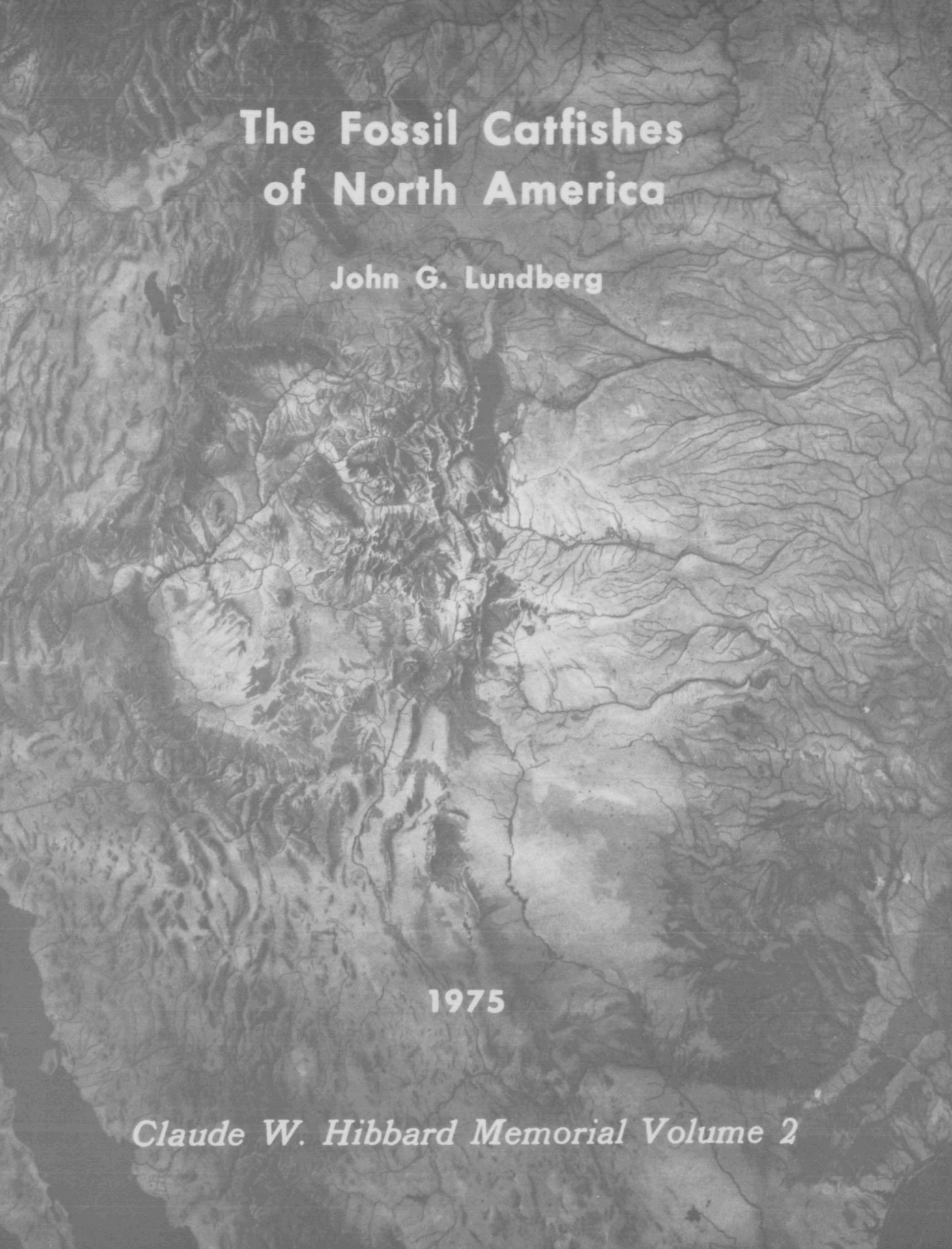


The Fossil Catfishes of North America

John G. Lundberg

1975

Claude W. Hibbard Memorial Volume 2

CLAUDE W. HIBBARD MEMORIAL VOLUMES (1-5)

Index and Bibliography of Late Cenozoic Freshwater Mollusca of Western North America
Dwight W. Taylor

The Fossil Catfishes of North America
John G. Lundberg

Studies on Cenozoic Paleontology and Stratigraphy
(Papers Presented at Hibbard Memorial Symposium, May, 1974, in Ann Arbor)

