

# FISHES OF A PLEISTOCENE LAKE IN SOUTH DAKOTA

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EAST LANSING

1973

PUBLICATIONS OF THE MUSEUM — MICHIGAN STATE UNIVERSITY

PALEONTOLOGICAL SERIES

Editorial Committee: Robert L. Anstey (Invertebrate Paleontology),  
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Cover Design by Dirk Gringhuis

Volume 1, Number 3, pp. 101-124, 4 plates, 1 figure in text

Published 20 December 1973

Price \$1.50

PUBLICATIONS OF THE MUSEUM, MICHIGAN STATE UNIVERSITY, PALEONTOLOGICAL SERIES, are issued at irregular intervals. Institutional libraries that wish to obtain copies of this series on an exchange basis should address the Exchange Librarian, Michigan State University Library, East Lansing, Michigan 48824. Individuals having a professional interest in the field of study to which this number pertains may obtain copies by addressing The Museum, Michigan State University, East Lansing, Michigan 48824, U.S.A.

PRINTED BY

LithoCrafters  
Ann Arbor, Michigan

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## ABSTRACT<sup>1</sup>

Pleistocene sediments (previously believed to be Oligocene) of the Cary-Mankato lake beds in Hand County, South Dakota, were examined and sampled paleontologically. Fossil fishes and geologic data were collected by the author during the summers of 1966 and 1969. The extent, thickness and stratigraphic relationships of the deposits were determined by geologic mapping and aerial observation.

Paleoecological analysis based on palynological evidence and fish faunal requirements indicate that the region resembled the **modern** high prairies in the area. Certain plant fossils suggest that the climate was more moist and slightly cooler than at present.

Evidence was collected which supports the premise that major portions of the modern upper Great Plains fish fauna were derived from the Mississippi River drainage, rather than the present Missouri River connections. The fossils recovered provide geographic range extensions for several species and the first fossil records for *Noturus* cf. *hildebrandi*, *Etheostoma exile*, *Percina* cf. *copelandi*, *Lepomis gibbosus* and *Lepomis macrochirus*.

## Introduction

Fossils were first reported at the Ree Heights locality by Cope (1891) and these remains sparked a controversy over the age of the deposit that has persisted to the present. The original fossils were described as Oligocene in age, but they had not been thoroughly investigated by modern workers, although sporadic trips had been made to the site by various workers. New interest developed after my field party collected several unreported species in 1966. More specimens were excavated in 1969 and provided ecological data that aided in the analysis of the fossil site.

This paper represents a revision of the fossil fish fauna of Ree Heights, South Dakota, as it relates to paleoecological and zoogeographical interpretations, and to the age and stratigraphy of the site.

### PREVIOUS WORK

The site was first reported in a mining claim filed in 1882 by Edwin Putnam. This claim (called the Ree Heights Chalk Stone Lode) was intended to provide matrix for lime burning, but the business failed and the claim was refiled in 1884 by two other parties. A third and final mining claim was filed in 1885 on the site, specifying a placer mining operation. This also failed and since that time the land has been utilized for the grazing of cattle.

In 1891, Edward D. Cope published an account of some fossil fishes sent to him from the Ree

Heights site by two local clergymen. Cope was unable to visit the site, and was misled into describing its age as Oligocene. This mistake was probably responsible for many of the inaccuracies in the nomenclature of his fossil species reported from the locality. His type materials are preserved in the American Museum of Natural History, New York, New York.

Correspondence preserved at the University of Nebraska State Museum, Lincoln, Nebraska, shows that the next collector at the site was A. G. Tagg of Highmore, South Dakota. He was hired in 1931 by E. H. Barbour (then Director, University of Nebraska State Museum) to collect samples. Later that summer Barbour also sent a party under C. Bertrand Schultz to Ree Heights. This resulted in a collection of approximately one hundred fishes. The collection was sent to W. K. Gregory (American Museum of Natural History) for identification in 1933 and assigned to an assistant, Anthony Q. Keasby. No report of this work survives (Bobb Schaeffer, American Museum of Natural History, *in litt.*) and the collection was returned to Nebraska in 1939 after Gregory left the American Museum.

David H. Dunkle visited the site in 1948 while in the field for the United States National Museum and made a small collection of fishes. He recognized that the site was not Oligocene, but was undecided about the correct assignment. At Dunkle's suggestion, Morris F. Skinner (American Museum of Natural History) visited the site in 1954 (Skinner, *in litt.*). Uyeno and Miller (1963) reported Skinner's conclusion that the site was Pleistocene. J. C. Hark-

<sup>1</sup>Contribution, in part, from the Department of Geology, Michigan State University.

sen (Associate Geologist of the South Dakota Geological Survey) also visited the site and concurred with Skinner's findings (Harksen, *in litt.*).

### MATERIALS AND METHODS

The fossil remains from Ree Heights are well preserved, abundant and provide much information about the ecology of the site. It is difficult to estimate the total number of fishes in the collections at hand, as the earlier collectors made no attempt to keep part and counterpart of individual fishes together. There are 521 identifiable fishes (268 identifiable to species and an additional 253 identifiable to genus only). Other vertebrates consist of eight frogs (*Rana cf. pipiens*) and a turtle that was destroyed in a house fire at the Leonard Fawcett ranch, Ree Heights, South Dakota. Badly crushed gastropods were occasionally observed, but few were collected. Several plant megafossils were recovered, but most of the botanical evidence came from diatoms, pollen and spores.

Special techniques were necessary to prepare the fishes for study. The matrix is a fine-grained, evenly bedded diatomite. The fossil fishes are generally preserved in lifelike positions with many fine details retained. The diatomite is very soft when freshly quarried and can be removed in blocks and split with a knife blade. Slabs with fossils were dried at the site and hardened with a mixture of white shellac and denatured ethyl alcohol (one part shellac to eight parts alcohol). This mixture penetrates well and does not warp the laminae when it dries.

The fossils were prepared for study with a needle, artist's brush and water. The techniques were modified for those specimens with only broken bones exposed. These fossils were coated with a water-soluble casein glue, embedded bone side down in a block of plaster of Paris, and the matrix removed normally from the back side of the slab. This technique exposed unbroken surfaces of previously undeterminable bones, allowing the identification of otherwise useless specimens. All diagnostic bones were coated with Alvar, a synthetic resin solution. Alvar tends to warp the laminae when dry and was not used to cover large areas of the matrix.

A basic part of the problem was the preparation of a representative comparative osteological collection. Most of the Ree Heights fishes are referable to modern species and must be identified by comparison with modern skeletal materials. Available collections of reference osteological materials are scarce and generally encompass only a few of the species in any given family. During the course of

this study, skeletons of more than 1200 fishes were prepared.

These skeletons were prepared by maceration in water, use of dermestid beetle colonies and especially by degrading the tissues with laundry enzyme "pre-soakers" (Ossian, 1970).

Terminology of the fish bones follows Harrington (1955). The phylogenetic arrangement of families, genera and species follows Moore (1957) whose treatment is a modification of Berg (1947). Plane table maps were prepared in the area of study to

TABLE I. Vertical Section in the Fossil Quarry

Depth from Top of Section (in cm)	Description
700	Mankato boulder-tills capping the lake beds and forming the tops of the Ree Hills at the site
731	Coarse gravel and sharp sand. Shows slight cross-bedding, but lacks fossils.
739	Clay layer with patches of fine sand, no fossils.
786	Poorly bedded diatomite, no fossils.
812	Coarse, cross-bedded sand with occasional pebbles. Contains lenses of sand and clay with fragments of diatomite buried at random angles in the matrix (fragments up to 38 cm. long), no fossils.
831	Poorly bedded, powdery diatomite, no fossils.
854	Weathered limonitic material, no fossils.
870	Well-laminated diatomite with good fossils, limonite band at the base.
899	Laminated diatomite with many fossil fishes.
914	Sandy diatomite, poorly laminated, no fossils.
943	Well-laminated diatomite with fossil fishes.
966	Sandy, cross-bedded diatomite, limonitic and unfossiliferous. This zone marks the end of the upper, shallow-water area. At the base of this layer is a series of gravel, sand, limonite and clay lenses.
1012	Well-laminated diatomite with scattered fossil fishes.
1059	Muddy, poorly laminated sand. Divided by limonitic bands into three nearly equal layers.
1074	Coarse, limonitic sand, no fossils.
1089	Clean, sharp, white sand, no fossils.
1111	Well-bedded diatomite with scattered fossils.
1124	Limonitic sand without fossils. Marks the lower limit of an intermediate depth zone.
1192	Well-laminated diatomite with scattered fossils.
1208	Limonitic sand layer without fossils.
1293+	Well-laminated diatomite with a few, large fossil fishes. Marks the limit of the excavation. The base of the pit did not penetrate this layer.*

\*Morris Skinner (*in litt.*) states that he bored to the base of the lake bed series with an auger and found gravels beneath the lake bed deposits at a depth of 32 feet.

show the major features of the site, determine the site's altitude in relation to the ancient drainages in the area, and to record the areal extent of the lake beds by their outcrop patterns. All traverses were tied into a United States Geological Survey bench mark approximately a mile from the site. Because exposures are limited locally, the cross section recorded as Table 1 was prepared from the walls of the excavations at the fossil quarry and may not be typical of the lake beds in general.

