | | | 17 | | | | | | | | | | | | |
| Pylodictis olivaris | | | | | | | | | | | | | | | | | | | | 33 | |
| Fundulus diaphanus | | | | | | | | | | | | | | | 18 | | | | | | |
| Fundulus sp. | | | | | | | | | | | 22 | | | | | | | | | | |
| Ambloplites rupestris | | | | | 8 | | | | | | | | | | | | | | | | |
| Lepomis cyanellus | | | 9 | | | | | | 17 | | 22 | 23 | 25 | | | | | 31 | | | |
| Lepomis gibbosus | | | | | | | | | | | | | | | 18 | | | | | | |
| Lepomis gulosus | | | | | 8 | | | | | | | | | | | | | | | | |
| Lepomis humilis | | 27 | | | 8 | | | | 17 | | | | 25 | | 18 | | | | | | |
| Lepomis macrochirus | | | | | | | | | | | | | | | 18 | | | | | | |
| Lepomis megalotis | | | | | 8 | | | | | | | | | | | | | | | | |
| Lepomis serratus | 1 | | | | | | | | | | | | | | | | | | | | |
| Lepomis sp. | | | | | | | | | | | | | | | | | | | 32 | | 32 |
| Micropterus salmoides | | | | | | | | | 17 | | | | 25 | | 18 | | | | | | |
| Micropterus sp. | | | | | 8 | | | | | | | | | | | | | | | | |
| Morone chrysops | | | | | 8 | | | | | | | | | | | | | | | | |
| Etheostoma exile | | | | | | | | | | | | | | | 18 | | | | | | |
| Etheostoma sp. | | | | | 8 | | | | | | | | | | | | | | | | |
| Perca flavescens | | | | | | | | 20 | | 23 | 22 | 23 | 25 | | 18 | | | | | | |
| Percina copelandi | | | | | | | | | | | | | | | 18 | | | | | | |
| Stizostedion vitreum | | | | | | | | 20 | | | | | | | | | | | | | |
| Aplodinotus grunniens | | | | | | | | | | | | | | | | | | 31 | | | 32 |

(rearrange sequence) →

Table 3. Correlation of an ③ absolute time scale, ① Cenozoic epochs, Neogene ④ ichthyofaunas, ② North American Land Mammal Ages, and overlapping traditional usages of North American glacial and interglacial nomenclature. ⑤



| | ① Epochs | ② North American Land Mammal Ages | | ③ MYBP | ④ Faunas TX | OK | KS | NE | SD | ⑤ Nebraskan | Aftonian | Kansan | Yarmouthian | Illinoian | Sangamonian |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Neogene | Pleistocene | Rancholabrean | | | 31-34 | | 28<br>24,25 | 27 | 26 | | | | | | |
| | | | | .11 | | | | | | | | | | | |
| | | Irvingtonian | Sheridanian | | | 22,23 | 19,21<br>18,20 | 17 | | | | | | I | I |
| | | | | .5 | | | | | | | | | | I | |
| | | | unnamed | | | | 16 | | | I | I | I | I | I | |
| | | | | 1 | | | | | | I | I | I | I | | |
| | | | Sappan | | | | | 15 | | I | I | I | I | | |
| | ? | | | | | | | | | I | I | I | I | | |
| | | Blancan | | 2 | | | | | | I | I | | I | | |
| | | | Senecan | | | | 13,14 | 12 | | I | I | | | | |
| | ? | | | | | | | | | I | I | | | | |
| | Pliocene | | Rexroadian | 3 | | | | 10<br>11 | | I | I | | | | |
| | | | | | | | 8,9 | | | | | | | | |
| | | | | 4 | | | | | | | | | | | |
| | | | | | | | 4,6 | | | | | | | | |
| | Miocene | | | 5 | | | | | | | | | | | |
| | | Hemphillian | | | | | 3,7 | 5,6 | | | | | | | |
| | | | | 10 | | | | | | | | | | | |
| | | Clarendonian | | | | 4 | 2 | 29 | 1 | | | | | | |
| | | Barstovian | | | | | | | | | | | | | |
| | | Hemingfordian | | 20 | | | | | | | | | | | |
| Paleogene | Oligocene | Arikareean | | | | | | | | | | | | | |
| | | Whitneyan | | | | | | | | | | | | | |
| | | Orellan | | 30 | | | | | | | | | | | |
| | | Chadronian | | | | | | | | | | | | | |
| | Eocene | Duchesnean | | 40 | | | | | | | | | | | |
| | | Uintan | | | | | | | | | | | | | |
| | | Bridgerian | | | | | | | | | | | | | |
| | | Wasatchian | | 50 | | | | | | | | | | | |
| | Paleocene | Clarkforkian | | | | | | | | | | | | | |
| | | Tiffanian | | 60 | | | | | | | | | | | |
| | | Torrejonian | | | | | | | | | | | | | |
| | | Puercan | | | | | | | | | | | | | |

TABLE 4. Distribution of Fishes in Nineteen Drainage Units, Physiographic Provinces and Habitats and Endemism in Western Mississippi River Drainages. (N=Native, U=Uncertain, D=Diadromous, A=Accidental, I=Introduced, ?=Questionable Validity, E=Extinct, P=Prevalent, M=Marginal, S=Sporatic and X=Present). Totals for each column represent total number of taxa in each.

| | DRAINAGE OCCURRENCE | | | | | | | | | | | | | | | | | | | ECOLOGY | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | RED | | ARKANSAS | | | | | | | MISSOURI | | | | | | | | | REGION | | | | | HABITAT | | | | |
| SPECIES | Ouachita R. | Lower Red R. | Upper Red R. | Lower Arkansas R. | Middle Arkansas R. | Canadian R. | Upper Arkansas R. | White R. | St. Francis-Little Rs. | Meramec-Miss Tribs. | Lower Missouri R. | Chariton-Nishnabotna Rs. | Kansas R. | Platte-Niobrara Rs. | Sioux-James Rs. | White-Lt. Missouri Rs. | Yellowstone R. | Upper Missouri R. | Mainstream Miss. R. | Coastal Plain | Interior Highlands | Central Lowlands | Great Plains | Rocky Mountains | Big River | Small River | Creek | Lake | Endemic |
| PETROMYZONTIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Ichthyomyzon castaneus | N | N | | N | N | | | N | N | N | N | N | N | | | | | | N | S | P | M | | | X | X | | X | |
| Ichthyomyzon fossor | | | | | | | | | | N | N | | | | | | | | | | P | | | | | X | X | | |
| Ichthyomyzon gagei | N | N | | N | N | | | N | | | N | | | | | | | | | S | P | | | | | X | X | | |
| Ichthyomyzon unicuspis | | | | | | | | | | | | | | N | | N | | | N | S | | S | | | X | | | | |
| Lampetra aepyptera | | | | | | | | N | N | N | | | | | | | | | | | P | | | | | | X | | |
| Lampetra appendix | | | | | | | | N | N | | | | | | | | | | | | P | | | | | X | X | | |
| CARCHARINIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Carcharinus leucas | | | | | | | | | | | | | | | | | | | A | S | | | | | | | | | |
| ACIPENSERIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Acipenser fulvescens | N | | | | | | | | N | | N | N | N | N | | | | | N | S | S | S | | | X | | | | |
| Scaphirhynchus albus | | | | | | | | | N | | N | N | N | N | | N | N | N | N | S | | P | P | | X | | | | X |
| Scaphirhynchus platorynchus | N | N | | N | N | | | N | | | N | N | N | N | N | N | N | N | N | P | P | P | P | | X | | | | |
| POLYODONTIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Polyodon spathula | N | N | | N | N | N | N | N | | | N | N | N | N | N | N | N | N | N | P | S | P | P | | X | | | X | |
| LEPISOSTEIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Atractosteus spatula | N | N | | N | | N | | N | N | | | | | | | | | | N | P | S | | | | X | | | | |
| Lepisosteus oculatus | N | N | N | N | N | N | N | N | N | | | | | | | | | | N | P | M | M | | | X | | | X | |
| Lepisosteus osseus | N | N | N | N | N | | N | N | N | N | N | N | N | N | N | | | | N | P | P | P | M | | X | X | | X | |
| Lepisosteus platostomus | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | | N | N | P | M | P | M | | X | X | | | |

TABLE 4. Continued.

| SPECIES | DRAINAGE OCCURRENCE | | | | | | | | | | | | | | | | | | | ECOLOGY | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | RED | | ARKANSAS | | | | | | | MISSOURI | | | | | | | | | REGION | | | | | HABITAT | | | | |
| | Ouachita R. | Lower Red R. | Upper Red R. | Lower Arkansas R. | Middle Arkansas R. | Canadian R. | Upper Arkansas R. | White R. | St. Francis-Little Rs. | Meramec-Miss Tribs. | Lower Missouri R. | Chariton-Nishnabotna Rs. | Kansas R. | Platte-Niobrara Rs. | Sioux-James Rs. | White-Lt. Missouri Rs. | Yellowstone R. | Upper Missouri R. | Mainstream Miss. R. | Coastal Plain | Interior Highlands | Central Lowlands | Great Plains | Rocky Mountains | Big River | Small River | Creek | Lake | Endemic |
| AMIIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Amia calva | N | N | | N | N | | | N | N | | I | I | I | | | | | | N | P | | | | | X | | | X | |
| ANGUILLIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Anguilla rostrata | D | D | D | D | D | D | D | D | D | D | D | D | D | D | D | | | | D | P | P | S | M | | X | X | | | |
| CLUPEIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Alosa alabamae | D | D | | D | D | | | | | D | D | | | | | | | | D | S | S | | | | X | X | | | |
| Alosa chrysochloris | N | N | | N | N | | | N | N | | N | N | N | N | | | | | N | P | S | S | | | X | | | | |
| Dorosoma cepedianum | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | | | N | P | S | P | M | | X | X | | X | |
| Dorosoma petenense | N | N | U | N | I | I | | N | N | | I | | | | | | | | N | P | M | M | | | X | | | X | |
| HIODONTIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Hiodon alosoides | N | N | N | N | N | | N | N | | | N | N | N | N | N | N | N | N | N | S | | P | P | | X | X | | | |
| Hiodon tergisus | N | N | | N | | | | N | N | N | N | N | | | | | | | N | P | M | M | | | X | X | | X | |
| SALMONIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Coregonus clupeaformis | | | | | | | | | | | | | | | | I | | I | | | | | S | | | | | X | |
| Oncorhynchus kisutch | | | | | | | | | | | | | | | | I | | I | | | | | S | | | | | X | |
| Oncorhynchus nerka | | | | | | | | | | | | | | I | | | I | I | | | | | | S | | X | | X | |
| Oncorhynchus tshawytscha | | | | | | | | | | | | | | | | I | | | | | | | S | | | | | X | |
| Prosopium williamsoni | | | | | | | | | | | | | | | | | N | N | | | | | | P | | X | X | | |
| Salmo aguabonita | | | | | | | | | | | | | | | | | I | I | | | | | S | | | | X | | |
| Salmo clarki | | | | | | N | N | | | | | | | N | | | N | N | | | | | | P | | | X | X | |
| Salmo gairdneri | I | I | | | I | I | I | I | | I | I | | I | I | I | I | I | I | | | | | | P | | X | X | X | |
| Salmo trutta | I | | | | I | I | I | I | | I | I | | | I | | I | I | I | | | | | | P | | X | X | X | |

TABLE ~~1~~ 4. Continued.