Geology and Paleontology of the Early Pleistocene Belleville Formation of North-Central Kansas
Ralph E. Eshelman

Fishes of the Pliocene Glenns Ferry Formation, Southwest Idaho
Gerald R. Smith
and
Fishes of the Miocene-Pliocene Deer Butte Formation, Southeast Oregon
Peter G. Kimmel

Museum of Paleontology
The University of Michigan
Ann Arbor, Michigan 48104

The Fossil Catfishes of North America

John G. Lundberg

PAPERS ON PALEONTOLOGY NO. 11

1975

Claude W. Hibbard Memorial Volume 2

PAPERS ON PALEONTOLOGY NO. 11

Museum of Paleontology
The University of Michigan
Ann Arbor, Michigan 48104

printed in Ann Arbor, Michigan
by Litho Crafters, Inc.

CONTENTS

ABSTRACT....iv

INTRODUCTION....1

PREVIOUS WORK....1

MATERIALS AND METHODS....1

ABBREVIATIONS USED IN ILLUSTRATIONS....2

SYSTEMATIC PALEONTOLOGY....2

Family Ariidae....2
Genus *Rhineastes* Cope....2
Rhineastes peltatus Cope....2
(?)*Rhineastes smithi* Cope....3
(?)*Rhineastes radulus* Cope....3

Genus *Arius*....3
Arius stauroforus (Lynn and Melland)....3
Arius felis (Linnaeus)....3

Genus *Bagre*....3
Bagre marinus (Mitchell)....3

Family Ictaluridae....4

Genus *Astephus* Cope....4
Astephus antiquus (Leidy)....7
Astephus calvus (Cope)....9
Astephus resimus, new species....9
Astephus, Indeterminate Species....11

Genus *Hypsidoris* Lundberg and Case....13
Hypsidoris farsonensis Lundberg and Case....13
Indeterminate Early Cenozoic Genera....15

Genus *Ictalurus* Rafinesque....17
Subgenus *Ictalurus* Rafinesque....17
Ictalurus rhaeas (Cope)....17
Ictalurus lambda Hubbs and Hibbard....17
Ictalurus furcatus (Lesueur)....19
Ictalurus punctatus (Rafinesque)....19
Ictalurus dugesi (Bean)....25
Ictalurus echinatus, new species....25
Indeterminate Species....27
Subgenus *Amiurus* Gill....27
Ictalurus pectinatus Cope....27
Ictalurus serracanthus Yerger and Relyea....29
Ictalurus catus (Linnaeus)....29
Ictalurus brunneus (Jordan)....29
Ictalurus macgrewi, new species....29
Ictalurus lavetti, new species....31
Ictalurus natalis (Lesueur)....35
Ictalurus leidyi, new species....35
Ictalurus nebulosus (Lesueur)....37
Ictalurus sawrockensis Smith....37
Ictalurus melas (Rafinesque)....38
Ictalurus peregrinus, new species....39
Ictalurus vespertinus Miller and Smith....41
Ictalurus (Amiurus), Indeterminate Spp....43
Ictalurus, Indeterminate Subgenus and Spp....44
Genus *Noturus* Rafinesque....45
Genus *Pylodictis*....45
Pylodictis olivaris (Rafinesque)....45

CONCLUSIONS....46

CLASSIFICATION OF FAMILY ICTALURIDAE....48

ACKNOWLEDGMENTS....49

LITERATURE CITED....50

ABSTRACT

The Cenozoic fossil record of the teleost order Siluriformes (catfishes) is reviewed. Fossils from freshwater deposits ranging from the late Paleocene through the Pleistocene represent two modern families: Ariidae and Ictaluridae.

The Eocene ariid genus *Rhineastes*, consisting of *R. peltatus* and *R. smithi*, has an uncertain relationship to modern lineages. *Rhineastes* constitutes an exceptional freshwater record for its primarily marine family. *Rhineastes radulus* is a *nomen dubium*. *Bagre marinus* and *Arius felis*, two living Atlantic and Gulf coast ariids, are known from late Pleistocene deposits. The Miocene *Arius stauroforus* is close to *A. felis*.

Astephus and *Hypsidoris* are extinct early Cenozoic genera of the Ictaluridae. *Astephus* (Paleocene-Oligocene) consists of three formally recognized species: *A. antiquus* (new combination), *A. calvus*, and *A. resimus* (described as new). *Rhineastes arcuatus* and *Ameiurus primaevus* are synonymized with *A. antiquus*. Much unnamed material is described which points to a greater diversity of the genus. *Hypsidoris* from the Eocene is currently monotypic but a few poorly preserved specimens may represent as yet unrecognized species.