In order to discuss the complete Ree Heights fauna, species are mentioned that were not collected by my parties. These are represented by Cope's American Museum of Natural History holotypes and bear AMNH numbers. All other specimens discussed (with the exception of the pollen samples) are deposited in the University of Nebraska State Museum and have UNSM numbers. The palynology samples were retained by Aureal T. Cross and are on file in the Department of Geology, Michigan State University.

#### LOCATION AND GEOLOGY

The fossil quarry (Fig. 1) is located in the southwestern quadrant of Hand County, South Dakota, on the Leonard L. Fawcett ranch (northeast quarter of section 21, Township 111 North, Range 70 West).

The area of study lies in the center of a region of high, rolling hills known locally as the Ree Hills. These are drained largely by the Elm and Crow creeks which flow southward to the Missouri River. The Ree Hills are terminated at the north by Wolf Creek and form a drainage divide between the Missouri River to the south and the James River to the northeast. The fossil site and adjacent sections are exposed in the highly dissected margins of the modern Elm Creek valley. The region displays topographic relief of about 450 feet, the Ree Hills being the highest area in the county (White *et al.*, 1963).

The Pleistocene strata of Hand County are complex and rest unconformably on a bedrock of upper Cretaceous shales. The outcrop of these bedrock units is locally limited to members of the Pierre Shale. These units form a glacially scoured surface over most of the county and provide the major constituent of the tills in the area (Flint, 1955). The Pierre Shale also forms the base of a local perched water table and its outcrop pattern can be determined by noting the location and elevation of springs in the sides of the hills. Recent exploratory drilling for agricultural water has disclosed the location of several east-west trending gravel-filled valleys in the subsurface incised into the surface of the Pierre Shale. These are transverse to the modern

north-south trending valleys in the region. These valleys were earlier postulated by Flint (1955) and others and help to substantiate several of the points below.

The Ree Hills and the neighboring Orient Hills to the north are prominent hilly regions representing erosional remnants of Tertiary and Pleistocene formations. Portions of the Ree Hills are said to be supported and capped in places by the Ogallala Pliocene (Flint, 1955). Flint also stated that these Pliocene materials were sandstones, quartzites, marls and silts. Trips on foot and by airplane failed to turn up evidence of these materials in the vicinity of the fossil site, however.

The outcrop area is largely composed of Wisconsinan tills with occasional patches of Illinoian strata (Flint, 1955). The Ree and Orient hills became divided and dissected during the Late Wisconsinan times by the eastward flowing Ancestral Bad River (White *et al.*, 1963). Flint stated that no evidence of Nebraskan or Kansan tills had been discovered in the county. Till boundaries beyond Hand County indicate that earlier glacial lobes overrode Hand County, but their deposits were removed by subsequent erosion or later glacial advances. Flint reported a site approximately 20 miles northeast of the study area which represented the only definite pre-Wisconsinan deposits recognized in Hand County.

The Iowan and Tazewell substages of the Wisconsinan have yet to be located in the county with certainty. The most prominent Pleistocene strata at the fossil site are members of the Cary glacial substage. The Cary sediments are divided locally into two units, each represented by a till topped by an erosional surface bearing meandering streamcourses. A thin veneer of Mankato deposits cover the northern two-thirds of Hand County, but only the first of the two Mankato advances reached the fossil site area (Flint, 1955).

In most places there is little to differentiate the first and second Cary units except the occasional channel fillings. The topographic expression at the time of the lower Cary erosional interval was low and the location of the fossil site probably already formed part of the floodplain of one of the Pleistocene rivers in the area. The upper Cary erosional surface is easily seen and was observed to be nearly flat (total relief less than 5 feet). In addition to the lake beds and marshes of the fossil site, there are two major contemporary channel fillings within a mile of the fossil excavations. These channels are filled with crossbedded particles of greatly disparate sizes (bedded particles include grains ranging from silt particles to boulders three or four feet in diameter). The gravels are quarried at the outcrops for





road metal, and walls approximately 30 feet high are exposed (the quarries do not expose the base of the gravels). Where the upper Cary surface is not covered by later sediments, Flint noted that it was covered with gentle swells and swales occupied in wet years by undrained basins and ponds, much as they must have been at the time the fossil site was being deposited.

The Mankato surface shows even less relief than the Cary, giving the surface of the Ree Hills (away from the dissected margins) the appearance of an unbroken plain. Flint (1955) stated that this surface also supported swells and swales, though gentler than those on the Cary surface.

The Cary rivers in Hand County appear to have been near a divide (Flint, 1955) and may have been drained to the south into the Ancestral White River or the east into the Ancestral Bad River (which joined the Ancestral White River south-southeast of the fossil site). These channels are only exposed for short intervals in Hand County, but may be traced from border to border from scattered outcrops. A channel to the south contains similar cross-bedded materials and is at nearly the same elevation as the lower Cary gravels. This southern stream parallels the modern Elm Creek drainage and was recognized by Flint (1955) as a tributary to the Ancestral White River. The Ancestral White River collected all the contemporary rivers in the area and trended southeast to the vicinity of the modern Big Sioux River of South Dakota and Iowa. Although traces have not been found east of this point, the Ancestral White River is believed to have followed

the Minnesota River basin or the Des Moines River basin to the Mississippi River (Flint, 1955).

There is some evidence for an earlier diversion of the regional drainage into the Hudson Bay area (Metcalf, 1966), utilizing the Cheyenne, Grand and Moreau River basins to move across southern Manitoba to join the pre-glacial Red River. Although evidence for this diversion is well documented (Lemke *et al.*, 1965), there is little reason to suggest that any of the modern South Dakota fish fauna was derived in this manner (Bailey and Allum, 1962). If any species were derived from this direction, they presumably were displaced by later glaciation and re-entered the area via the Missouri or Mississippi River connections.

The Ancestral White River with its Mississippi River connections was interrupted and its tributaries captured by the Missouri River (Flint, 1955). The Missouri River was open throughout the Wisconsinan glaciation and provided a logical path for the recolonization of eastern South Dakota when the ice retreated.

These Mississippi River connections have been analyzed by an examination of the modern fish fauna (Bailey and Allum, 1962). They found that 55 of the 93 extant South Dakota species appeared to be native to the Mississippi River, while only 28 seemed to have been derived from the Missouri River route. Their idea has been tested by others with equally convincing results (Underhill, 1957 = darters, minnows and madtoms; Leonard, 1959 = gastropods; and Metcalf and Distler, 1961 = crayfish).

## Systematic Paleontology

### Family CYPRINIDAE

#### *Proballostomus longulus* Cope

(Plate 1 - A)

*Material.* Partial skeleton (AMNH 8090). Holotype.

*Geologic Range.* Wisconsinan. Restricted to Ree Heights.

*Remarks.* Cope considered *Proballostomus longulus* to be a cyprinodontid fish, and Rosen and Gordon (1953) concurred on the basis of a supposed gonopodium. This structure was later shown to be a crack in the matrix (T. Uyeno, University of Michigan, pers. comm.). After examination, Uyeno and Miller (1963) assigned this fish to the family Cyprinidae and Rosen (*l. c. cit.*, p. 14) agreed. Most of the fishes from Ree Heights are representatives of living species, and Uyeno and Miller point out that

*P. longulus* also probably belongs to an extant species.

Cope's specimen is difficult to analyze due to its poor state of preservation. Uyeno and Miller (1963) reexamined the holotype in their review of the late Cenozoic fishes of North America, and noted a tripus and modified fourth rib of a Weberian apparatus ("more slender than in any catostomid," G. R. Smith, pers. comm.). These structures accompanied by intramuscular bones in the trunk, a hypural plate composed of more than two hypural bones, and an anal fin more anteriorly placed than in any catostomid prove that this specimen is a cyprinid. The specimen is too poor for more precise assignment.

The author did not collect this species, so there are no data concerning habitat choice. The other minnows were collected mainly from the shallow zone and further specimens of *P. longulus* will probably be found there, too.

*?Sardinus blackburni* Cope

(Plate 3 - B)

*Material.* Holotype (AMNH 8091), lacking the head.

*Geologic Range.* Wisconsinan. Restricted to Ree Heights.

*Remarks.* Cope (1891) reservedly believed this fish to be a sardine, but the author has recently examined it, as have Uyeno and Miller (1963) with the conclusion that it cannot belong to this genus. It is referable to the family Cyprinidae, but it is presently impossible to assign it to any lower taxon.

Cope gave a set of characters for this form and, although they are rather general due to the taxonomic uncertainty of the taxon, they might bear listing here. They are as follows: strongly cycloid scales; vertebrae with longitudinal fossae; well developed and distinct hypural bones; dorsal fin commences above the ventrals and is of moderate length; spaces between the caudal haemal spines are traversed by a slender rod obliquely downwards and backwards (? intramuscular bones. C. R. Ossian); dorsal fin rays 1 - 7 (or 8), eight anal fin rays, at least six pelvic fin rays; six caudal vertebrae and a series of proportional measurements which may be taken from the photograph in Plate 3 — B (this publication), if desired.