| | DRAINAGE OCCURRENCE | | | | | | | | | | | | | | | | | | | ECOLOGY | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | RED | | ARKANSAS | | | | | | | MISSOURI | | | | | | | | | REGION | | | | | HABITAT | | | | |
| SPECIES | Ouachita R. | Lower Red R. | Upper Red R. | Lower Arkansas R. | Middle Arkansas R. | Canadian R. | Upper Arkansas R. | White R. | St. Francis-Little Rs. | Meramec-Miss Tribs. | Lower Missouri R. | Chariton-Nishnabotna Rs | Kansas R. | Platte-Niobrara Rs. | Sioux-James Rs. | White-Lt. Missouri Rs. | Yellowstone R. | Upper Missouri R. | Mainstream Miss. R. | Coastal Plain | Interior Highlands | Central Lowlands | Great Plains | Rocky Mountains | Big River | Small River | Creek | Lake | Endemic |
| Salvelinus fontinalis | | | | | | I | I | | | | | | | I | | I | I | I | | | | | | P | | | X | X | |
| Salvelinus namaycush | | | | | | | | | | | | | | I | | | I | I | | | | | | S | | | | X | |
| Thymallus arcticus | | | | | | | | | | | | | | I | | | I | N | | | | | | M | | X | X | X | |
| OSMERIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Osmerus mordax | | | | | | | | | | | I | I | | I | | I | I | I | I | S | | S | S | | X | | | X | |
| UMBRIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Umbra limi | | | | | | | | | N | | | | | | N | I | | | N | M | | P | | | | | | X | |
| ESOCIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Esox americanus | N | N | | N | | | | N | N | N | N | | | N | | | | | N | P | P | M | S | | | X | X | X | |
| Esox lucius | I | I | I | | | | I | I | I | I | I | I | I | N | N | I | I | I | N | | | P | P | | X | | | X | |
| Esox masquinongy | I | | | | | | | I | | | I | | | | | | | | | | S | | | | | | | X | |
| Esox niger | N | N | U | N | | | | N | N | | | | | | | | | | N | P | | | | | | X | | X | |
| CHARACIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Astyanax mexicanus | | I | I | | I | | | | | | | | | | | | | | | S | S | S | | | X | X | | | |
| CYPRINIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Campostoma anomalum | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | | | N | S | P | P | M | P | | X | X | | |
| Campostoma oligolepis | | | | | I | | | N | N | N | N | | | | | | | | N | | P | | | | | X | X | | |
| Carassius auratus | I | | I | I | I | | I | I | I | I | | I | I | I | | | I | I | | | | | | | X | X | | X | |
| Couesius plumbeus | | | | | | | | | | | | | | N | | N | N | N | | | | | P | P | | X | X | X | |
| * Ctenopharyngodon idella | I | I | I | I | I | I | I | I | I | | I | I | I | I | I | | | | I | P | M | | | | X | | | X | |
| Cyprinus carpio | I | I | I | I | I | I | I | I | I | I | I | I | I | I | I | I | I | I | I | M | M | P | P | | X | X | | X | |
| Ericymba buccata | | | | | | | | | N | N | | | | | | | | | | | M | | | | | X | | | |

TABLE ~~1~~4. Continued.

| | DRAINAGE OCCURRENCE | | | | | | | | | | | | | | | | | | | ECOLOGY | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | RED | | ARKANSAS | | | | | | | MISSOURI | | | | | | | | | REGION | | | | | HABITAT | | | | |
| SPECIES | Ouachita R. | Lower Red R. | Upper Red R. | Lower Arkansas R. | Middle Arkansas R. | Canadian R. | Upper Arkansas R. | White R. | St. Francis-Little Rs. | Meramec-Miss Tribs. | Lower Missouri R. | Chariton-Nishnabotna Rs. | Kansas R. | Platte-Niobrara Rs. | Sioux-James Rs. | White-Lt. Missouri Rs. | Yellowstone R. | Upper Missouri R. | Mainstream Miss. R. | Coastal Plain | Interior Highlands | Central Lowlands | Great Plains | Rocky Mountains | Big River | Small River | Creek | Lake | Endemic |
| Gila atraria | | | | | | | | | | | | | | | | | | I | | | | | | P | | X | | X | |
| Gila pandora | | | | | | I | | | | | | | | | | | | | | | | | | M | | X | X | | |
| Hybognathus argyritis | | | | | | | | | | | N | N | N | N | N | N | N | N | N | | | P | P | | X | X | | | X |
| Hybognathus hankinsoni | | | | | | | | | | | | N | N | N | N | N | N | N | | | | P | P | | | | X | | |
| Hybognathus hayi | N | N | | N | | | | N | N | | | | | | | | | | N | P | | | | | X | X | | | |
| Hybognathus nuchalis | N | N | | N | | | | N | N | N | | | | | | | | | N | P | M | M | | | X | X | | | |
| Hybognathus placitus | | N | N | N | N | N | N | | | | N | N | N | N | | N | N | N | N | | | P | P | | X | X | | | |
| Hybopsis aestivalis | N | N | N | N | N | N | N | N | N | | N | N | N | N | | | | | N | P | | P | P | | X | X | | | |
| Hybopsis amblops | | | | N | N | | | N | N | N | | | | | | | | | | | P | | | | | X | X | | |
| Hybopsis dissimilis | | | | | | | | N | N | | | | | | | | | | | | P | | | | X | X | | | |
| Hybopsis gelida | | | | | | | | | | | N | N | N | N | | N | N | N | N | | | P | P | | X | X | | | X |
| Hybopsis gracilis | | | | | | N | N | | | | N | N | N | N | N | N | N | N | N | | | M | P | M | X | X | | | |
| Hybopsis meeki | | | | | | | | | | | N | N | N | N | | N | N | N | N | | | M | P | | X | | | | |
| Hybopsis storeriana | N | N | N | N | N | N | N | N | | N | N | N | N | N | N | | | | N | P | S | P | M | | X | | | | |
| Hybopsis x-punctata | N | | | | N | | | N | | N | N | | | | | | | | N | | P | M | | | | X | | | |
| Nocomis asper | N | N | | | N | | | | | | | | | | | | | | | | P | M | | | | X | X | | X |
| Nocomis biguttatus | | | | | | | | N | N | N | N | | N | N | N | | | | | | P | S | S | | | X | X | | |
| Notemigonus crysoleucas | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | I | I | I | N | | S | P | S | | | X | X | X | |
| Notropis amnis | N | N | | N | | | | N | N | N | | | | | | | | | N | P | M | | | | X | X | | | |
| Notropis atherinoides | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | P | S | P | S | | X | X | | X | |
| Notropis atrocaudalis | | N | | | | | | | | | | | | | | | | | | P | M | | | | | X | X | | |
| Notropis bairdi | | N | N | | | | I | | | | | | | | | | | | | S | | P | M | | | X | | | X |
| Notropis blennius | | U | U | N | N | | N | | | | N | N | N | N | N | | | | N | S | | P | M | | X | X | | | |
| Notropis boops | N | N | N | N | N | N | N | N | N | N | N | | | | | | | | N | M | P | M | | | | X | X | | |
| Notropis buchanani | N | N | N | N | N | N | N | N | | | N | N | N | | | | | | N | P | | P | | | X | X | | | |
| Notropis camurus | | | | N | N | | N | | | | | | | | | | | | | | P | M | | | | X | X | | |
| Notropis chalybeus | N | N | | | | | | N | N | | | | | | | | | | | P | | | | | | | X | | |

H. a. tetranemus now considered extirpated in Colorado

TABLE ~~1~~ 4. Continued.

| SPECIES | DRAINAGE OCCURRENCE | | | | | | | | | | | | | | | | | | ECOLOGY | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | RED | | ARKANSAS | | | | | | | MISSOURI | | | | | | | | | REGION | | | | | HABITAT | | | |
| | Ouachita R. | Lower Red R. | Upper Red R. | Lower Arkansas R. | Middle Arkansas R. | Canadian R. | Upper Arkansas R. | White R. | St. Francis-Little Rs. | Merāmec-Miss Tribs. | Lower Missouri R. | Chariton-Nishnabotna Rs. | Kansas R. | Platte-Niobrara Rs. | Sioux-James Rs. | White-Lt. Missouri Rs. | Yellowstone R. | Upper Missouri R. | Mainstream Miss. R. | Coastal Plain | Interior Highlands | Central Lowlands | Great Plains | Rocky Mountains | Big River | Small River | Creek | Lake | Endemic |
| Notropis chrysocephalus | N | N | | N | N | | | N | N | N | N | | | | | | | | | M | P | M | | | | X | X | | |
| Notropis cornutus | | | | | | | | | | | N | N | N | N | N | N | | | | | M | P | S | | | X | X | | |
| * Notropis dorsalis | | | | | | | H | | | N | N | N | N | N | N | N | | | N | | | P | P | | X | X | X | | |
| Notropis emiliae | N | N | | N | | | | N | N | | | | | | | | | | N | P | M | M | | | | X | X | X | |
| Notropis fumeus | N | N | | N | N | | | N | N | | | | | | | | | | N | P | | M | | | | X | X | X | |
| Notropis galacturus | | | | | | | | N | N | | | | | | | | | | | | P | | | | | X | | | |
| Notropis girardi | | | I | N | N | N | N | | | | | | | | | | | | | | | P | P | | | X | | | X |
| Notropis greenei | | | | N | N | | | N | N | N | N | | | | | | | | | M | P | | | | | X | | | X |
| Notropis heterolepis | | | | | | | ? | | | | N | | ? | N | N | | | | | | S | S | S | | | X | X | X | |
| Notropis hubbsi | N | N | | N | | | | | | | | | | | | | | | | P | | | | | | X | X | X | X |
| Notropis hudsonius | | | | | | | | | | | | | | | N | I | | | N | | | P | | | X | | | X | |
| Notropis longirostris | N | | | | | | | | | | | | | | | | | | | M | | | | | | X | X | | |
| Notropis lutrensis | N | N | N | N | N | N | N | | N | N | N | N | N | N | N | N | | | N | P | | P | P | | X | X | X | X | |
| Notropis maculatus | N | N | | N | | | | N | N | | | | | | | | | | N | P | | | | | X | X | | X | |
| Notropis nubilus | | | | N | N | | | N | N | N | N | | | | | | | | N | | P | | | | | X | X | | |
| Notropis ortenburgeri | N | N | | N | N | N | | | | | | | | | | | | | | M | P | M | | | | X | X | | X |
| Notropis oxyrhynchus | | | N | | | | | | | | | | | | | | | | | | | S | | | | X | | | |
| Notropis ozarcanus | | | | | I | | | N | N | | | | | | | | | | | | P | | | | X | X | | | X |
| Notropis perpallidus | N | N | | | | | | | | | | | | | | | | | | | P | | | | | X | | | X |
| Notropis pilsbryi | | N | | | N | | | N | | | | | | | | | | | | | P | M | | | | X | X | | X |
| Notropis potteri | | N | N | | | | | | | | | | | | | | | | N | P | | P | | | X | | | | |
| Notropis rubellus | N | N | | | N | | N | N | N | N | N | | N | | | | | | | | P | M | | | | X | X | | |
| Notropis sabinae | N | N | | | | | | N | N | | | | | | | | | | | P | | | | | | X | X | | |
| Notropis shumardi | | N | | N | | | | | | | N | N | N | N | | N | | | N | P | | P | M | | X | | | | |
| Notropis spilopterus | | | | | N | | | | | N | N | | | | I | | | | N | | P | | | | | X | X | | |
| Notropis stramineus | | N | N | | N | N | N | | | N | N | N | N | N | N | N | N | | N | | M | P | P | M | X | X | X | | |
| Notropis telescopus | | | | | | | | N | N | | | | | | | | | | | | P | | | | | X | | | |

TABLE ~~1~~ 4. Continued.