Astephus and *Hypsidoris* share specializations of the pelvic fin and girdle with modern ictalurids. However, the extinct genera are strikingly more primitive in their possession of vomerine teeth, constant development of a rib on the fifth vertebra, and the absence of jaw muscle origin on the skull roof. *Hypsidoris* apparently has maxillary teeth, which indicates that this dentition was retained beyond the "*Diplomystes*-grade" of catfish evolution. *Astephus* is probably closer by common ancestry to modern ictalurids than is *Hypsidoris*.

The living ictalurids form a monophyletic group that is especially well characterized by extensive jaw muscle origin on the skull roof. Seven major lineages of modern ictalurids are recognized: the subgenera *Ictalurus* and *Amiurus* of *Ictalurus*, and the genera *Noturus, Pylodictis, Prietella, Satan,* and *Trogloglanis*. The last three are rare troglodytes, none of which is known as fossil.

The earliest known occurrence of the subgenus *Ictalurus* is with *I. rhaeas* (new combination) of the Oligocene Cypress Hills Formation. *Ameiurus cancellatus* and *Ameiurus maconnellii* are synonymized with *I. rhaeas*. An unnamed Oligocene fossil from South Dakota may also be an early representative of this lineage. Beyond these forms, the subgenus has left an excellent record which documents a marked evolutionary conservatism. The distinctive Mio-Pliocene *I. echinatus* (described as new) is one of two known extinct species of the subgenus *Ictalurus*. *Ictalurus lambda*, from the Pliocene, is very similar to the living *I. furcatus*. The living channel catfish, *I. punctatus*, is known from well-preserved fossils throughout the late Cenozoic, beginning in the middle Miocene. *Ictalurus decorus* from the Miocene is placed in synonymy with *I. punctatus*. The Mexican *I. dugesi* has been recorded from lake deposits of late Pleistocene age.

The earliest known member of the subgenus *Amiurus* (bullheads) is the Oligocene *Ictalurus pectinatus* (new combination) from the Florissant lake beds. Three of the four members of the *I. catus* species group (*I. catus, I. serracanthus,* and *I. brunneus*) have left late Pleistocene remains in Atlantic and Gulf coast drainages. No known extinct species pertain to this group.

The most diverse fossil record of any ictalurid group has been left by the *I. natalis* species group of *Amiurus*. The three living species are known from the Pleistocene: *I. natalis* (Wisconsinan), *I. nebulosus* (Wisconsinan), and *I. melas* (Kansan). There are six extinct species. *Ictalurus macgrewi*, described as new, is the oldest, coming from middle Miocene deposits. *Ictalurus lavetti*, described as new, from the lower Pliocene is close to the lineage leading to *I. natalis*. The Mio-Pliocene *I. leidyi* is described as a new species, lying close to the *I. nebulosus-I. melas* lineage. *Ictalurus sawrockensis* is a Plio-Pleistocene form closely related to *I. melas*. *Ictalurus benderensis* has been placed in synonymy with *I. sawrockensis*. *Ictalurus peregrinus* is described as new from the Pliocene of Oregon. This species, and the closely related *I. vespertinus* from the Plio-Pleistocene of Idaho and Oregon, occur well outside of the geographical range of living ictalurids.

Noturus, the most species rich subgroup of the Ictaluridae, has left a meager Pleistocene fossil record.

The monotypic *Pylodictis* has a history that parallels that of *Ictalurus punctatus*. *Pylodictis olivaris* is known from middle Miocene and younger deposits, and over this period it has undergone no detectable osteological change.

THE TELEOST order Siluriformes, the catfishes, comprises nearly 2000 species that are currently classified in 31 families. This group has major centers of diversity in the tropical freshwaters of South America, Africa, and Asia. Temperate North America is peripheral to this diversity and has a single catfish family, the Ictaluridae. The Recent Ictaluridae, with about 43 species, rank first in size among endemic North American freshwater fish families, but compared to other catfish groups they are only moderately speciose. Also, in temperate North America the Ariidae, a primarily marine catfish family, are represented by a few coastal species. Nearly a century ago the first North American fossil catfishes were discovered and described. Since then, almost entirely through the collecting efforts of paleomammalogists, the continental Cenozoic deposits of North America have yielded what may be the most extensive fossil record for any group of Nearctic fishes. In spite of their abundance and potential systematic value, however, these fossils have been largely ignored by paleontologists and ichthyologists.