No specimens of this fish were collected by the author. Because of this and the uncertain taxonomic situation, no comments can be made about the stratigraphic position in the lake beds, distribution of the species or its ecological requirements.

**Family ICTALURIDAE***Ictalurus melas* Rafinesque - Black Bullhead

(Plate 3 - C)

*Material.* Five complete or nearly complete skulls (UNSM 71132-71136), six fragmentary skulls (UNSM 71143-71148), five dentaries (UNSM 71149-71150, 71152-71153, and 71159), two angulars (UNSM 71153, both on same slab), a partial hyoid apparatus (UNSM 71154), six cleithra bearing spines (UNSM 71137-71142) and five slabs bearing series of vertebrae and ribs (UNSM 71155-71158, and 71160).

*Geologic Range.* Illinoian (C. L. Smith, 1954, 1958; G. R. Smith, 1963) to Recent. The specimens represent the first Ree Heights records.

*Remarks.* Identification of *I. melas* is based primarily on the morphology of the pectoral spines, cleithra and the neurocrania. The terminology of Hubbs and Hibbard (1951) will be used for the spines, while that of C. L. Smith (1961) will be used for the neurocrania.

Pectoral spines have been widely used to define ictalurid species in the past, but Lundberg (pers. comm.) has stated that specific variation is frequently so great that pectoral spines must be used with caution. The six spines at hand from Ree Heights, however, all fall within the range of variation of *I. melas*.

The shaft of a catfish spine may bear dentations on both the anterior and posterior edges. *I. melas* has dentations only on the posterior edge, and these are situated on the rim of the basal recess, but never in the recess. Modern ictalurids may bear notches on the anterior edge of the shaft near the tip. *I. melas* shows either a single notch or none, and in this as in the other characters, the Ree Heights specimens agree (Paloumpis, 1963).

The posterior tip of the ictalurid cleithrum terminates in a three-pointed projection, two of the points forming a Y-shaped fork at the tip of the bone, while the third projects at a lower level. This last projection is termed the humeral process (Taylor, 1969) and its proportions are species constant. In *I. melas*, the humeral process tends to be smaller and less strongly developed than in other ictalurids (except in some species of *Noturus*). Below the humeral process, the cleithrum bends sharply. The outer edge of this curve is sculptured to varying degrees in ictalurids, and the Ree Heights specimens are similar to *I. melas*. This species has a less rugose sculpture than any other catfish examined.

The ictalurid neurocranium has structures that are useful in the identification of species. The most obvious feature of the skull roof is the pair of dorsal foramina which cross most of the length of the skull roof. The posterior dorsal foramen opens nearly to the transverse crest at the rear of the skull, and continues further backwards as two raised ridges which join to form a paper-thin crest extending far beyond the main body of the neurocranium (this is the supraoccipital spine of C. L. Smith, 1961). In all other northern ictalurids, this foramen either closes before reaching the transverse crest, the ridges on the edges of the closed foramen become depressed, or these ridges are produced backwards as a heavy, massive crest. The well-preserved Ree Heights specimens all show the conditions found in *I. melas*.

The lower jaw apparatus was found intact in several specimens and the angulars proved useful. The fossils were compared with all northern ictalurids and found to match the *I. melas* condition in which the rear projection (point beyond the articulation with the quadrate) was found to be shorter and less well developed than in any species except *I. natalis*.

None of the Ree Heights catfishes was recovered from strata lower than 8 feet from the top of the lake beds. This is the point where the fauna shifts from shallow-water to deep-water fishes (fry and minnows are no longer evident). The specimens were restricted to the diatomite layers that would have provided the muddy bottom environment preferred by modern bullheads. None was found in the sandy intervals. The presence of what appear to be fossil cattails near two of the skeletons indicates that the depth of water at that time was not more than 3 feet (Benton and Werner, 1958).

*I. melas* is a common fish in South Dakota today and may be found living in habitats very similar to those found in the Ree Heights fossil beds (Bailey and Allum, 1962).

*Noturus* cf. *Noturus hildebrandi* Bailey and Taylor

#### Least Madtom

(Plate 2 — A, B and C)

**Material.** One nearly complete fish (UNSM 71130) preserved as part and counterpart. A second specimen (UNSM 71131) is represented by a cleithrum and a pectoral spine.

**Geologic Range.** Wisconsinan to Recent. Fossil occurrence restricted to Ree Heights.

**Remarks.** North American freshwater catfishes are divided into two groups: *ktalurus-like* catfishes and bullheads; and madtoms and stonecats of the genus *Noturus* (Taylor, 1969). Madtoms have a rear extension of the underside of the premaxilla, an elongate snout, and a modified caudal fin to distinguish them from the other ictalurids (Lundberg, pers. comm.). Standard ictalurid caudal fins have a principal ray count of ten, while madtoms always have a higher number of principal rays (Taylor, 1969; Lundberg, *in litt.*). UNSM 71130 has been damaged in this area, but shows at least 25 countable principal caudal fin rays.

Madtoms have recently been divided into three subgenera by Taylor (1969) on the basis of a number of characters, several of them osteological. The Ree Heights madtoms can be keyed into the subgenus *Rabida*, because the pectoral spines have dentations on both the anterior and posterior edges. Of the 13 species in the *Rabida* group, the fossils can be assigned to *Noturus hildebrandi* on the basis of the following characters: a short and blunt humeral process on the cleithrum (shorter than the diameter of the pectoral spine, not including the dentations); the tooth patch on the premaxilla is rectangular and has rounded posterior corners; and a pectoral spine with the anterior dentations reduced in size and number, and whose posterior dentations (with the exception of the first) are retrorse (Taylor, 1969; Lundberg, pers. comm.).

Taylor lists vertebral counts for all the species of *Noturus*, and while the count of 36 for the fossil madtom lies within the range of *N. hildebrandi*, this is not sufficient to separate it from several other species.

Work in progress on recent catfishes by John Lundberg (Duke University) indicates that the species of *Noturus* cannot be separated confidently by the use of pectoral spines. The osteology of the Ictaluridae is being examined by Lundberg, and positive assignment should await the outcome of this study. Therefore the name *Noturus hildebrandi* should be considered tentative.

In Mississippi, *N. hildebrandi hildebrandi* is typically found in relatively shallow, clear gravel or pebble-bottomed riffles in currents; while *N. hildebrandi lautus* in Tennessee is found over shifting sand in shallow water (Taylor, 1969). One Tennessee habitat was over mud, sand and silt. As has been mentioned above, there were adjacent drainages in Cary times that probably provided areas with these habitats. The presence of the species in the Ree Heights lakes is probably due to introduction during floodtimes.

The species is presently restricted to limited areas in western Tennessee, northern Mississippi and southwestern Kentucky.

The madtom fossils were recovered from the shallow-water area of the quarry, accompanied by minnows and fry, but there are too few specimens to support conclusions about habitat preferences.

#### Family CYPRINODONTIDAE

##### *Fundulus diaphanus* (LeSueur) - Banded Killifish

(Plate 1 - B)

**Material.** Holotype (AMNH 8089), a well-preserved, complete fish. A second specimen was collected by the author's party in 1966 and tentatively identified with this species. This specimen could not be located again after the Vertebrate Paleontology Laboratory at The University of Nebraska State Museum made a recent move to new quarters and is presumed lost.

**Geologic Range.** Wisconsinan to Recent. Fossil occurrence restricted to Ree Heights.

**Remarks.** Cope (1891) recognized that AMNH 8089 was a cyprinodont, but failed to recognize it as a member of the genus *Fundulus* and erected the taxon *Gephyrura concentrica*. R. M. Bailey (University of Michigan) with the concurrence of T. Uyeno and R. R. Miller reexamined the specimen and noted characters that assigned it to the species *Fundulus diaphanus* (Uyeno and Miller, 1963).

The osteology and relationships of this taxon have been exhaustively treated (Cope, 1891, Uyeno

and Miller, 1963) and need not be repeated here.

The specimen collected in 1966 came from the shallow margin of the lake accompanied by fossil reed and other shallow-water indicators (frogs, gastropods and fry). Recent members of this species prefer the same quiet, reedy, environment throughout their range (Hubbs and Lagler, 1949). *F. diaphanus* presently occurs in eastern South Dakota, but not in the vicinity of Ree Heights.

### Family CENTRARCHIDAE

#### *Micropterus salmoides* (Lacépède) - Largemouth Bass

(Plate 3 — A)

*Material.* Partial skeleton (UNSM 71037).

*Geologic Range.* Illinoian (G. R. Smith, 1963) to Recent. This specimen represents the second occurrence in the fossil record.

*Remarks.* The generic assignment was made primarily on the basis of the shape of the angular and urohyal bones. The angular bone of *Micropterus* is more elongate than in other centrarchids. In addition to being generally more robust than in related species, the lower portion of this bone is terminated anteriorly by a sharply lunate edge. G. R. Smith (pers. comm.) suggests that this character will not serve to separate this species from *Pomoxis*, but the identification can be confirmed by the use of other characters listed below.