| | DRAINAGE OCCURRENCE | | | | | | | | | | | | | | | | | | | ECOLOGY | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | RED | | ARKANSAS | | | | | | | MISSOURI | | | | | | | | | REGION | | | | | HABITAT | | | | |
| SPECIES | Ouachita R. | Lower Red R. | Upper Red R. | Lower Arkansas R. | Middle Arkansas R. | Canadian R. | Upper Arkansas R. | White R. | St. Francis-Little Rs | Meramec-Miss Tribs. | Lower Missouri R. | Chariton-Nishnabotna Rs | Kansas R. | Platte-Niobrara Rs. | Sioux-James Rs. | White-Lt. Missouri Rs. | Yellowstone R. | Upper Missouri R. | Mainstream Miss. R. | Coastal Plain | Interior Highlands | Central Lowlands | Great Plains | Rocky Mountains | Big River | Small River | Creek | Lake | Endemic |
| Notropis texanus | N | N | | N | | | | N | N | | | | | | | | | | N | P | | | | | X | X | | | |
| Notropis topeka | | | | | N | | N | | | | N | N | N | N | N | | | | | | | P | S | | | | X | | |
| Notropis umbratilis | N | N | | N | N | N | N | N | N | N | N | N | N | | | | | | N | P | P | P | | | | X | X | | |
| Notropis venustus | N | N | N | N | | | | N | N | | | | | | | | | | N | P | M | M | | | X | X | | | |
| Notropis volucellus | N | N | | N | N | | N | N | N | N | N | | | | | | | | N | P | M | P | | | X | X | | X | |
| Notropis whipplei | N | N | | N | N | N | | N | N | N | | | | | | | | | | M | P | M | | | | X | | | |
| Notropis zonatus | | | | | | | | N | N | N | N | | | | | | | | | | P | | | | | X | X | | X |
| Phenacobius mirabilis | | N | N | N | N | N | N | ? | N | N | N | N | N | N | N | N | | | N | M | M | P | P | S | X | X | X | | |
| Phoxinus eos | | | | | | | U ? | | | | | | | N | N | N | N | N | | | | S | S | S | | | X | X | |
| Phoxinus erythrogaster | | U | U | | N | U | U N? | N | N | N | N | | N | | N | | | | | | P | S | | S | | | X | | |
| Phoxinus neogaeus | | | | | | | | | | | | | | N | | N | | N | | | | | P | M | | | X | X | |
| Pimephales notatus | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | I | | | N | | P | P | S | | | X | X | X | |
| Pimephales promelas | I | U | N | I | N | N | N | I | I | N | N | N | N | N | N | N | N | N | N | | S | P | P | | X | X | X | X | |
| Pimephales tenellus | N | N | | N | N | | N | N | N | | | | | | | | | | | | P | P | | | | X | X | | X |
| Pimephales vigilax | N | N | N | N | N | N | N | N | N | N | | | I | | I | | | | M | P | | P | | | X | X | | | |
| Rhinichthys atratulus | | | | | | | | | | | | U | | N | N | N | | | | | | S | S | | | | X | | |
| Rhinichthys cataractae | | | | | | N | N | | | | | | | N | | N | N | N | | | | | P | P | | X | X | | |
| Richardsonius balteatus | | | | | | | | | | | | | | | | | | I | | | | | | P | | | X | X | |
| Semotilus atromaculatus | N | N | | N | N | N | N | N | N | N | N | N | N | N | N | N | N | | N | P | P | P | P | M | | | X | | |
| Semotilus margarita | | | | | | | | | | | | | | N | | N | N | N | | | | M | P | | | | X | X | |
| CATOSTOMIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Carpiodes carpio | N | N | N | N | N | N | N | N | N | | N | N | N | N | N | N | N | N | N | S | S | P | P | | X | X | | X | |
| Carpiodes cyprinus | N | N | | | | | U | N | | N | N | N | N | N | N | | | | N | S | S | P | M | | X | X | | X | |
| Carpiodes velifer | N | | U | N | N | | N | N | N | N | N | N | N | N | | | | | N | | P | P | | | | X | | X | |
| Catostomus catostomus | | | | | | | U | | | | | | | N | | N | N | N | | | | | M | P | | X | X | X | |
| Catostomus commersoni | | | | | N | N | N | N | | N | N | N | N | N | N | N | N | N | | | S | P | P | P | | X | X | X | |

TABLE ~~X~~ 4. Continued.

| SPECIES | DRAINAGE OCCURRENCE | | | | | | | | | | | | | | | | | | | ECOLOGY | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | RED | | ARKANSAS | | | | | | | MISSOURI | | | | | | | | | REGION | | | | | HABITAT | | | | |
| | Ouachita R. | Lower Red R. | Upper Red R. | Lower Arkansas R. | Middle Arkansas R. | Canadian R. | Upper Arkansas R. | White R. | St. Francis-Little Rs. | Meramec-Miss Tribs. | Lower Missouri R. | Chariton-Nishnabotna Rs | Kansas R. | Platte-Niobrara Rs. | Sioux-James Rs. | White-Lt. Missouri Rs. | Yellowstone R. | Upper Missouri R. | Mainstream Miss. R. | Coastal Plain | Interior Highlands | Central Lowlands | Great Plains | Rocky Mountains | Big River | Small River | Creek | Lake | Endemic |
| Catostomus platyrhynchus | | | | | | | | | | | | | | N | | N | N | N | | | | | M | P | | X | X | | |
| Cycleptus elongatus | N | N | N | N | N | | | N | | N | N | N | N | N | N | N | N | N | N | M | M | P | S | | X | | | X | |
| Erimyzon oblongus | N | N | | N | N | N | | N | N | N | | | | | | | | | N | S | P | M | | | | | X | | |
| Erimyzon sucetta | N | N | | | | | | N | N | N | | | | | | | | | | P | S | | | | | | X | X | |
| Hypentelium nigricans | N | | | N | N | | | N | N | N | N | | | | | | | | N | | P | | | | | X | X | | |
| Ictiobus bubalus | N | N | N | N | N | | N | N | N | N | N | N | N | N | N | N | N | N | N | P | | P | S | | X | X | | X | |
| Ictiobus cyprinellus | N | N | N | N | N | N | N | N | N | | N | N | N | N | N | N | N | N | N | P | | P | S | | X | X | | X | |
| Ictiobus niger | N | N | N | N | N | N | N | N | N | | N | N | N | N | N | | | | N | P | M | P | | | X | X | | | |
| Lagochila lacera | | | | | | | | N | | | | | | | | | | | | | S | | | | | X | | | |
| Minytrema melanops | N | N | | N | N | N | N | N | N | N | I | | | | | | | | | P | S | P | | | | X | X | X | |
| Moxostoma anisurum | | | | | | | | N | N | N | N | | | | | | | | N | | P | | | | X | X | | | |
| Moxostoma carinatum | N | N | | N | N | | N | N | N | N | N | | U | | N | | | | N | | P | M | | | | X | | | |
| Moxostoma duquesnei | N | N | | N | N | | | N | N | N | N | | | | | | | | | | P | | | | | X | | | |
| Moxostoma erythrurum | N | N | N | N | N | N | N | N | N | N | N | N | | | N | | | | | M | P | P | | | | X | X | | |
| Moxostoma macrolepidotum | | | I | | N | | N | N | N | N | N | N | N | N | N | N | N | N | N | M | P | P | P | | X | X | | | |
| Moxostoma poecilurum | N | N | | | | | | | | | | | | | | | | | | P | | | | | X | X | | X | |
| ICTALURIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Ictalurus catus | I | I | | I | | | | I | I | | | | | | | | | | | S | | | | | | X | | X | |
| Ictalurus furcatus | N | N | N | N | N | | | N | N | | N | N | N | N | | N | | | N | P | | P | | | X | | | X | |
| Ictalurus melas | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | I | I | N | P | S | P | P | | | X | X | X | |
| Ictalurus natalis | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | I | I | I | N | P | P | P | S | | | X | X | X | |
| Ictalurus nebulosus | U | U | | U | I | | | U | U | | I | I | I | I | I | | | | | M | M | M | | | | X | | X | |
| Ictalurus punctatus | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | P | S | P | P | | X | X | | X | |
| Noturus albater | | | | | | | | N | N | | | | | | | | | | | | P | | | | | X | | | X |
| Noturus eleutherus | N | N | | | | | | N | N | | | | | | | | | | N | M | P | | | | X | X | | | |
| Noturus exilis | | N | | N | N | | | N | N | N | N | N | N | | | | | | | | P | M | | | | X | X | | |

TABLE 4. Continued.

| | DRAINAGE OCCURRENCE | | | | | | | | | | | | | | | | | | | ECOLOGY | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | RED | | ARKANSAS | | | | | | | MISSOURI | | | | | | | | | REGION | | | | | HABITAT | | | | |
| SPECIES | Ouachita R. | Lower Red R. | Upper Red R. | Lower Arkansas R. | Middle Arkansas R. | Canadian R. | Upper Arkansas R. | White R. | St. Francis-Little Rs. | Meramec-Miss Tribs. | Lower Missouri R. | Chariton-Nishnabotna Rs | Kansas R. | Platte-Niobrara Rs. | Sioux-James Rs. | White-Lt. Missouri Rs. | Yellowstone R. | Upper Missouri R. | Mainstream Miss. R | Coastal Plain | Interior Highlands | Central Lowlands | Great Plains | Rocky Mountains | Big River | Small River | Creek | Lake | Endemic |
| Noturus flavater | | | | | | | | N | | | | | | | | | | | | | P | | | | | X | | | X |
| Noturus flavus | | | | | N | | | | | N | N | N | N | N | N | N | N | N | N | | M | P | P | | X | X | X | | |
| Noturus gyrinus | N | N | N | N | N | | | N | N | | N | N | N | N | N | | | | N | P | | P | | | | | X | X | |
| Noturus lachneri | N | | | | | | | | | | | | | | | | | | | | P | | | | | | X | | X |
| Noturus miurus | N | | | N | N | | | N | N | | | | | | | | | | | P | M | P | | | | X | X | X | |
| Noturus nocturnus | N | N | N | N | N | N | N | N | N | N | N | | | | | | | | | P | M | P | | | | X | X | | |
| Noturus phaeus | N | N | | | | | | | | | | | | | | | | | | P | | | | | | | X | | |
| Noturus placidus | | | | | N | | | | | | | | | | | | | | | | | P | | | | X | | | X |
| Noturus taylori | N | | | | | | | | | | | | | | | | | | | | P | | | | | | X | | X |
| Pylodictis olivaris | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | | | N | P | | P | M | | X | X | | | |
| AMBLYOPSIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Amblyopsis rosae | | | | | N | | | N | | | | | | | | | | | | | P | | | | | | | | X |
| Chologaster agassizi | | | | | | | | | N | | | | | | | | | | | M | | | | | | | | | |
| Typhlichthys subterraneus | | | | | | | | N | | | N | | | | | | | | | | P | | | | | | | | |
| APHREDODERIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Aphredoderus sayanus | N | N | | N | | | | N | N | | | | | | | | | | | P | M | | | | | X | X | X | |
| PERCOPSIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Percopsis omiscomaycus | | | | | | | | | | | N | N | | N | N | | | | N | | | P | | | | X | | X | |
| GADIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Lota lota | | | | | | | | | | | N | N | N | N | N | N | N | N | | | | S | P | M | X | | | X | |
| BELONIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Strongylura marina | | | | | | | | | | | | | | | | | | | A | S | | | | | | | | | |

TABLE 4. Continued.

| | DRAINAGE OCCURRENCE | | | | | | | | | | | | | | | | | | | ECOLOGY | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | RED | | ARKANSAS | | | | | | | MISSOURI | | | | | | | | | REGION | | | | | HABITAT | | | | |
| SPECIES | Ouachita R. | Lower Red R. | Upper Red R. | Lower Arkansas R. | Middle Arkansas R. | Canadian R. | Upper Arkansas R. | White R. | St. Francis-Little Rs. | Meramec-Miss Tribs. | Lower Missouri R. | Chariton-Nishnabotna Rs. | Kansas R. | Platte-Niobrara Rs. | Sioux-James Rs. | White-Lt. Missouri Rs. | Yellowstone R. | Upper Missouri R. | Mainstream Miss. R. | Coastal Plain | Interior Highlands | Central Lowlands | Great Plains | Rocky Mountains | Big River | Small River | Creek | Lake | Endemic |
| CYPRINODONTIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Cyprinodon rubrofluviatilis | | | N | | | I | | | | | | | | | | | | | | | | | P | | | X | X | | |
| Fundulus blairae | | N | | | | | | | | | | | | | | | | | | P | | | | | | X | X | X | |
| Fundulus catenatus | N | N | | | N | | | N | N | N | N | | | | | | | | N | | P | | | | | X | X | | |
| Fundulus chrysotus | N | N | | | | | | N | N | | | | | | | | | | | P | | | | | | X | X | X | |
| Fundulus diaphanus | | | | | | | | | | | | | | | N | | | | | | | M | | | | | X | X | |
| Fundulus dispar | N | | | | | | | N | N | | | | | | | | | | N | P | | | | | | | X | X | |
| Fundulus notatus | N | N | N | N | N | N | N | N | N | N | N | | | | | | | | N | P | | P | | | | X | X | X | |
| Fundulus olivaceus | N | N | | N | N | N | | N | N | N | N | | | | | | | | | P | P | M | | | | X | X | | |
| Fundulus sciadicus | | | | | N | | | | | | N | | I | N | N | N | | | | | P | P | P | | | | X | | X |
| Fundulus zebrinus | | | N | | | N | N | | | | N | N | N | N | | I | I | I | | | | P | P | | X | X | X | | |
| POECILIIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Gambusia affinis | N | N | N | N | N | N | I | N | N | I | I | I | I | | | | | | N | P | M | M | | | | | X | X | |
| Poecilia mexicana | | | | | | | | | | | | | | | | | | I | | | | | | S | | | | X | |
| Xiphophorus helleri | | | | | | | | | | | | | | | | | | I | | | | | | S | | | | X | |
| Xiphophorus variatus | | | | | | | | | | | | | | | | | | I | | | | | | S | | | | X | |
| ATHERINIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Labidesthes sicculus | N | N | N | N | N | N | N | N | N | N | N | | | | | | | | N | P | P | S | | | X | X | | X | |
| Menidia beryllina | N | N | N | N | I | I | I | | N | | I | | | | | | | | N | P | S | S | | | X | | | X | |
| GASTEROSTEIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Culaea inconstans | | | | | | U | U | | | | | | | N | N | N | N | N | | | | S | S | S | | | X | X | |