It is the purpose of this paper to catalogue and describe these remains of fossil catfishes from North America. The probable evolutionary relationships among the fossil and Recent ictalurids is also noted. However, a more detailed discussion of phylogeny is presented elsewhere (Lundberg, 1970 and in preparation).

Previous Work

The earliest reports of Paleogene catfishes can be credited almost entirely to Cope, Leidy, and Eastman. This work consists mainly of brief descriptions. Isolated bones from the Eocene Bridger and Green River Formations were described by Cope (1872, 1873, 1884) and Leidy (1873a, 1873b). Eastman (1917) gave an account of a nearly complete catfish skeleton from the Green River shales. A catfish from the Oligocene deposits near Florissant, Colorado was reported by Cope (1874 and 1884) and additional Oligocene material from the Cypress Hills, Saskatchewan was described in 1891 by Cope. More recently, Cavender (1968) and Lundberg and Case (1970) described additional specimens and began a more critical comparison of these to living catfishes. There has been much confusion surrounding the systematic position of these early Cenozoic fossils. Some or all of them have been referred (or compared) to the Ariidae (Jordan, 1923), Ictaluridae (Eastman, 1917), Bagridae (Frizzell and Dante, 1965), Pimelodidae and Doradidae (Cope, 1884), and Diplomystidae (Gardiner, 1966). It is now possible to conclude that at least two families are represented, the Ariidae and the Ictaluridae (Lundberg and Case, 1970). Fossils representing the Ariidae occur in freshwater Eocene, and coastal Miocene and Pleistocene deposits. The Ictaluridae are best represented in Eocene, and Miocene through Pleistocene deposits, and there are a few Paleocene and Oligocene records. In addition, the usual problematical specimens are present about which little can be said until more suitable material is collected.

The major contributions toward the anatomy and systematics of the late Cenozoic ictalurids have been by Hubbs and Hibbard (1951), C. L. Smith (1961, 1962), Uyeno and Miller (1962), Miller and G. R. Smith (1967), and Swift (1968b). Elsewhere these authors and others have also listed numerous records of fossil ictalurids. My studies indicate, however, that the diversity and abundance of late Tertiary and Pleistocene catfishes have been underestimated.

Reports of Cretaceous catfishes from Hell Creek deposits of Montana (Brown, 1907) have been neither verified nor discredited here but it is possible that these records are based on the heavily ossified first pectoral rays of sturgeons which are abundant in these deposits and are somewhat similar to catfish pectoral spines. Upper Cretaceous otoliths from the Fox Hills Formation, South Dadota, which were questionably referred to the Siluriformes by Frizzell (1965) have not been examined. Also, the Eocene otoliths which formed the basis for the description of a new genus and species of catfish (Frizzell and Dante, 1965) were not reexamined. Hence this material is not listed below. The formal description of fossil taxa based solely on otoliths cannot be strongly recommended. Otolith structure in ictalurids and bagrids appears to be too variable intraspecifically to serve as a source for reliable characters in descriptive taxonomy.

MATERIALS AND METHODS

The material examined in this study has come from numerous collections. The abbreviations listed here are those used throughout the text in referring to the materials.

AMNH, American Museum of Natural History
F:AM, Frick Collection at the American Museum of Natural History
KU, University of Kansas Museum of Natural History
MCZ, Museum of Comparative Zoology, Harvard University
MSU, Michigan State University
NMC, National Museum of Canada, Ottawa
PF, Field Museum of Natural History, Chicago

PU, Princeton University
SDSM, South Dakota School of Mines and Technology
SMUMP, Shuler Museum of Paleontology, Southern Methodist University
TMM, Texas Memorial Museum, Austin
UC, University of California, Berkeley
UF, University of Florida, Gainesville
UMMP, University of Michigan, Museum of Paleontology
UMMZ, University of Michigan, Museum of Zoology
UNSM, University of Nebraska, State Museum
UO, University of Oregon
USNM, United States National Museum, Smithsonian Institution
UW, University of Wyoming
YPM, Peabody Museum, Yale University