Urohyal bones are among the more variable bones in this family. Species of *Lepomis* have urohyals that are usually either unforked and blunt anteriorly, or are forked with an angle of 90 degrees or greater between the branches of the fork. In *Micropterus*, the tip of this bone is always forked in juveniles and young adults (there is some tendency toward bluntness in very large adults) and has an angle of less than 90 degrees between the branches (typically less than 60 degrees). The Ree Heights specimen is approximately 45 mm in standard length and has a urohyal resembling the young *Micropterus*-type and is, therefore, a sub-adult fish.

Dorsal and anal fin ray counts are in the proper range for this species (Bryan, 1969), separating this specimen from the genus *Pomoxis* which always has more than three anal fin spines and fewer than ten dorsal fin spines. There are at least 28 vertebrae.

The only other member of the genus occurring in the area today is the smallmouth bass, *Micropterus dolomieu*. These resemble each other closely osteologically, but comparison with all modern material at hand suggests that the fossil is closer to *M. salmoides* than *M. dolomieu*.

The Ree Heights specimen was collected from the shallow region near the top of the exposure. This area preserves a habitat that is similar to that

chosen by young *Micropterus* in recent faunas (Hubbs and Lagler, 1949). *M. salmoides* is a common fish in South Dakota today, but Bailey and Allum (1962) suggest that the recent populations may represent human introductions during this century.

#### *Lepomis humilis* (Girard) - Orange-spotted sunfish

(Plate 3 — D)

*Material.* Thirty-three nearly complete fishes (UNSM 70676 - 70709), 57 skulls (UNSM 70710 - 70767) the holotype of *Oligoplarchus squamipinnis* Cope (AMNH 8078), and three paratypes (AMNH 8080, 8081 and 8083).

*Geologic Range.* Possibly Late Minoian (G. R. Smith, 1963, *L. humilis* ?) to Recent. Ree Heights is the only site with confidently identified *L. humilis* materials.

*Remarks.* This species was reported by Cope (1891) as *Oligoplarchus squamipinnis*, though he was aware of its similarities with the genus *Lepomis*. R. M. Bailey examined the type materials during a review of the family Centrarchidae (Unpub. Doctoral Diss., Univ. Mich., 1938) and determined that the fossil was close to or identical with *L. humilis* (Uyeno and Miller, 1963). After examining the large series of fossils listed above, I can find no difference between the fossils and skeletons of recent *L. humilis*.

Distinguishing osteological characters for the species of *Lepomis* are taken from the following authors: Branson and Moore, 1962; Moore, 1957; Trautman 1957 and Cross, 1967.

The genus *Lepomis* may be distinguished from the percids by their spinous and soft-rayed portions of the dorsal fins. In centrarchids, these portions are continuous, not separated. Percids have two or fewer anal spines, while centrarchids always have three or more (three in *Lepomis*). General features that separate *Lepomis* from the other centrarchids are: a preopercle whose limbs form an angle of less than 100 degrees (about 90 degrees), no teeth on the pterygoids, and modally they have 12 precaudal vertebrae. It should be borne in mind that some of the characters used in this discussion are variable. Therefore, the sum total of characters is more important than any single osteological feature.

*L. humilis* is osteologically very distinct from the other species in its group. The most useful characteristics of the genus are the large lateral line canal pores. In *L. humilis* the pore openings on the frontal bones and dentaries are very large in proportion to the bones, the diameter of the openings being greater than the width of bone between adjacent pores. In other members of the genus, the pores are

always narrower than the bony spaces between them. This character is clearly visible in all specimens of *L. humilis* from Ree Heights.

The preopercles of sunfishes may bear small serrations on the posterior and ventral edges of this bone. In the fossil *L. humilis*, these serrations are restricted to an area extending from the upper edge of the lateral-line pore at the angle of the bone to the posterior margin of the anterior-most aperture of the preopercle.

The pharyngeal tooth plates of the fossil *L. humilis* are not massive as in *L. gibbosus*, but are long and narrow as in the majority of sunfishes. *L. humilis* has a long dentary (shared only with *L. cyanellus* and *Chaenobryttus* among the sunfishes), other sunfishes having relatively short and stout dentaries. The vertebral count is modally 27.

This species is probably the commonest fish at the site, and was collected everywhere in the shallow region at the top of the lake beds, but not from the deeper zones. *L. humilis* is a common fish in eastern South Dakota (Bailey and Allum, 1962), and is probably part of the native pre-glacial fish fauna of the Great Plains region.

#### *Lepomis gibbosus* (Linnaeus) - Pumpkinseed sunfish

(Not illustrated)

**Material.** Six nearly complete fishes (UNSM 70767 - 70772), and 14 skulls and partial skeletons (UNSM 70773 - 70787).

**Geologic Range.** Wisconsinan to Recent. Restricted as a fossil to Ree Heights.

**Remarks.** Characters separating the genus *Lepomis* from related fishes have been discussed above. Distinguishing osteological features of *L. gibbosus* are as follows:

The preopercle of *L. gibbosus* is also distinctively serrated. The serrae are restricted to an area only slightly above to slightly below the angle made by the limbs of the preopercle. The edge of the opercle is produced as a smooth arc, minutely serrated, not extended backwards into an "ear-flap" as in several closely related species.

The lateral-line openings in the dentary and frontal bones are much smaller in proportions than those of *L. humilis* (the diameter of the pores is always less than the width of the bones between adjacent pores). The dentary in *L. gibbosus* is of the short-jawed variety (see *L. humilis*, Remarks).

In *L. gibbosus*, the pharyngeal tooth plates are broad and massive, bearing blunt pavement teeth. Bean and Weed (1911) demonstrated that the characters of the pharyngeal mill are constant, regardless

of age of the individual, and can be used to differentiate the youngest sunfishes with confidence.

The otoliths, or ear bones, have been used by several authors to identify genera and species from many ages and localities. Fifteen specimens from Ree Heights have well preserved otoliths identical with those of the modern *L. gibbosus*.

The *L. gibbosus* fossils were located in the lower portions of the shallow zone where the water may have been 3 to 5 feet in depth. *L. gibbosus* was accompanied by a few fossils of *L. humilis*, some large minnows and medium-sized *Perca flavescens* (100 to 150 mm in standard length). Although living *L. gibbosus* are found in the area today, Bailey and Allum (1962) state that they believe their presence there is due to human introductions.

#### *Lepomis macrochirus* (Rafinesque) - Bluegill sunfish

(Plate 1 - C)

**Material.** Three skulls and partial skeletons (UNSM 71034 - 71036).

**Geologic Range.** Wisconsinan to Recent. Fossils are restricted to Ree Heights.

**Remarks.** The characters that distinguish the genus *Lepomis* have been mentioned above. *L. macrochirus* can be distinguished osteologically as follows:

The preopercle of *L. macrochirus* displays a distinctive serration along the posterior and ventral borders. These edges bear alternate patches of large and small serrae, and the body of the preopercle anterior to the serrae is striated.

The urohyal bone has a unique manner of branching, with the anterodorsal process extending from the axis of the bone at an angle of about 70 degrees. This side branch is longer than the axial branch.

*L. macrochirus* is one of the "short-jawed" sunfishes (see *L. humilis*, Remarks). The dentary and the frontal bones in this species have small lateral-line pores like those in *L. gibbosus*. The pharyngeal mill and its teeth are of the slender, sharp-toothed variety found in *L. humilis* and some other sunfishes, not the massive sort of *L. gibbosus*.

All three specimens of *L. macrochirus* came from the deeper portions of the deposit (believed to represent water deeper than 5 feet), but there are too few fossils to support definite comments about the habitat of this taxon. The only fossils recovered with *L. macrochirus* were large *Perca flavescens*. *L. macrochirus* is common in the area today, but appears to have been introduced by early settlers (Bailey and Mum, 1962).

## Family PERCIDAE

*Perca flavescens* (Mitch ill) - Yellow Perch

(Plate 4 - C)

*Material.* Six complete fishes (UNSM 70652 - 70654, 70674 - 70675), 8 partial skeletons (UNSM 70656, 70664, 70666, 70668 - 70669, 70671 - 70673), 15 skulls (UNSM 70655 - 70661, 71172 - 71180), 1 *preopercle* (UNSM 70665) and 1 cleithrum (UNSM 70663). The holotype of *Mioplosus multidentatus* Cope (AMNH 8075) was also examined.

*Geologic Range.* Illinoian (C. L. Smith, 1954, 1958; and G. R. Smith, 1963) to Recent.

*Remarks.* *Perca flavescens* was collected by Cope's correspondents, but he incorrectly assigned it to the taxon *Mioplosus multidentatus* (Cope 1891). He had erected this genus for the perch-like fishes of the Eocene Green River beds of Wyoming (Cope, 1884). Both fishes are similar in some respects, but the correct relationships were overlooked. Curiously enough, the species name referred to the serrate lower edge of the preopercle, the most easily identifiable bone in the perch skull (well preserved and visible in the holotype).

The Ree Heights fossils display the typical percid dorsal fin, consisting of separate spinous and soft-rayed portions. In those specimens with complete dorsal fins, the spinous and soft-ray counts match those of the living *P. flavescens*. This species can be separated from other percids by the serrate margins on several of the skull bones. These are the *preopercle*, subopercle, post-temporal, cleithrum and supracleithrum. Serrae on the lower edge of the preopercle are especially robust and are directed forward.