TABLE ~~1~~ 4. Continued.

| SPECIES | DRAINAGE OCCURRENCE | | | | | | | | | | | | | | | | | | ECOLOGY | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | RED | | ARKANSAS | | | | | | | MISSOURI | | | | | | | | REGION | | | | | HABITAT | | | | |
| | Ouachita R. | Lower Red R. | Upper Red R. | Lower Arkansas R. | Middle Arkansas R. | Canadian R. | Upper Arkansas R. | White R. | St. Francis-Little Rs. | Meramec-Miss Tribs. | Lower Missouri R. | Chariton-Nishnabotna Rs. | Kansas R. | Platte-Niobrara Rs. | Sioux-James Rs. | White-Lt. Missouri Rs. | Yellowstone R. | Upper Missouri R. | Mainstream Miss. R. | Coastal Plain | Interior Highlands | Central Lowlands | Great Plains | Rocky Mountains | Big River | Small River | Creek | Lake | Endemic |
| SYNGNATHIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Syngnathus scovelli | | | | | | | | | | | | | | | | | | | A | S | | | | | | | | | |
| PERCICHTHYIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Morone americana | | | | | | | | | | | | | | I | | | | | | | | S | | | | X | | X | |
| Morone chrysops | N | N | U | N | N | U | U | N | N | | N | N | U | I | U | I | | | N | P | S | S | S | | X | | | X | |
| Morone mississippiensis | N | N | | | I | | | N | N | | | I | | | I | | | | N | P | | | | | X | | | X | |
| Morone saxatilis | I | I | I | I | I | I | I | I | I | | I | | I | I | | | | | I | S | S | S | S | | | | | X | |
| CENTRARCHIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Ambloplites ariommus | N | N | | | | | | N | N | | | | | | | | | | | M | P | | | | | X | X | | |
| Ambloplites constellatus | | | | | | | | N | | | I | | | | | | | | | | P | | | | | X | X | | X |
| Ambloplites rupestris | | | | I | I | | | | | N | I | | | | N | I | I | | | | P | S | S | | | X | X | | |
| Centrarchus macropterus | N | N | | N | | | | N | N | | | | | | | | | | N | P | | | | | | X | X | X | |
| Elassoma zonatum | N | N | | N | | | | N | N | | | | | | | | | | N | P | | | | | | | X | X | |
| Lepomis auritus | I | I | | I | | | | I | I | | | | | | | | | | | P | S | | | | | X | | X | |
| Lepomis cyanellus | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | U | I | I | N | P | P | P | P | | X | X | X | X | |
| Lepomis gibbosus | | | | | | | | | | I | | I | I | I | U | I | I | I | | | S | S | S | S | | X | X | X | |
| Lepomis gulosus | N | N | N | N | N | N | U | N | N | N | N | | U | | | | | | N | P | S | P | | | | | X | X | |
| Lepomis humilis | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | | | N | M | S | P | P | | X | X | X | X | |
| Lepomis macrochirus | N | N | N | N | N | U | N | N | N | N | N | U | U | U | U | I | I | I | N | P | S | M | | | X | X | X | X | |
| Lepomis marginatus | N | N | | N | | | | N | N | | | | | | | | | | N | P | | | | | | | X | X | |
| Lepomis megalotis | N | N | N | N | N | N | N | N | N | N | N | | U | | | | | | N | M | P | P | S | | | X | X | X | |
| Lepomis microlophus | N | N | U | N | U | U | I | N | N | N | I | | I | I | | | | | N | P | S | M | S | | X | X | | X | |
| Lepomis punctatus | N | N | | | I | I | | N | N | | | | | | | | | | N | P | | M | | | | X | | X | |
| Lepomis symmetricus | N | N | | N | | | | N | N | | | | | | | | | | N | P | | | | | | | | X | |

TABLE 4. Continued.

| | DRAINAGE OCCURRENCE | | | | | | | | | | | | | | | | | | | ECOLOGY | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | RED | | | ARKANSAS | | | | | | | MISSOURI | | | | | | | | | REGION | | | | | HABITAT | | | | |
| SPECIES | Ouachita R. | Lower Red R. | Upper Red R. | Lower Arkansas R. | Middle Arkansas R. | Canadian R. | Upper Arkansas R. | White R. | St. Francis-Little Rs. | Meramec-Miss Tribs. | Lower Missouri R. | Chariton-Nishnabotna Rs | Kansas R. | Platte-Niobrara Rs. | Sioux-James Rs. | White-Lt. Missouri Rs | Yellowstone R. | Upper Missouri R. | Mainstream Miss. R. | Coastal Plain | Interior Highlands | Central Lowlands | Great Plains | Rocky Mountains | Big River | Small River | Creek | Lake | Endemic |
| Micropterus coosae | | | | | | | | I | | | | | | | | | | | | | | S | | | | | | X | |
| Micropterus dolomieui | N | N | | N | N | | | N | N | N | N | | I | I | U | I | I | I | | | P | | | | | X | X | X | |
| Micropterus punctulatus | N | N | N | N | N | N | N | N | N | | I | I | | | | | | | N | M | P | M | | | | X | X | X | |
| Micropterus salmoides | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | I | I | I | N | P | P | P | S | | X | X | X | X | |
| Pomoxis annularis | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | I | I | I | N | P | S | P | S | | X | X | | X | |
| Pomoxis nigromaculatus | N | N | I | N | N | I | I | N | N | N | N | I | I | I | N | I | I | I | N | P | S | P | S | | X | X | | X | |
| PERCIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Ammocrypta asprella | N | N | | | | | | N | N | N | N | | | | | | | | | P | M | | | | X | X | | | |
| Ammocrypta clara | N | N | | | | | | N | N | | | | | | | | | | N | P | | | | | X | X | | | |
| Ammocrypta vivax | N | N | | N | | | | N | N | | | | | | | | | | | P | M | | | | X | X | | | |
| Etheostoma asprigene | N | N | | N | | | | N | N | N | | | | | | | | | N | P | | | | | X | | | X | |
| Etheostoma blennioides | N | | | N | N | | | N | N | N | N | | | | | | | | | | P | M | | | | X | X | | |
| Etheostoma caeruleum | | | | | I | | | N | N | N | N | | | | | | | | | | P | | | | | X | X | | |
| Etheostoma chlorosomum | N | N | | N | N | N | | N | N | | N | | | | | | | | N | P | | M | | | | | X | X | |
| Etheostoma collettei | N | N | | | | | | | | | | | | | | | | | | P | P | | | | | | X | | |
| Etheostoma cragini | | | | | N | | N | | | | | | | | | | | | | | M | S | S | | | | X | | X |
| Etheostoma euzonum | | | | | | | | N | | | | | | | | | | | | | P | | | | | X | | | X |
| Etheostoma exile | | | | | | | | | | | | | | N | N | N | N | N | | | | P | P | | | X | | X | |
| Etheostoma flabellare | | | | N | N | | | N | N | N | N | | | | | | | | | | P | M | | | | X | X | | |
| Etheostoma fusiforme | N | N | | | | | | | N | | | | | | | | | | | P | S | | | | | X | | X | |
| Etheostoma gracile | N | N | N | N | N | N | N | N | N | | N | | | | | | | | N | P | S | M | | | | | | X | |
| Etheostoma histrio | N | N | | N | | | | N | N | | | | | | | | | | | P | M | | | | | X | X | | |
| Etheostoma juliae | | | | | | | | N | | | | | | | | | | | | | P | | | | | X | | | X |
| Etheostoma microperca | | N | | | N | | | | | N | N | | | | | | | | | | S | S | | | | | X | X | |
| Etheostoma moorei | | | | | | | | N | | | | | | | | | | | | | P | | | | | X | X | | X |
| Etheostoma nianguae | | | | | | | | | | | N | | | | | | | | | | P | | | | | X | X | | X |

TABLE 4. Continued.

| SPECIES | DRAINAGE OCCURRENCE | | | | | | | | | | | | | | | | | | | ECOLOGY | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | RED | | ARKANSAS | | | | | | | MISSOURI | | | | | | | | | REGION | | | | | HABITAT | | | | |
| | Ouachita R. | Lower Red R. | Upper Red R. | Lower Arkansas R. | Middle Arkansas R. | Canadian R. | Upper Arkansas R. | White R. | St. Francis-Little Rs | Meramec-Miss Tribs. | Lower Missouri R. | Chariton-Nishnabotna Rs | Kansas R. | Platte-Niobrara Rs. | Sioux-James Rs. | White-Lt. Missouri Rs. | Yellowstone R. | Upper Missouri R. | Mainstream Miss. R. | Coastal Plain | Interior Highlands | Central Lowlands | Great Plains | Rocky Mountains | Big River | Small River | Creek | Lake | Endemic |
| Etheostoma nigrum | N | N | | N | N | | | N | N | N | N | N | N | N | N | | | | N | | M | P | S | | | X | X | | |
| Etheostoma pallididorsum | N | | | | | | | | | | | | | | | | | | | | P | | | | | | X | | X |
| Etheostoma parvipinne | N | N | | N | | | | N | N | | | | | | | | | | | P | | | | | | | X | | |
| Etheostoma proeliare | U | N | U | N | | N | | N | N | | | | | | | | | | N | P | M | M | | | | | X | X | |
| Etheostoma punctulatum | | | | | N | | | N | N | | N | | | | | | | | | | P | | | | | | X | X | X |
| Etheostoma radiosum | N | N | | | | | | | | | | | | | | | | | | | P | M | | | | X | X | | X |
| Etheostoma spectabile | | N | N | N | N | N | N | N | N | N | N | N | N | N | | | | | | | P | P | S | | | X | X | | |
| Etheostoma stigmaeum | N | N | | N | N | | | N | N | | | | | | | | | | | | P | | | | | X | X | | |
| Etheostoma tetrazonum | | | | | | | | | | N | N | | | | | | | | | | P | | | | | X | X | | X |
| Etheostoma whipplei | N | N | | N | N | N | | N | | | | | | | | | | | | | P | P | | | | X | X | | |
| Etheostoma zonale | N | | | N | N | | | N | N | N | N | | | | | | | | | | P | | | | | X | X | | |
| Perca flavescens | | | | | | | | | | | | | I | I | N | I | I | I | N | | | P | P | | | | | X | |
| Percina caprodes | N | N | N | N | N | N | N | N | N | N | N | | N | | N | | | | | | P | P | | | | X | X | X | |
| Percina copelandi | N | N | | N | N | | N | | | | | | | | | | | | | M | P | P | | | X | X | | | |
| Percina cymatotaenia | | | | | | | | | | | N | | | | | | | | | | P | | | | | X | X | | X |
| Percina evides | | | | | | | | N | N | N | N | | | | | | | | | | P | | | | | X | | | |
| Percina macrolepida | | N | N | | | | | | | | | | | | | | | | | S | | P | | | | X | | X | |
| Percina maculata | N | N | | N | N | | | N | N | | N | N | N | N | N | | | | | M | M | P | | | | X | X | | |
| Percina nasuta | N | | | N | N | | | N | N | | | | | | | | | | | | P | | | | | X | | | X |
| Percina ouachitae | N | | | | | | | N | N | | | | | | | | | | | P | M | | | | X | X | | | |
| Percina pantherina | | N | | | | | | | | | | | | | | | | | | | P | | | | | X | | | X |
| Percina phoxocephala | | N | | N | N | | N | | | N | N | | | | | | | | | | M | P | | | | X | | | |
| Percina sciera | N | N | N | N | N | | | N | N | | | | | | | | | | | P | M | M | | | X | X | | | |
| Percina shumardi | N | N | | N | N | | | N | N | | | | | | | | | | N | P | | S | | | X | | | | |
| Percina uranidea | N | | | | | | | N | N | | | | | | | | | | | P | M | | | | X | X | | | |
| Stizostedion canadense | N | N | | N | N | | | N | N | N | N | N | N | N | N | N | N | N | N | | M | P | P | | X | X | | X | |
| Stizostedion vitreum | I | I | I | I | U | I | I | U | U | N | U | U | U | U | N | N | I | I | N | | P | P | P | | X | X | | X | |