Abbreviations Used In Illustrations

AAPS, adductor arcus palatini scar on parasphenoid
AF, anterior cranial fontanelle
ant. dents., anterior dentations of pectoral spine
BR, basal recess at origin of fourth transverse process for anterior limb of tripus
CHYO, cranial facet for hyomandibular
CL, cleithrum
EPB, epiphyseal bar
EPO, epiotic
FLA, foramen for lateral accessory branch of facial nerve
FOP, optic nerve foramen
FR, frontal
FRC, frontal crests
FSCL, supracleithrum facet of fourth transverse process
LE, lateral ethmoid
LSOC, longitudinal crests for jaw muscle origin on supraoccipital
NS4, neural spine of fourth vertebra
OS, orbitosphenoid
PAS, parasphenoid
PF, posterior fontanelle
PFLE, palatine facet of lateral ethmoid
PMX, premaxilla
PMXP, sublateral posterior process of premaxilla
post. dents., posterior dentations of pectoral spine
PRO, prootic
PTO, pterotic
PTT, posttemporal
Q, quadrate
SE, supraethmoid
SCL, supracleithrum
SOC, supraoccipital
SP, sphenotic
SPP, sphenotic process
TP4, transverse process of fourth vertebra
TP5, transverse process of fifth vertebra
TSL, ossified transcapular ligament
TSOC, transverse crest of muscle origin on supraoccipital
V, vomer
VL, vertical lamina of Weberian complex

SYSTEMATIC PALEONTOLOGY

Family **Ariidae**

Genus *Rhineastes* Cope

Rhineastes.— Cope, 1872, p. 486.

Diagnosis.— Catfishes of the family Ariidae with the supraoccipital highly convex; dorsum covered with prominent, evenly distributed tuberculations. Anterior edge of the dorsal spine with multiple rows of dentations; posterior edge with a deep median groove and small dentations.

Type Species.— *Rhineastes peltatus* Cope, 1872, p. 486, by original designation.

Remarks.— In 1872 Cope described two species of fossil catfishes of the genus *Rhineastes* both of which appear to belong to the Ariidae. In 1873 he described additional species which were referred to this genus, but they were placed in the subgenus *Astephus*. It is concluded herein that the members of Cope's *Astephus* belong to the Ictaluridae; hence, *Astephus* is accorded generic rank. *Rhineastes* is restricted to include *R. peltatus*, and perhaps one other form, *R. smithi*.

Rhineastes peltatus Cope

(Fig. 1 A; Pl. II B, C)

Rhineastes peltatus.— Cope, 1872, p. 486 (original description; Bridger Formation, South Bitter Creek, Wyoming). Hay, 1929, p. 727 (list of previous references).

Diagnosis.— As for genus.

Holotype.— USNM 3984, supraoccipital bone and dorsal spine.

Horizon and Type Locality.— Bridger Formation, middle Eocene. South Bitter Creek, almost certainly in south-central Sweetwater County, Wyoming.

Description and Remarks.— The holotype and only known specimen consists of a partial supraoccipital bone and the mid-section of the dorsal spine. The surface of the supraoccipital is covered with prominent, evenly spaced tuberculations. The posterior cranial fontanelle is a deep, closed groove that extends longitudinally across the anterior half of the bone. The supraoccipital spine is broken off at the base, but it appears to have been quite broad. On the posterior face of the bone a median vertical lamina separates the paired foramina of the lateral accessory nerves. Beneath each of these foramina a strong horizontal shelf is developed. Among the Recent catfishes examined these horizontal shelves have been found only in the ariid genera *Arius* and *Potamarius*.

The dorsal spine is strongly compressed laterally. The

sides of the spine are finely striate. Along the anterior edge there are multiple rows of prominent dentations that are irregularly spaced. Along the posterior edge there is a deep median groove and a few small evenly spaced dentations.

The extreme development of the dermal tubercles in *R. peltatus* almost certainly excludes the possibility of close relationship with the Ictaluridae. The only catfish families that exhibit such well-developed dermal tubercles, at least in some species, are the Ariidae, Bagridae, Pimelodidae, and Doradidae. The characters of the fossil, however, are most closely approached by some species of *Arius*. On this basis the fossil form is referred to the Ariidae. The species of *Arius* examined differ from the fossil in having a single median row of dentations on the anterior edge of the dorsal spine and the posterior part of the supraoccipital is angular at the midline rather than smoothly convex.

Fossil ariids are known from early Tertiary marine and freshwater deposits in Europe and Africa (Casier, 1960). This family at present is primarily restricted to brackish water habitats but there are freshwater representatives on all continents except Europe and the United States and Canada.