All percids known to inhabit South Dakota and adjacent areas were examined. *P. flavescens* has an *opercle*, dentary, angular, quadrate, maxilla and premaxilla that differ from related species in their proportions, serration and *lateral-line* pore arrangement.

*P. flavescens* was recovered from nearly all levels of the excavation. The only segregation noted was that the larger fishes were recovered from the deeper water area of the deposit, while the smaller fishes were restricted to the shallow zones. This was expected, as modern perch fry tend to remain in the shallow areas until they are large enough to cope with predators in the deeper regions. Yellow perch were the largest fishes recovered from the lake beds, ranging in standard length to more than 300 mm.

The species is common in the area today and probably is part of the ancestral fish fauna of the Great Plains and may have been present in pre-glacial times (Bailey and Allum, 1962).

*Percina* cf. *Percina copelandi* (Jordan) - Channel darter

(Plate 4 - A)

*Material.* A single headless specimen (UNSM 71170) preserved as part and counterpart (incomplete).

*Geologic Range.* Wisconsinan to Recent. This and *Etheostoma exile* (this publication) are the only known fossil darters.

*Remarks.* Although this specimen is unique and incomplete, characters are present that seem to justify giving a tentative name. The fish is covered with fine ctenoid scales that are much smaller, in proportion to the size of the fish, than those on the fossil *Etheostoma exile*. The pelvic fins are close together and have a ray count of one spine and five or six soft rays. The pectoral fins appear to be complete and are larger than those seen on most darters in the *Etheostoma* group. The dorsal fin shows the typically divided spinous and soft-rayed portions and the segments are well separated. The dorsal fin-ray count consists of 10 spines and 10 or 11 soft rays. The anal fin appears to have two spines and eight soft rays, and is somewhat smaller than the soft-rayed portion of the dorsal fin. Most of the fin spines are broken away, but have left sharp impressions in the matrix that are visible with low-angle lighting. Thirty-eight vertebrae are visible, although there may have been a few more in the missing portion of the slab.

The fossil is more elongate than the other darters in the collection that were assigned to the genus *Etheostoma*. Its ratio of body depth to estimated body length is  $5\frac{1}{2}$  to 6, more than most darters in the genus *Etheostoma*, but less than those in the genus *Ammocrypta*. The above data suggest that the fossil should be assigned to the genus *Percina*. G. R. Smith (*pers*, comm.) suggested that the characters and inferred habitat at Ree Heights indicated that the fossil might be *P. copelandi*. I agree that this possibility is a good one. This species is presently all restricted to the south and east of South Dakota, but with the near total lack of information of darter distribution in the Pleistocene, this may or may not represent disjunct distribution.

The unique specimen of the species was collected in 1966 from float blocks at the foot of the outcrop. At the time of collection, the only matrix exposed at the surface was material from the uppermost few feet of the lake beds. Therefore, the fish must have come from the very last, shallow portions of the lake and occupied a habitat similar to that in which *Etheostoma exile* was collected at Ree Heights. Various members of the genus *Percina* live in South Dakota today, but are normally collected from gravel riffles. *P. copelandi*, however, is a lake

species and is collected from areas with sluggish water movements and sandy bottoms. This habitat at Ree Heights would seem to have been a tolerable one for *P. copelandi*, reinforcing the identification. As noted in the cross section of the fossil beds (Table 1), the upper latter stages of the lake's history were marked by periodic influxes of sand and show evidence of disturbance by running water. This fish may have entered the lake during one of the fluvial periods, if it should later be found that the above identification was incorrect and the fish belongs in a different species.

*Etheostoma exile* (Girard) - Iowa darter

(Plate 4 - B)

*Material.* Seven complete fishes (UNSM 71162 - 71169), and two partial skeletons with skulls (UNSM 71170 - 71171).

*Geologic Range.* Wisconsinan to Recent. Fossil occurrence restricted to Ree Heights.

*Remarks.* These fossils were assigned to the genus *Etheostoma* on the basis of a divided dorsal fin composed of spinous and soft-rayed portions, large ctenoid scales and an unserrated preopercle. The fossils are not as elongate as fishes of the genus *Percina* or *Ammocrypta*, but are more so than those of the genera *Perca* or *Stizostedion*.

The genus *Etheostoma* is a large and diverse group whose relationships are still imperfectly known. It is not always possible to differentiate the numerous species of modern darters without careful study. Because of these difficulties, the fossils were not only compared with those darters most likely to have inhabited South Dakota at some time in the past, but also those in adjacent areas. All darters known to live currently in South Dakota, North Dakota, Nebraska, Iowa, Minnesota and most of the darters of Kansas were examined. These included: *Ammocrypta asperella*, *A. clara*, *Etheostoma asprigene*, *E. blennoides*, *E. caeruleum*, *E. chlorosomum*, *E. exile*, *E. flabellare*, *E. microperca*, *E. nigrum*, *E. punctulatum*, *E. spectabile*, *E. zonale*, *Percina caprodes*, *P. evides*, *P. maculata*, *P. nigrofasciata*, *P. phoxocephala* and *P. shumardi*.

The characteristics of the fossils include: scaled cheeks, pelvic fins placed closely together, two anal fin spines and seven to eight anal soft rays. The pelvic fins have one spine and five soft rays. There are approximately 44 vertebrae.

Four bones from the head region of recent darters were chosen as good species indicators for two reasons: they were both highly species specific and were preserved on most of the specimens. These bones were the opercle, premaxilla, angular and the dentary. When the series of recent skeletons was examined, it became apparent that the fossils were part of the genus *Etheostoma*. In the fossils, the opercle has a smoothly convex posterior border with the entire opercle ossified. The dorsal border of the opercle rises gently posteriad to a maximum height three-quarters of the way along a horizontal ridge, and then falls away sharply in a lunate curve that merges with the spine on the posterior edge. In *Ammocrypta* the upper border is either absent (no expansion above the spine) or the border parallels the spine. The condition in *Percina* varied from a smoothly arched border to one that formed a hook at the maximum expansion, but never approached the condition found in the fossils. Various species of *Etheostoma* resembled the fossil darters, but otherwise differed in ways discussed below.

The premaxilla of the fossil is an elongate bone with the upper margin rising to a high point two-thirds of the way back from the anterior end. The vertical process at the anterior end is rather short, rising only slightly above the bulbular expansion adjacent to its base. In *Ammocrypta* the premaxilla is short, stout and massive, and does not resemble the fossils. Several species of *Percina* and *Etheostoma* were like the fossil in a few points, but differed in others.

The shape of the fossil darter's angular is markedly different from the condition in *Ammocrypta*, *Percina* and nearly all the species of *Etheostoma* examined. Only *E. exile*, *E. flabellare*, *E. caeruleum* and *E. blennoides* had angulars similar in shape to those on the fossils.

A diagnostic feature observed on the dentary was the vertical expansion of the upper tooth-bearing limb of the bone. In the fossil form there is a paddle-like development seen only on the genus *Etheostoma* and only in the species *E. exile* and *E. flabellare*. However, *E. flabellare* was seen to have an opercle and premaxilla differing from the fossil form, while *E. exile* agrees with the fossils in all respects. The vertebral count (35 - 37) is within the range recorded for modern populations of *E. exile* (Bailey and Gosline, 1955).

# Discussion

## PALEOECOLOGY

Extrapolating from Recent habitat preferences, most of the Ree Heights fishes preferred lentic (standing water) situations (see Table 2). *Etheostoma exile* is said by Harlan and Speaker (1956) to be especially common in ponds and lakes that are adjacent to major rivers, a situation like the one at Ree Heights in Cary times.

TABLE 2. Habitat Preferences of the Modern Counterparts of the Ree Heights Fishes

	Lentic Environments	Lentic Environments Both Habitats with Pref. for Lentic	Shallow Water Zero to 5 ft.	Deeper Water 5 ft. or More
<i>Proballostomus longulus</i> (habits unknown)				
<i>Sardinus blackburni</i> (habits unknown)				
<i>Fundulus diaphanus</i>		A*	▲	
<i>Ictalurus melas</i>		A	A	
<i>Noturus hildebrandi</i>	A		A	
<i>Etheostoma exile</i>		A	A	
<i>Perca flavescens</i>		A		A
<i>Percina copelandi</i>		A	A	
<i>Micropterus salmoides</i>		A	Y	A
<i>Lepomis humilis</i>		A	A	
<i>Lepomis gibbosus</i>		A	A	
<i>Lepomis macrochirus</i>		A	Y	A

\*Y = immature individuals; A = adults

*Noturus* cf. *hildebrandi* is the only Ree Heights fish restricted to rivers (Taylor, 1969), presently occupying two southern river systems. In one of these, the bottom consists of gravel to pebble-sized grains in a swift current. In the other system, the current is slower and the bottom is composed of shifting sand, mud and silt (Taylor, 1969). Neither of these environments is represented in the lake beds, but similar sediments can be found in the nearby ancient river channels. The lake beds were probably situated on the floodplains of those channels, and the *N. hildebrandi* specimens were probably swept into the lake beds during periods of high water.