TABLE ~~1~~ 4. Continued.

| | DRAINAGE OCCURRENCE | | | | | | | | | | | | | | | | | | | ECOLOGY | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | RED | | ARKANSAS | | | | | | | MISSOURI | | | | | | | | | REGION | | | | | HABITAT | | | | |
| SPECIES | Ouachita R. | Lower Red R. | Upper Red R. | Lower Arkansas R. | Middle Arkansas R. | Canadian R. | Upper Arkansas R. | White R. | St. Francis-Little Rs. | Meramec-Miss Tribs. | Lower Missouri R. | Chariton-Nishnabotna Rs | Kansas R. | Platte-Niobrara Rs. | Sioux-James Rs. | White-Lt. Missouri Rs. | Yellowstone R. | Upper Missouri R. | Mainstream Miss. R | Coastal Plain | Interior Highlands | Central Lowlands | Great Plains | Rocky Mountains | Big River | Small River | Creek | Lake | Endemic |
| SCIAENIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Aplodinotus grunniens | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | N | P | | P | M | | X | X | | X | |
| MUGILIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Mugil cephalus | | | | A | | | | | | | | | | | | | | | A | S | | | | | | | | | |
| COTTIDAE | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Cottus bairdi | | | | | | | | N | N | N | N | | | | | | | | | | P | | | | | X | X | | |
| Cottus carolinae | | | | | N | | | N | N | N | N | | | | | | | | | | P | | | | | X | X | | |

TABLE 5. Matrices of Numbers of shared Species and Similarities of Species Composition (expressed as percent) Among Selected Drainages, Physiographic Regions, Habitats and Endemic Species in the Western Mississippi River Basin. Only native species (N) are used in comparisons and ~~between drainages and prevalent (P) distributions in Physiographic Regions are used~~ in calculations. Upper right triangular matrix is number of shared species, lower left matrix is percent similarity, and diagonal is number of native species ~~or prevelant taxa~~ in ~~that catagory~~ the drainage unit.

| DRAINAGES | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 Ouachita R. | 133 | 118 | 45 | 104 | 83 | 47 | 47 | 116 | 110 | 61 | 69 | 43 | 42 | 38 | 36 | 20 | 12 | 12 | 87 | 109 | 96 | 87 | 35 | 2 | 60 | 98 | 67 | 68 | 10 |
| 2 Lower Red R. | 89 | 133 | 52 | 104 | 84 | 51 | 51 | 109 | 103 | 62 | 71 | 47 | 46 | 41 | 38 | 24 | 14 | 13 | 87 | 109 | 92 | 94 | 41 | 4 | 62 | 99 | 65 | 67 | 9 |
| 3 Upper Red R. | 57 | 66 | 56 | 48 | 48 | 41 | 43 | 44 | 43 | 34 | 44 | 35 | 35 | 33 | 30 | 20 | 11 | 11 | 46 | 46 | 37 | 55 | 33 | 3 | 35 | 46 | 26 | 33 | 1 |
| 4 Lower Arkansas R. | 84 | 84 | 63 | 117 | 91 | 51 | 53 | 105 | 100 | 63 | 73 | 47 | 45 | 41 | 37 | 23 | 13 | 13 | 83 | 92 | 86 | 90 | 40 | 3 | 55 | 90 | 57 | 59 | 6 |
| 5 Middle Arkansas R. | 69 | 69 | 64 | 80 | 111 | 52 | 60 | 92 | 82 | 69 | 85 | 51 | 52 | 46 | 45 | 28 | 18 | 17 | 69 | 67 | 90 | 95 | 45 | 6 | 45 | 87 | 63 | 47 | 12 |
| 6 Canadian R. | 58 | 63 | 72 | 66 | 68 | 58 | 48 | 47 | 44 | 37 | 44 | 34 | 34 | 33 | 29 | 21 | 14 | 13 | 44 | 44 | 43 | 55 | 33 | 8 | 28 | 46 | 36 | 31 | 2 |
| 7 Upper Arkansas R. | 54 | 59 | 72 | 64 | 74 | 79 | 64 | 48 | 45 | 42 | 53 | 41 | 42 | 40 | 36 | 24 | 17 | 16 | 47 | 43 | 46 | 62 | 40 | 8 | 35 | 56 | 34 | 32 | 3 |
| 8 White R. | 82 | 77 | 54 | 80 | 72 | 56 | 54 | 150 | 130 | 78 | 85 | 45 | 46 | 40 | 39 | 21 | 14 | 14 | 88 | 99 | 118 | 88 | 38 | 4 | 59 | 116 | 74 | 64 | 14 |
| 9 St. Francis-Little Rs. | 81 | 76 | 54 | 79 | 66 | 54 | 51 | 90 | 139 | 76 | 78 | 41 | 42 | 37 | 35 | 19 | 10 | 10 | 86 | 99 | 104 | 83 | 34 | 4 | 57 | 106 | 70 | 64 | 8 |
| 10 Meramec-Miss. Tribs. | 56 | 57 | 49 | 61 | 69 | 52 | 56 | 68 | 69 | 92 | 78 | 38 | 40 | 35 | 39 | 22 | 12 | 11 | 58 | 49 | 83 | 68 | 39 | 6 | 37 | 82 | 56 | 39 | 3 |
| 11 Lower Missouri R. | 56 | 58 | 59 | 63 | 76 | 57 | 65 | 66 | 62 | 77 | 114 | 65 | 65 | 62 | 54 | 37 | 24 | 23 | 75 | 60 | 89 | 91 | 57 | 8 | 53 | 91 | 63 | 46 | 10 |
| 12 Chariton-Nishnabotna Rs. | 49 | 53 | 58 | 56 | 62 | 55 | 63 | 49 | 46 | 49 | 78 | 66 | 62 | 59 | 48 | 37 | 25 | 24 | 56 | 43 | 42 | 66 | 52 | 7 | 47 | 50 | 28 | 31 | 3 |
| 13 Kansas R. | 48 | 52 | 58 | 53 | 63 | 55 | 65 | 50 | 47 | 52 | 78 | 94 | 66 | 59 | 49 | 37 | 25 | 24 | 53 | 40 | 43 | 66 | 52 | 8 | 45 | 50 | 31 | 29 | 3 |
| 14 Platte-Niobrara Rs. | 39 | 42 | 51 | 44 | 51 | 50 | 58 | 40 | 38 | 42 | 68 | 84 | 84 | 76 | 55 | 49 | 34 | 34 | 54 | 39 | 40 | 70 | 66 | 15 | 45 | 52 | 39 | 39 | 4 |
| 15 Sioux & James Rs. | 41 | 43 | 50 | 44 | 54 | 47 | 55 | 43 | 39 | 51 | 65 | 73 | 74 | 78 | 66 | 37 | 24 | 23 | 48 | 34 | 42 | 66 | 55 | 10 | 37 | 47 | 34 | 38 | 2 |
| 16 White-Little Missouri Rs. | 28 | 33 | 38 | 33 | 41 | 39 | 43 | 28 | 26 | 34 | 53 | 65 | 65 | 81 | 65 | 50 | 33 | 33 | 35 | 24 | 22 | 45 | 48 | 14 | 33 | 33 | 24 | 25 | 4 |
| 17 Yellowstone R. | 22 | 25 | 26 | 24 | 34 | 32 | 38 | 25 | 18 | 24 | 45 | 55 | 55 | 71 | 52 | 80 | 35 | 33 | 22 | 13 | 13 | 29 | 33 | 13 | 22 | 23 | 16 | 19 | 3 |
| 18 Upper Missouri Rs. | 21 | 23 | 25 | 24 | 31 | 29 | 35 | 24 | 17 | 21 | 42 | 52 | 52 | 70 | 49 | 79 | 93 | 36 | 21 | 13 | 12 | 28 | 33 | 13 | 22 | 24 | 16 | 21 | 3 |
| 19 Mainstream Miss. R. | 71 | 71 | 61 | 72 | 62 | 57 | 58 | 68 | 69 | 57 | 66 | 67 | 64 | 59 | 58 | 50 | 41 | 38 | 113 | 86 | 68 | 91 | 52 | 5 | 73 | 76 | 41 | 64 | 3 |
| 20 Coastal Plain | 84 | 84 | 52 | 76 | 55 | 50 | 45 | 73 | 75 | 46 | 49 | 46 | 41 | 39 | 38 | 28 | 18 | 19 | 73 | 122 | 75 | 83 | 37 | 3 | 66 | 83 | 51 | 64 | 5 |
| 21 Interior Highlands | 67 | 64 | 39 | 65 | 67 | 45 | 45 | 78 | 71 | 72 | 65 | 42 | 41 | 37 | 43 | 24 | 17 | 16 | 53 | 56 | 150 | 92 | 42 | 6 | 50 | 120 | 86 | 50 | 27 |
| 22 Central Lowlands | 63 | 68 | 60 | 70 | 73 | 60 | 62 | 60 | 59 | 61 | 69 | 68 | 64 | 67 | 70 | 50 | 39 | 39 | 73 | 64 | 64 | 139 | 71 | 10 | 66 | 98 | 69 | 67 | 13 |
| 23 Great Plains | 36 | 41 | 45 | 43 | 48 | 45 | 52 | 37 | 34 | 46 | 60 | 68 | 65 | 82 | 74 | 68 | 54 | 55 | 57 | 39 | 41 | 72 | 77 | 14 | 44 | 56 | 40 | 40 | 7 |
| 24 Rocky Mountains | 6 | 13 | 11 | 10 | 19 | 28 | 27 | 12 | 13 | 20 | 25 | 24 | 27 | 51 | 35 | 49 | 49 | 49 | 16 | 10 | 19 | 31 | 48 | 18 | 4 | 11 | 17 | 9 | 0 |
| 25 Big R. | 58 | 59 | 46 | 56 | 45 | 37 | 43 | 54 | 54 | 42 | 53 | 59 | 54 | 54 | 48 | 45 | 35 | 36 | 76 | 66 | 46 | 63 | 55 | 13 | 84 | 60 | 12 | 39 | 4 |
| 26 Small R. | 65 | 66 | 47 | 65 | 62 | 47 | 53 | 73 | 69 | 68 | 64 | 48 | 46 | 47 | 47 | 35 | 30 | 32 | 57 | 59 | 76 | 65 | 53 | 34 | 54 | 166 | 89 | 57 | 26 |
| 27 Creek | 52 | 50 | 29 | 47 | 52 | 41 | 36 | 55 | 53 | 53 | 51 | 30 | 32 | 39 | 38 | 28 | 23 | 23 | 35 | 42 | 64 | 53 | 42 | 54 | 12 | 63 | 122 | 47 | 18 |
| 28 Lake | 62 | 61 | 42 | 57 | 45 | 39 | 38 | 56 | 58 | 42 | 44 | 38 | 34 | 45 | 47 | 33 | 29 | 33 | 63 | 61 | 44 | 61 | 48 | 30 | 45 | 48 | 45 | 91 | 2 |
| 29 Endemic | 18 | 16 | 2 | 11 | 23 | 4 | 6 | 25 | 15 | 6 | 19 | 6 | 6 | 8 | 4 | 9 | 7 | 7 | 6 | 9 | 49 | 24 | 15 | 0 | 8 | 46 | 34 | 4 | 34 |