(?) *Rhineastes smithi* Cope

(Fig. 1 B)

Rhineastes smithii.– Cope, 1872, p. 486 (original description; Bridger Formation, South Bitter Creek, Wyoming). Hay, 1929, p. 727 (list of previous references).

Diagnosis.– A catfish, perhaps belonging to the genus *Rhineastes*, that differs from other fossil catfishes, as far as known, in having strong, regularly spaced anterior and posterior dentations on a flattened or compressed pectoral spine.

Holotype.– USNM 3977, right pectoral spine.

Horizon and Type Locality.– Bridger Formation, middle Eocene. Mammoth Buttes, South Bitter Creek, Wyoming.

Material, Localities, and Horizons.– USNM 3978, basal half of left pectoral spine, from type locality (Cope, 1884, pl. 5, fig. 10).

USNM 3979, fragment of dentary bone, from type locality. (Tentative identification based on association, Cope, 1884, pl. 5, fig. 11).

USNM 167587, portion of right cleithrum and basal part of pectoral spine, from Wyoming.

PU 19326 (part), right pectoral spine, from Henry's Fork, Sweetwater County, Wyoming. Upper White Layer of Bridger D Formation.

Description and Remarks.– The character of the anterior and posterior dentations and the flattened form of the pectoral-spine shaft are unique among fossil and living North American catfishes. The posterior process of the cleithrum is broad and nearly completely covered basally with well-developed but fine tubercles.

The ornamentation of the pectoral spine and cleithral process of *Astephus* is very different from that of *R. smithi*. There are no pectoral spines associated with the holotype of *R. peltatus*, and it is possible that spines of *R. smithi* are actually those of *R. peltatus*. Usually in catfishes the degree of development of ornamentation of dorsal and pectoral spines are positively correlated, and *R. peltatus* is known to have a highly ornamented dorsal spine. The material of both *R. peltatus* and *R. smithi* is known only from the Bridger Formation in the vicinity of South Bitter Creek, Wyoming.

Nomen dubium

Rhineastes radulus Cope, 1873, p. 639.

The type of *R. radulus*, USNM 4099, comprises four bone fragments, unidentifiable to element, but bearing dermal ornamentation similar to that found in some catfishes. This material is insufficient to permit confident identification. Cope (1884) questioned his earlier reference of these bones to *Rhineastes*. Smith-Woodward (1901) also expressed doubt as to the validity of *R. radulus*.

Genus *Arius*

Arius stauroforus (Lynn and Melland)

Felichthys stauroforus.– Lynn and Melland, 1939, p. 14 (original description; Calvert Formation, Maryland).

Holotype.– USNM 15746, partial neurocranium.

Horizon and Type Locality.– Calvert Formation, Zone 12, Miocene. Three mi S of Plum Point, Maryland.

Remarks.– The holotype was not examined but based on the original description and figures this form appears to be closely related to the Recent *Arius felis*.

Arius felis (Linnaeus)

Material, Localities, and Horizons.– Vero fauna. Vero Beach, Florida, center SW¼ Sec. 35, T 32 S, R 39 E, Bed 3 of Vero deposits, late Pleistocene (Weigel, 1963). AMNH 2935 (part), pectoral and dorsal spines.

Remarks.– These spines are not structurally distinct from those of Recent specimens of *A. felis*.

Genus *Bagre*

Bagre marinus (Mitchell)

Material, Localities, and Horizon.– Pectoral spines (not examined), Pleistocene deposits, Florida. Swift (1968a) reported spines of *Bagre marinus*.