Fossil fishes were found only in the finely laminated diatomite layers of the lake beds, never in the clastic zones (see Table 1). These fine-grained sedi-

ments accumulated evenly with little or no disturbance for long periods of time. Fishes as small as 11 mm in total length were preserved intact. The damage seen in most specimens is only the slight disarticulation caused by compaction of the matrix after deposition.

In most aquatic ecosystems, scavengers consume dead fishes and scatter their bones. The perfection seen in some of the specimens suggests that they may have been victims of a winterkill or a drought. In either case, the cadavers might have escaped scavengers for a while, perhaps long enough to accumulate the diatomite cover that protected them.

*Paleoecology of Other Fossils.* Vertebrate fossils other than fishes are rare in the area, but do not prevent one from envisioning a landscape very much like that near Ree Heights today. The only fossil mammals reported by Flint (1955) were *Rangifer* (caribou), *Equus* sp. (small form said to be like those of the late Pleistocene of Alaska, according to C. B. Schultz, in Flint, 1955), and *Archidiskodon* sp. (a mammoth). These were interpreted by Flint as indicative of subarctic types living near the edge of a retreating ice sheet. However, references in Hall and Kelson (1959) suggest that caribou do not necessarily indicate this at all. They cite records of specimens and populations recently living as far south as Minden City, Michigan (taken there as recently as 1942). If the caribou records are meaningful, then climatic conditions at the site need not have been very different from those experienced there today.

Pakobotanical evidence supports the idea that the site does indeed represent a lake and provides climatic indicators that suggest that the area may have been cooler and more moist than at present. A. T. Cross (Michigan State University) and his students, R. E. Taggart and L. E. Eames, examined the matrix for pollen and spores, noting that the sediment was an impure diatomite. Some diatoms are known to be very specific in habitat and may be used to determine environmental conditions at their sites of collection, provided there has not been significant transport. Table 3 points out that five of the recorded diatom genera tend to inhabit still or slow-moving water (lentic conditions). The others are nonspecific types (ubiquitous in the habitat), but none indicates rapidly moving water (lotic conditions).

Spruce (*Picea*) and Pine (*Pinus*) were detected by their pollen. Conifers are uncommon in the area today and were probably equally uncommon in



TABLE 3. Ecological Data from Botanical Sources

	O	me.	Lotic and Lentic Environments	Non-specific Forms	Moist Lowlands	May not be Local Easily Transported
<b>Diatoms</b>						
<i>Cocconeis</i>				X		
<i>Cymbella</i>				X		
<i>Denticula</i>				X		
<i>Fragilaria</i>		X				
<i>Gomphonema</i>				X		
<i>Navicula</i>				X		
<i>Pinnularia</i>	X					
<i>Stephanodiscus</i>	X					
<i>Surirella</i>						
<i>Tabellaria</i>	X					
<b>Other algae</b>						
<i>Pediastrum</i>						
<b>Higher plants</b>						
Pteridophyte (fern)				X	X	
<i>Equisetum</i>				X		
<i>Picea</i>				X		X
<i>Pinus</i>		X				
<i>Carya</i>				X		
<i>Tilia</i>				X		
<i>Quercus</i>				X	X	
<i>Betula</i>				X		X
Grasses, various types			X			
Composites			X			
<i>Myriophyllum</i>	X					

*Carya* times. Cross (pers. comm.) states that conifer pollen can travel great distances and the Ree Heights materials could have been derived from sources as remote as the Black Hills of South Dakota or even the Front Range of the Rocky Mountains. This pollen is common in the sample and could represent a local source, as Flint (1955) cites a fossil spruce forest of about the same age from a site north of the Ree Heights locality.

Hickory (*Carya*) pollen was recognized, but this tree is not common to the Great Plains either. In this region, the genus is presently limited to the Missouri River channel as far north as the central, eastern border of Nebraska (Pool, 1961). Oak (*Quercus*) leaves and pollen were also found, but were not precise indicators of habitat. The oak appears to be the bur oak, *Quercus macro carpa* Michaux, a common tree of the area today. Bur

oaks are most common on the moist lowlands, but do well in the drier uplands as well (Pool, 1961).

Birch (*Betula*) pollen was also detected and indicates a cool, moist growing site. Birches are rare in the area today, the nearest living groves are found in canyons tributary to the Niobrara River at Valentine, Nebraska. This Nebraska stand has been interpreted as a relict forest left behind by a retreating glacier (Pool, 1961).

Several undetermined genera of grasses are present, accompanied by a number of composite plants (represented by pollen). These fossils are so difficult to differentiate and so wide-ranging in the present Great Plains region that they provide little ecological data. Pollen was noted from the submerged aquatic plant, *Myriophyllum*. This common "waterweed" tends to inhabit slow-moving or still water, and is unlikely to flourish over a gravel bottom. *Myriophyllum* is a fragile plant that cannot stand much transport and probably grew in place.

Based on ecological requirements of the fishes and the botanical evidence, the fossil site was situated on a high prairie region similar to that in the Hand County region today. Grasses and composites covered most of the highlands, with trees confined to the lowlands and stream courses. The area around the lake beds was probably lightly wooded and formed part of the floodplain of the adjacent rivers. The fossil site was a series of shallow, marshy ponds probably connected by channels of slow-moving water. Occasional floods invaded these waters, depositing layers of sand derived from the load of the nearby river beds.

### SOURCE OF THE FISH FAUNA

The majority of the Ree Heights fishes used an eastern connection with the Mississippi River to reach this part of South Dakota (see Table 4). This access may have been across either northern Iowa or southern Minnesota (Flint, 1955; Underhill, 1957; Bailey and Allum, 1962).

Only two of the Ree Heights species were more likely derived from the Missouri River route. *Lepomis humilis* is known from deposits of Illinoian age in Kansas (G. R. Smith, 1963) and this species probably forms part of the ancestral Great Plains fish fauna. *L. humilis* occupies slow-moving streams at times and might well have ascended the Missouri River. *ktalurus melas* is also known from the Great Plains Pleistocene (C. L. Smith, 1954, 1958; G. R. Smith, 1963), and also may have used the Missouri River to reach South Dakota.

Several of the fishes might have been derived from either system. *Perca flavescens* is found in the Great Plains Pleistocene and together with *P. cope-*

TABLE 4. Drainage Connections to South Dakota (largely from Bailey and Allum 1962)

	Dr Mississippi River	Dr Tennessee River	Dr Ohio River	Dr Missouri River
<i>Pro ballostomus longulus</i> (source unknown)				
<i>Sardinus blackburni</i> (source unknown)				
<i>Fundulus diaphanus</i>				
<i>Ictalurus melas</i>	X	X	X	X
<i>Noturus hildebrandi</i>				
<i>Etheostoma exile</i>	X	X	X	X
<i>Percina copelandi</i>				
<i>Perca flavescens</i>			X	X
<i>Micropterus salmoides</i>	X	X	X	X
<i>Lepomis humilis</i>			X	X
<i>Lepomis gibbosus</i>			X	X
<i>Lepomis macrochirus</i>				

\*During their extended drainage in the Pleistocene, the Des Moines and Minnesota Rivers may have provided routes for those South Dakota fishes believed derived from the Mississippi River system.

*landi* and *M. salmoides* (believed native to Nebraska by R. E. Johnson, in Bailey and Allum, 1962) might have ascended either the Missouri or Mississippi Rivers. *Etheostoma exile* has been reported from the lower Great Plains recent fauna, but apparently in error (Cross, 1967).

*Noturus* cf. *hildebrandi* presents problems of another sort, as does *Percina* cf. *copelandi*. These fishes are both found far from their present ranges. *N. hildebrandi*, as mentioned above, is not known now outside of Mississippi, Tennessee and parts of Kentucky. *P. copelandi* is known from a broad arcuate region beginning in Ohio and extending to Oklahoma, but only slightly closer than *N. hildebrandi* (Trautman, 1957). This disparate distribution was greater than anticipated, but probably only reflects the total lack of knowledge concerning the fossil distribution of these two fishes.

With the exception of *N. cf. hildebrandi*, none of the fishes is out of place ecologically, although several are beyond their present geographic ranges. Identifications in this study represent range extensions for *Lepomis gibbosus*, *L. macrochirus*, *Noturus* cf. *hildebrandi* and *Percina* cf. *copelandi*. *Fundulus diaphanus* presently occurs only in the northeast corner of South Dakota (Bailey and Allum, 1962). The discovery at Ree Heights constitutes a minor range extension for this species as well.

The present South Dakota fish fauna began its

dispersal into the region at some time prior to the Wisconsinan glaciation. The fishes were probably temporarily displaced southwards during one or more of the Wisconsinan advances. Those species found at Ree Heights, but not now native to South Dakota are still mostly living nearby. These are probably still in the process of recolonization.

ACKNOWLEDGMENTS

I wish to acknowledge the assistance offered by Dr. J. Alan Holman (The Museum, Michigan State University) and Dr. Gerald R. Smith (Museum of Paleontology, University of Michigan).