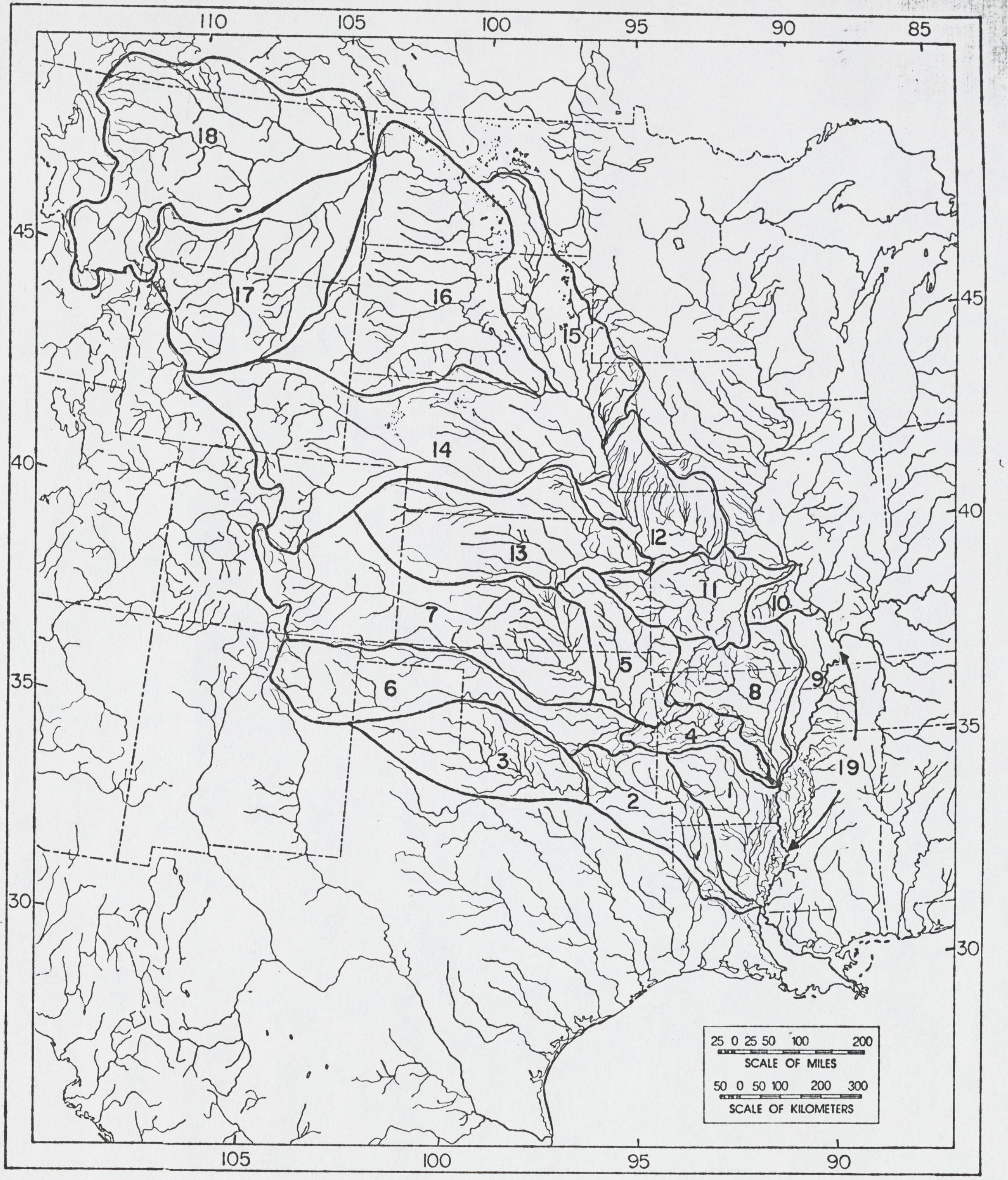


Figure 1. Cross _et_ _al_.

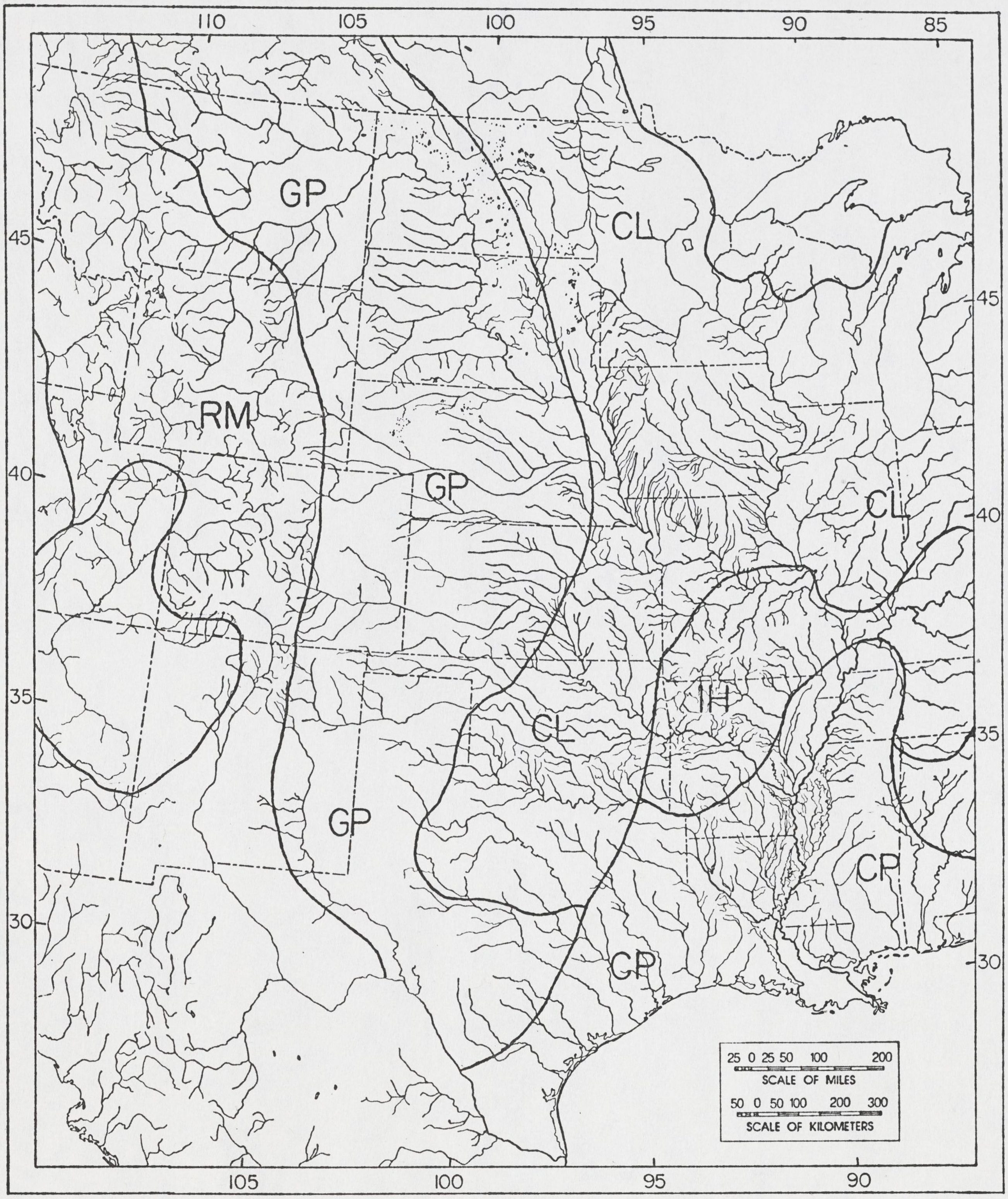


Figure 2. Cross *et al*.