Drs. Reeve M. Bailey and Robert R. Miller (Museum of Zoology, University of Michigan) helped clarify taxonomic problems and provided comparative materials from the recent collections in their control. Professor Edward D. Cope's type specimens were on loan to Dr. Miller and he gave me access to them for study and photography.

Dr. C. B. Schultz (formerly Director, University of Nebraska State Museum) generously supported my field work, provided laboratory space during part of my study and authorized the loan of Ree Heights materials under his care.

Other assistance was offered by Dr. Aureal T. Cross and his students Ralph E. Taggart and Leonard E. Eames (Geology Department, Michigan State University) in the identification of botanical materials. Dr. John Lundberg (Duke University) aided me with some of the catfish problems.

Thanks are also due to Mr. Leonard L. Fawcett, owner of the fossil site, and his family. Mr. Fawcett offered every assistance during the 1966 and 1969 field seasons. My field crews were guests in his home, used his ranch lands at will, and were taken aloft in his private plane to make aerial surveys of the fossil site and its surroundings. The success of this study is due in large part to his interest and generosity.

Field work during the 1969 season was aided by grants from the Society of the Sigma Xi and the American Society of Ichthyologists and Herpetologists. Some of the field supplies were provided by the Museum, Michigan State University. The entire cost of the 1966 field season and the expense of my assistant for the 1969 season were borne by the University of Nebraska State Museum.

I wish to thank my wife, Eleanor, who has aided me in the field, assisted with the mapping and the collection of fossil and recent fishes, and offered suggestions and encouragement throughout the span of the investigation.

Lastly, although I have profited greatly by discussions with many specialists, the conclusions stated in this paper are my own.

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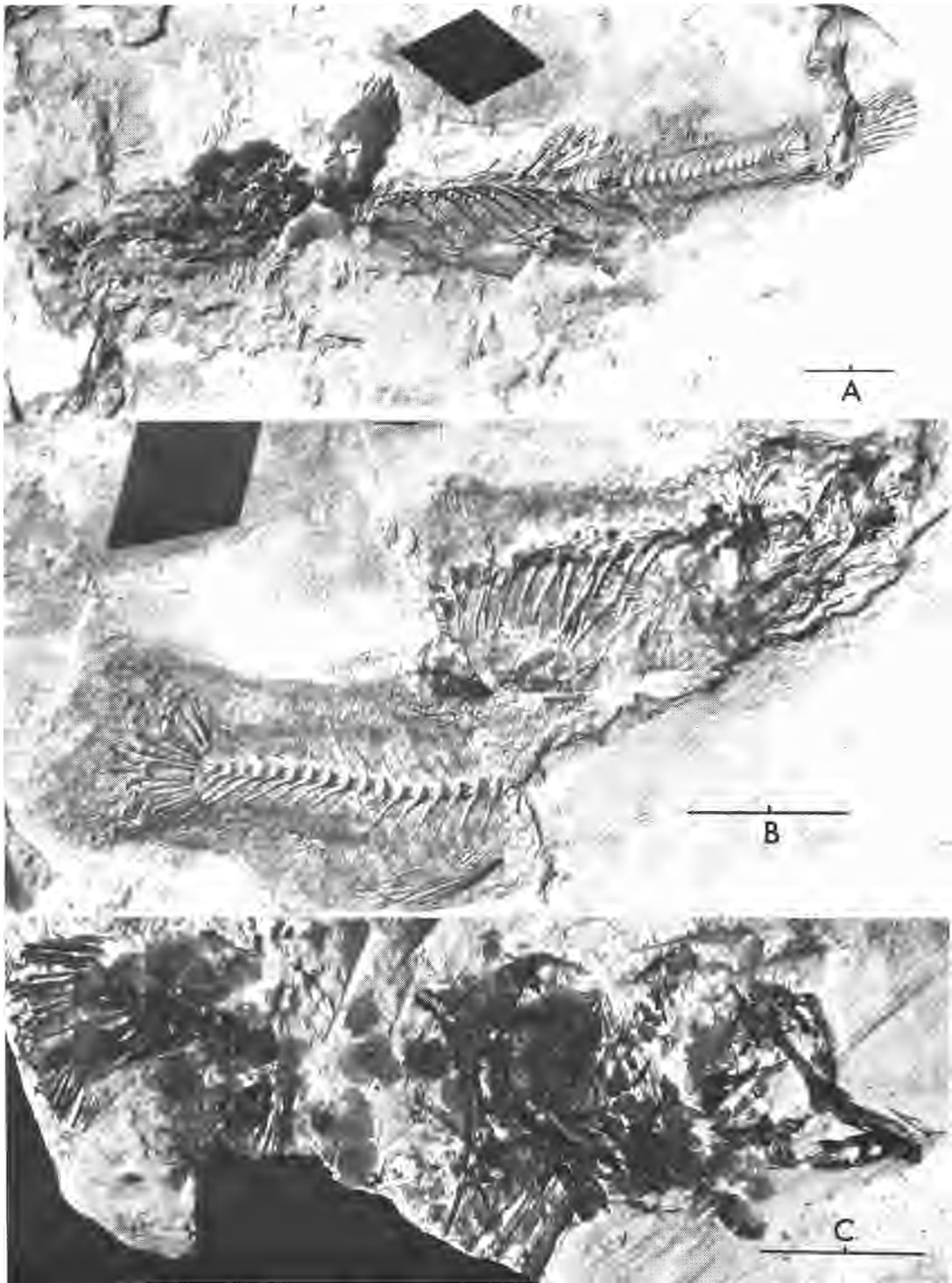


Plate 1. Ree Heights fishes. (A) *Proballostomus longulus* Cope AMNH 8090; (B) *Fundulus diaphanus* (Le Sueur) AMNH 8089; (C) *Lepomis macrochirus* (Rafinesque) UNSM 71034. Each line equals 10 mm.

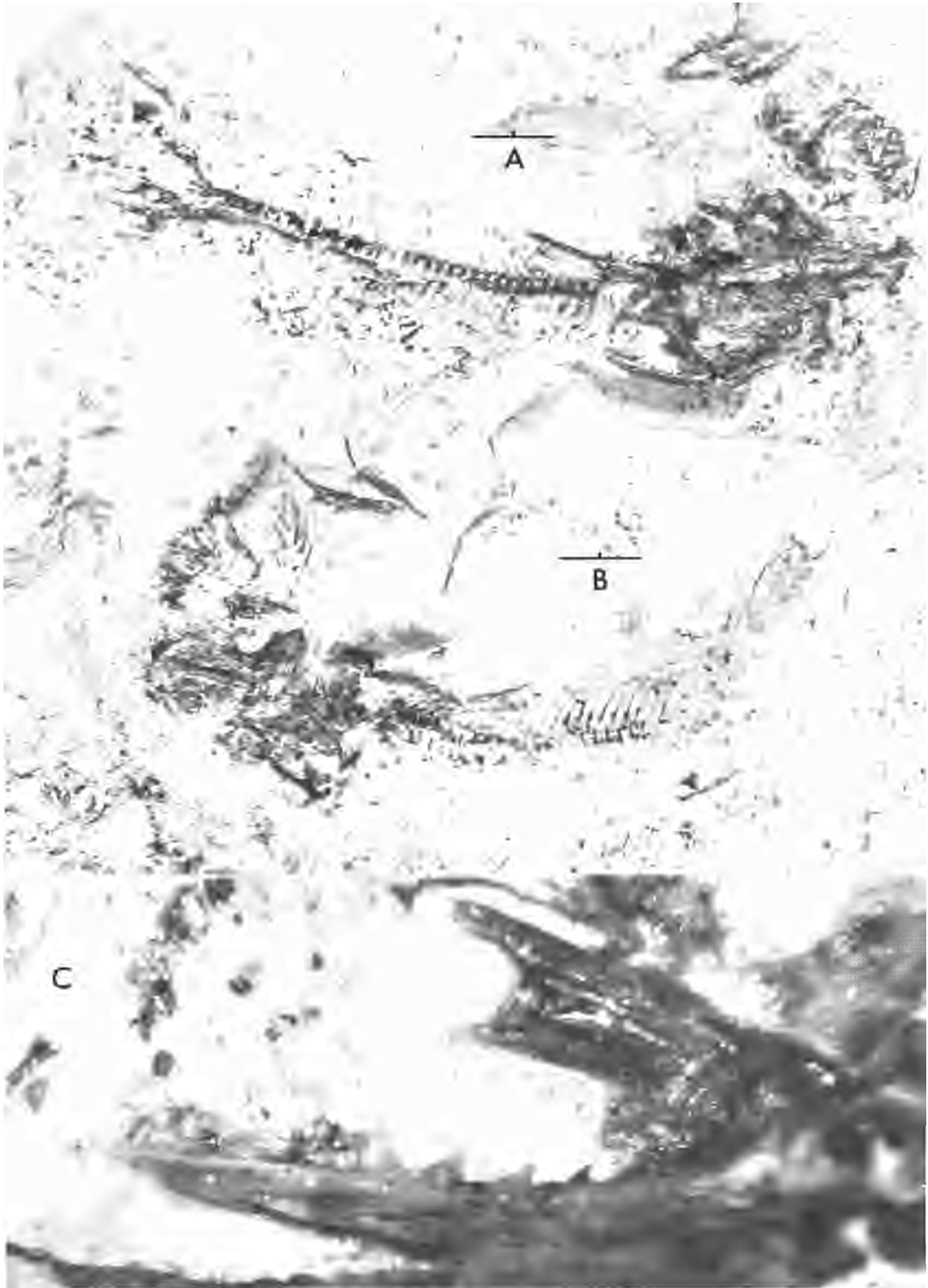


Plate 2. Ree Heights fishes. (A) and (B) *Noturus* cf. *hildebrandi* Bailey and Taylor, part and counterpart of UNSM 71130; (C) detail of pectoral region of (A) showing pectoral spine, dentations and humeral process of the cleithrum (X 13). Each line equals 10 mm.

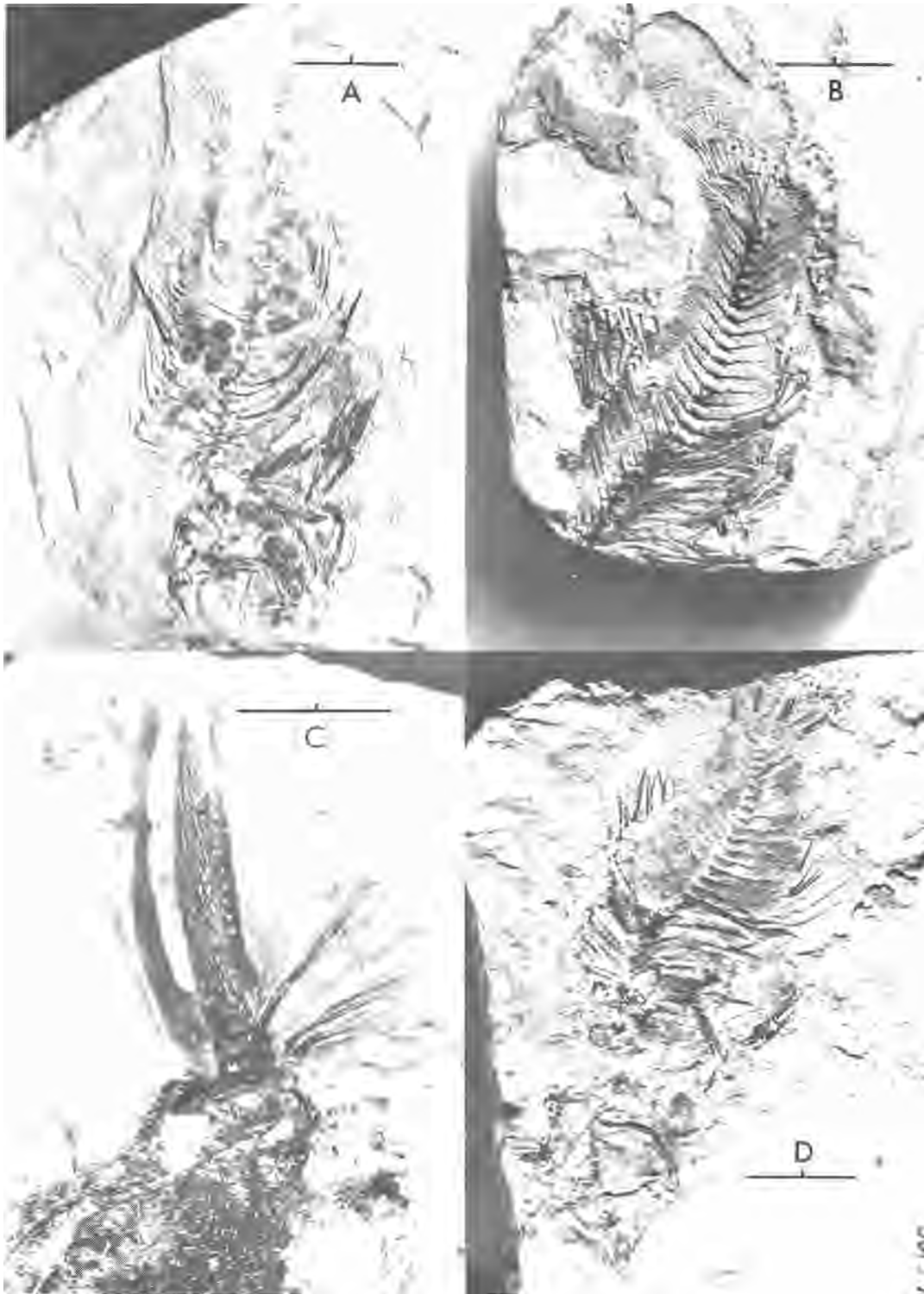


Plate 3. Ree Heights fishes. (A) *Micropterus salmoides* (Lacépède) UNSM 71037; (B) *Sardinus blackburni* Cope AMNH 8091; (C) *Ictalurus melas* Rafinesque UNSM 71139 (detail of left pectoral spine); (D) *Lepomis humilis* (Girard) UNSM 70682. Each line equals 10 mm.

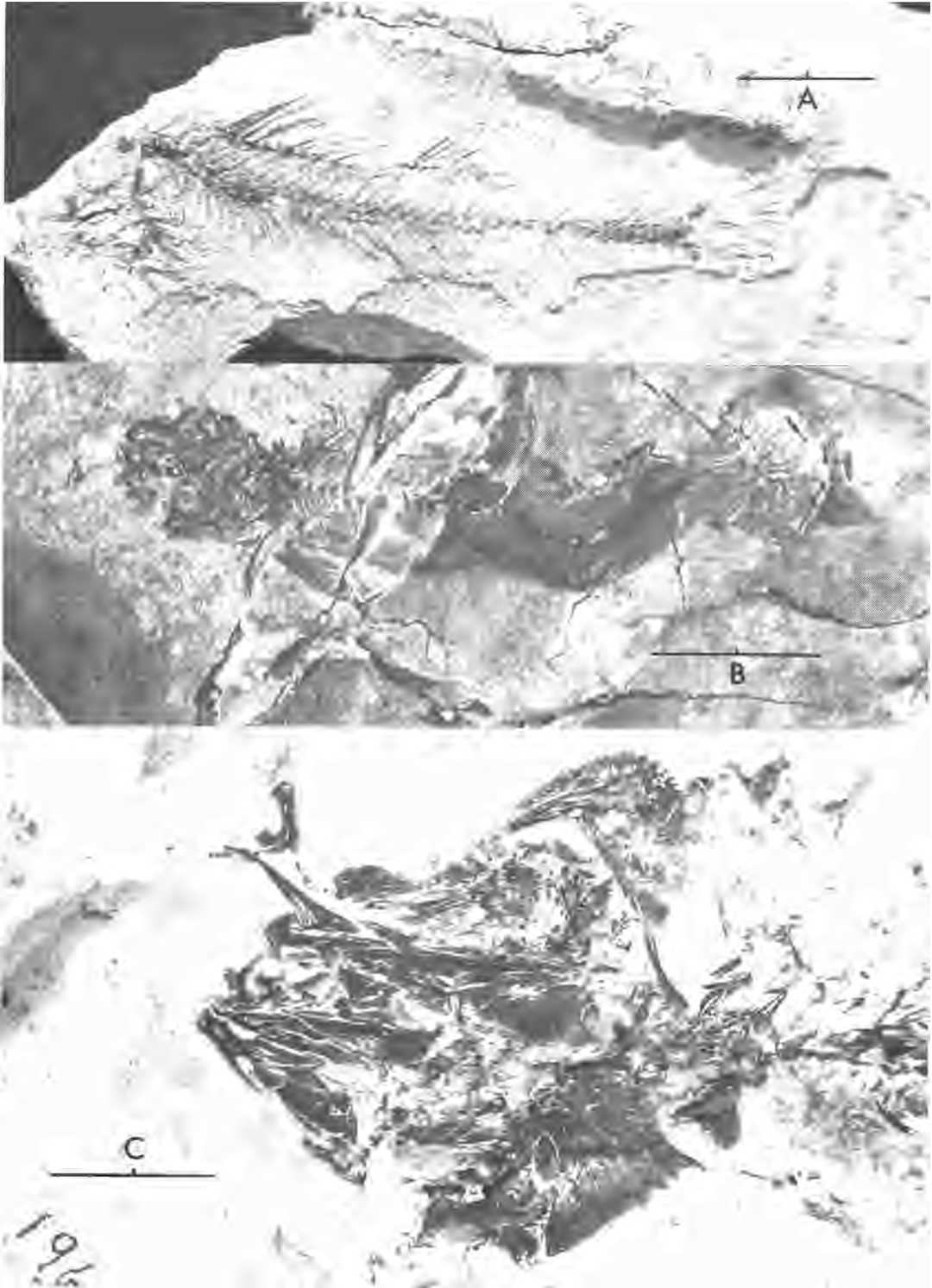


Plate 4. Ree Heights fishes. (A) *Percina* cf. *copelandi* (Jordan) UNSM 71130; (B) *Etheostoma* *exile* (Girard) UNSM 71164; (C) *Perca flavescens* (Mitchill) UNSM 71177. Each line equals 10 mm.

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