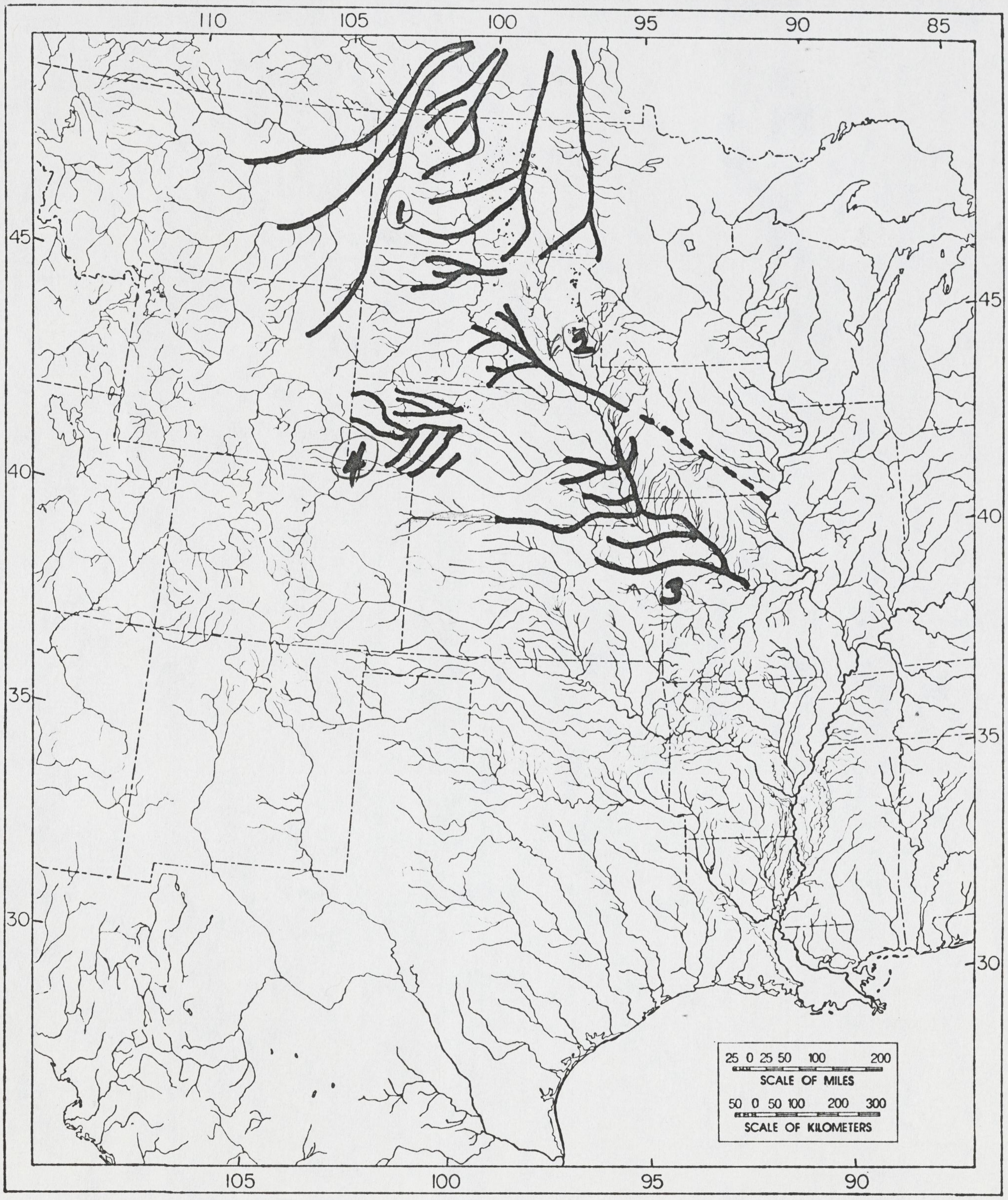

110
105
100
95
90
85
45
40
35
30
1
2
3
4
25 0 25 50 100 200
SCALE OF MILES
50 0 50 100 200 300
SCALE OF KILOMETERS

Fig 3A

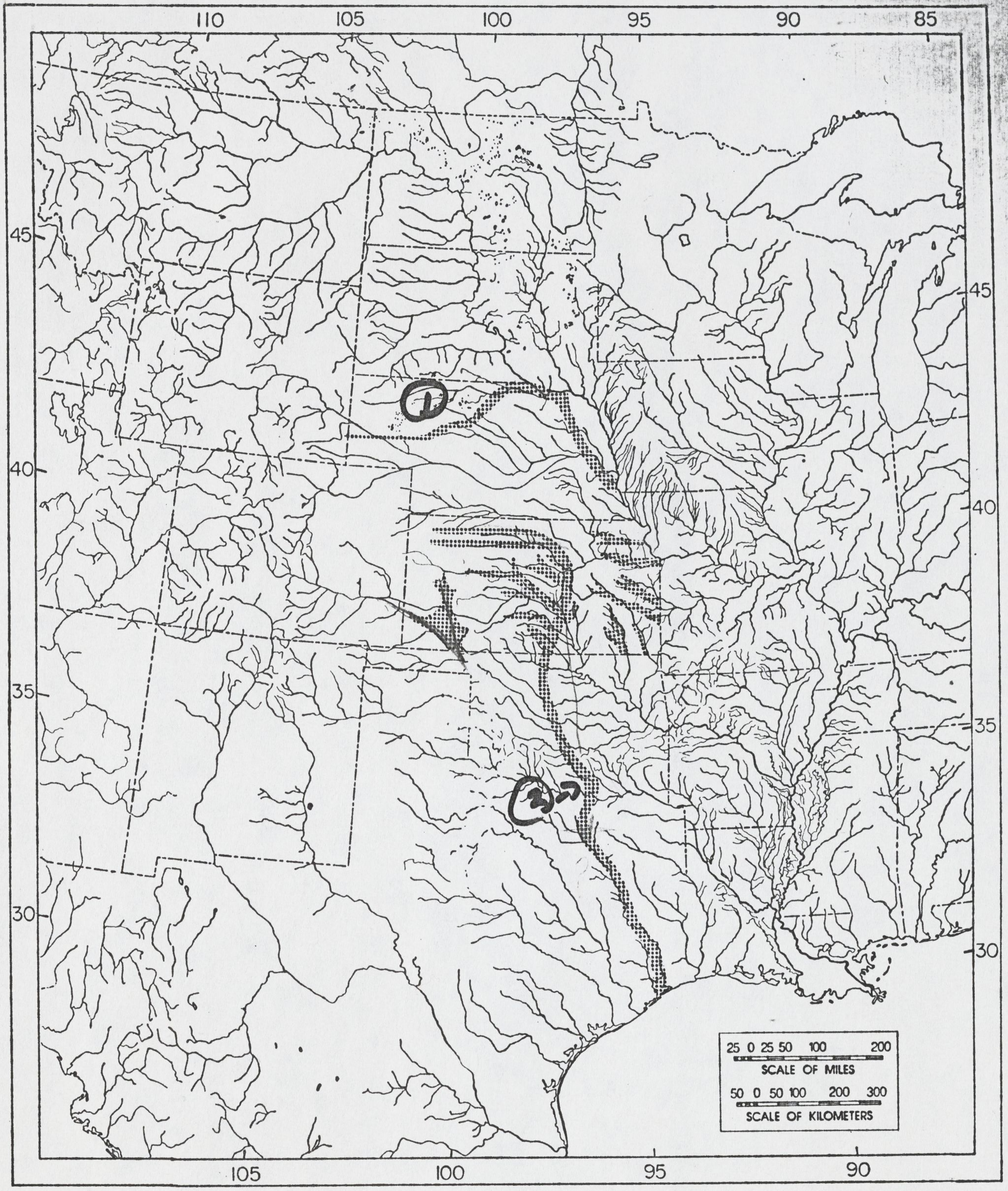
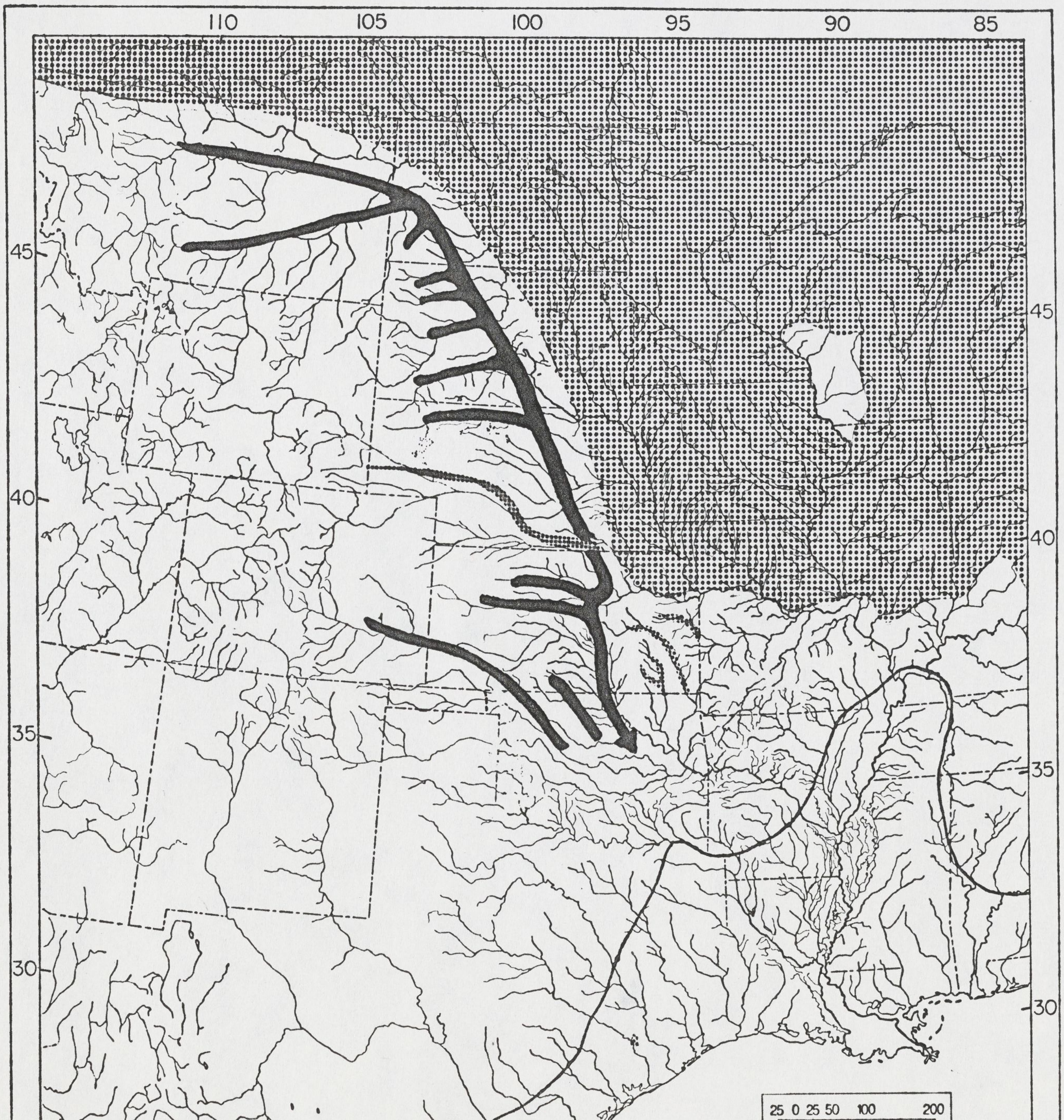


Figure 3B. Cross et al.

Figure 3C. Cross et al.



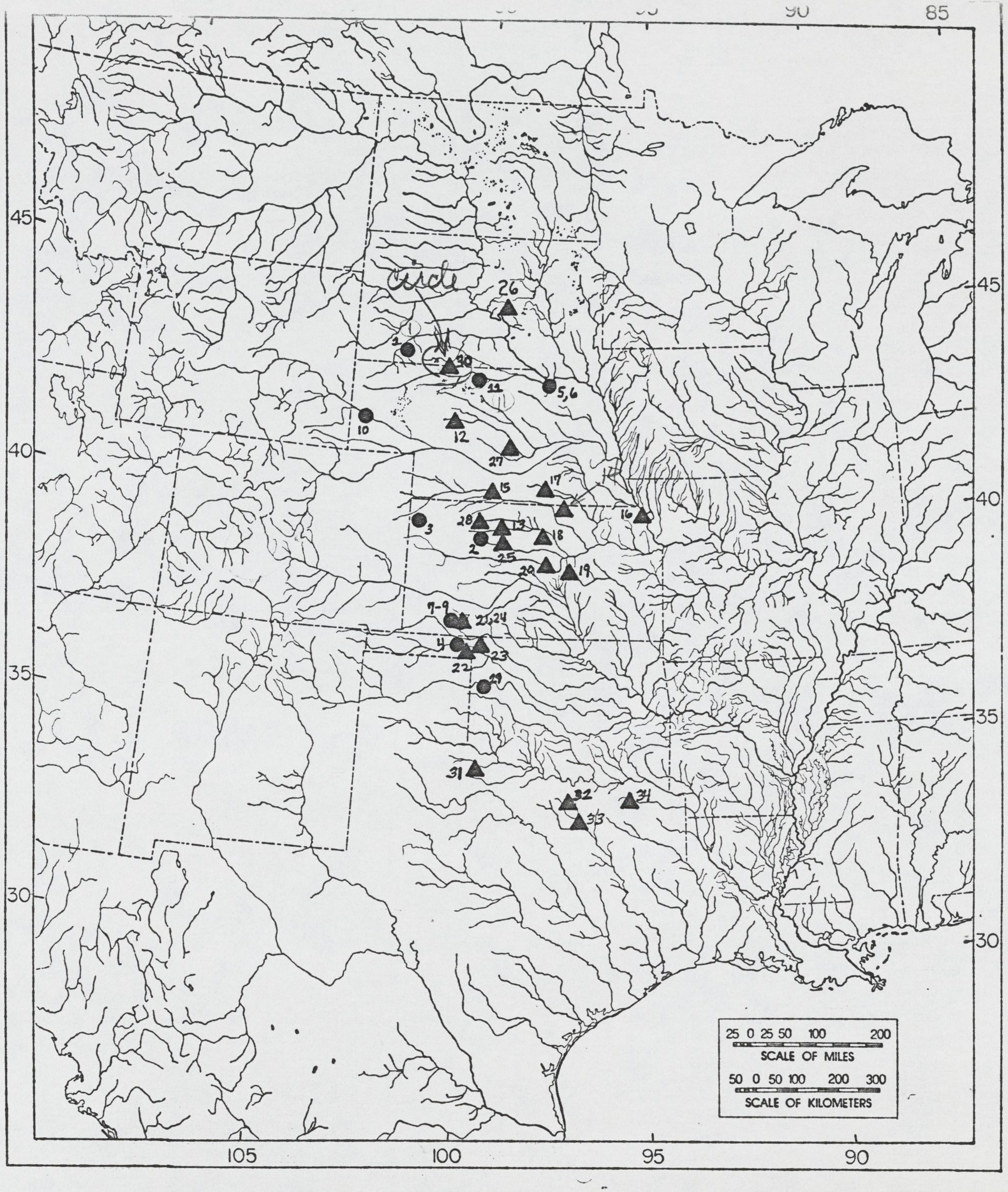
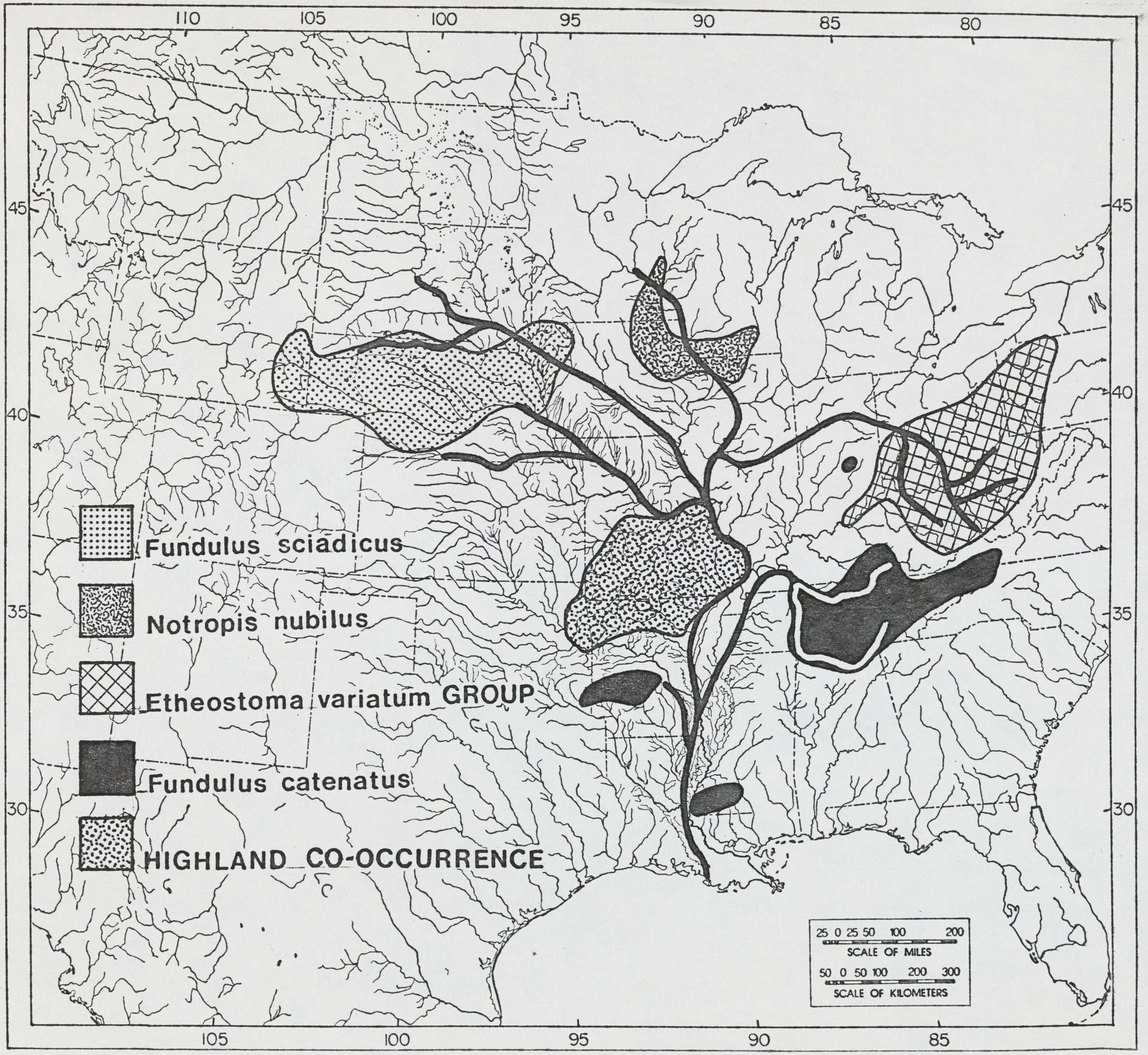


Figure 4. Cross *et al*.

Figure 5. Cross et al.



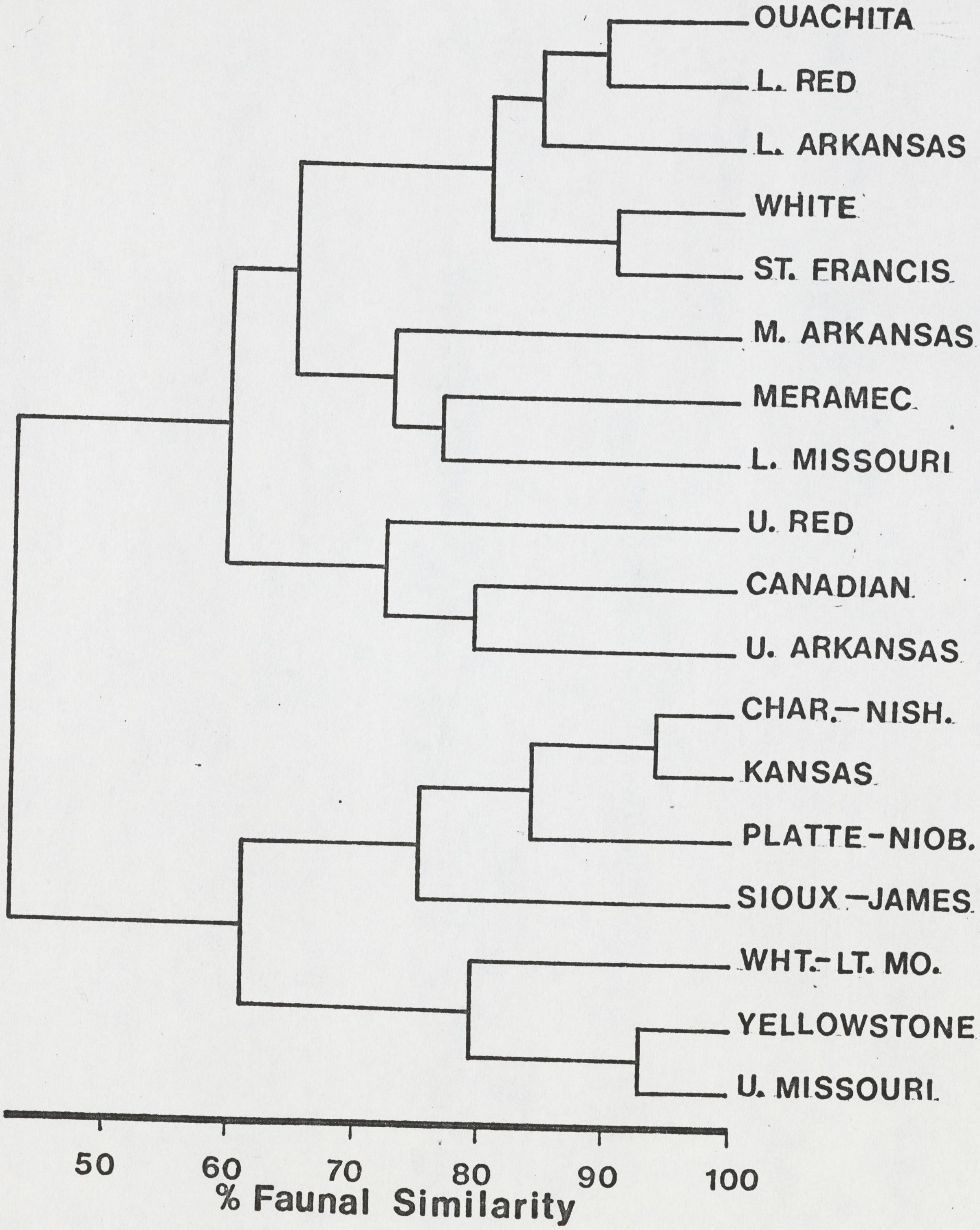


Figure 6. Cross et al.

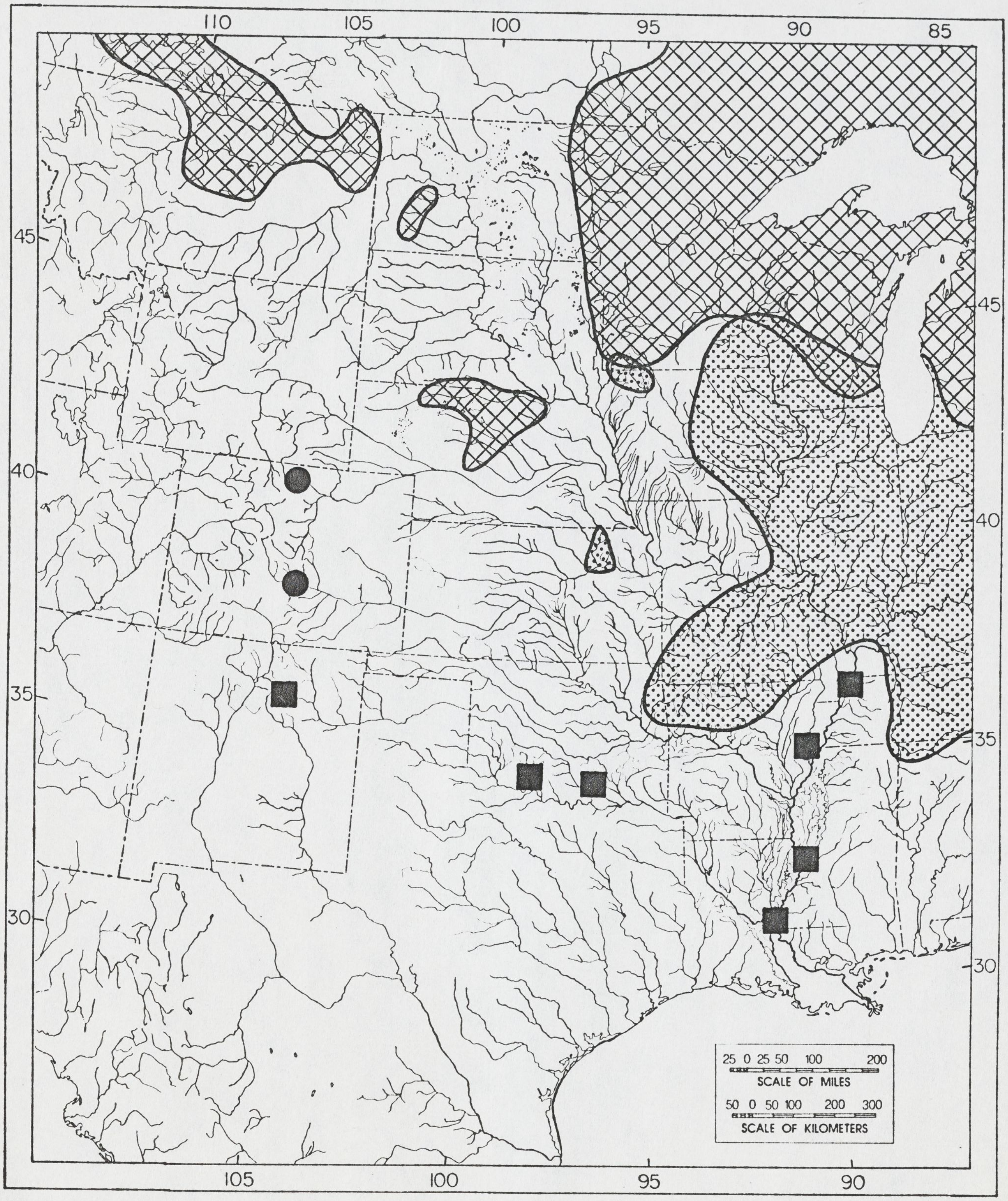


Figure 7. Cross _et_ _al_.

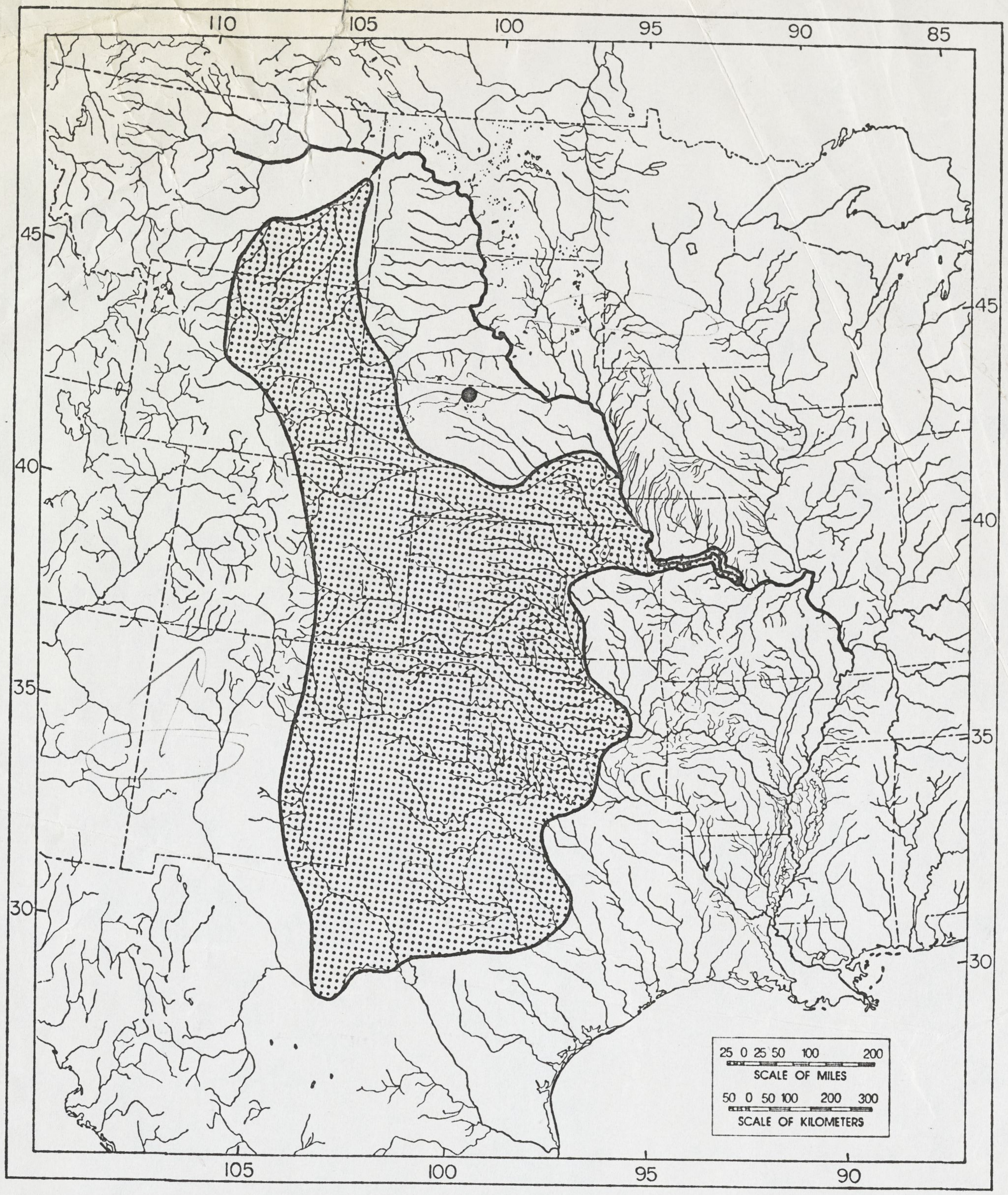


Figure 8. Cross et al.