FIGURE 1

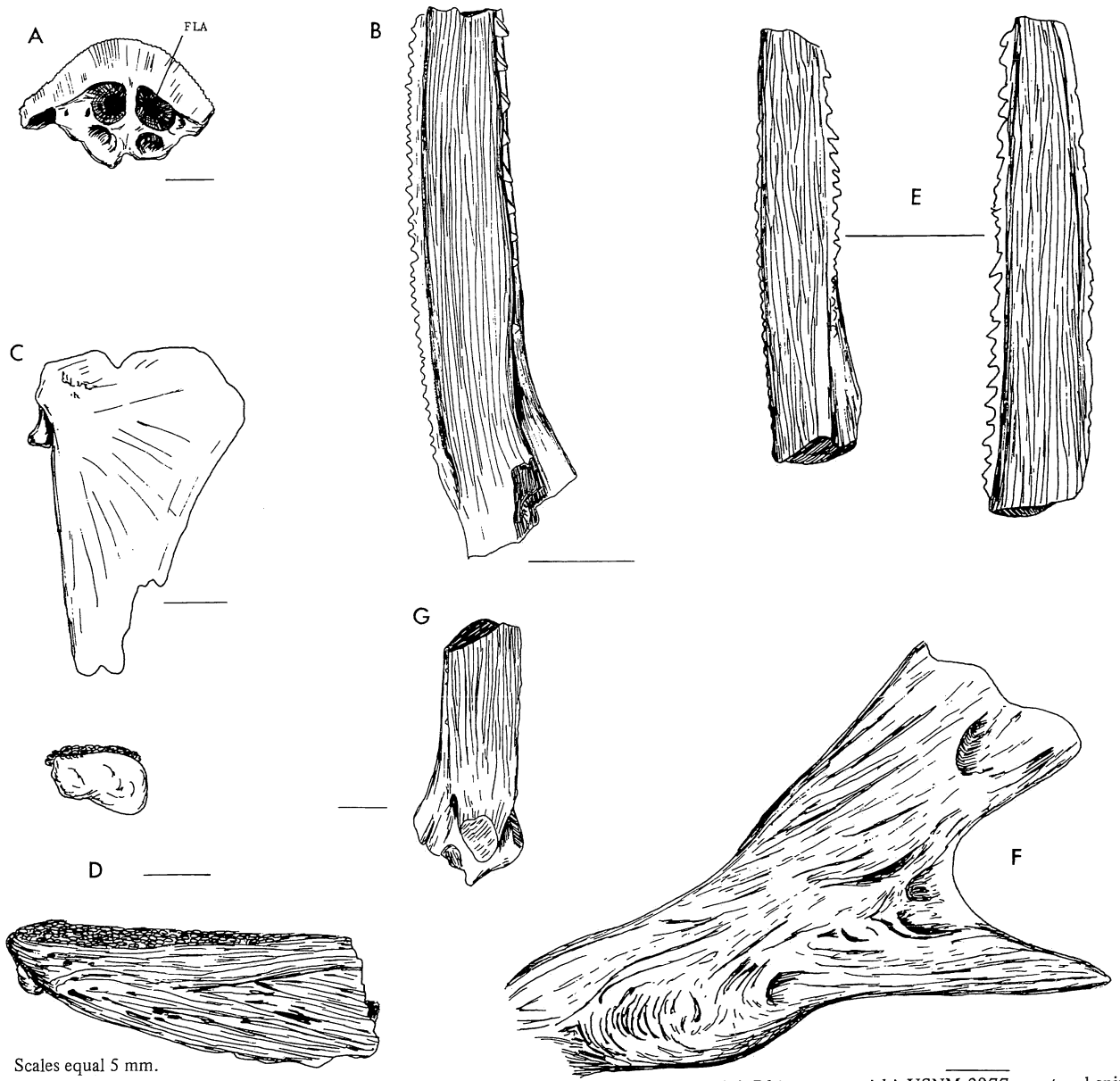


Fig. 1. (A) *Rhineastes peltatus*, USNM 3984, supraoccipital bone, posterior view. (B) *Rhineastes smithi*, USNM 3977, pectoral spine. (C) *Astephus antiquus*, UMMP V57981, opercle. (D) *Astephus antiquus*, USNM 2179, dentary, symphyseal and lateral view. (E) *Astephus antiquus*, UMMP V57980, two pectoral spines. (F) *Astephus* sp., AMNH 6060, left cleithrum, lateral view. (G) *Astephus* sp., SDSM 6948, pectoral spine base, Slim Buttes, South Dakota.

Family **Ictaluridae**

Genus *Astephus* Cope

Astephus.– Cope, 1873, p. 638 (proposed as a subgenus of *Rhineastes*). Jordan, 1923, p. 146 (recognized *Astephus* as a genus of ariid catfishes).

Diagnosis.– An extinct genus of ictalurid catfishes that differs from living genera in the possession of villiform vomerine teeth, the constant development of a rib on the fifth vertebra, and the lack of jaw-muscle origin on the temporal region of the skull roof.

Astephus differs from other extinct North American

catfishes in the broad supraethmoid, single transverse band of vomerine teeth, full development of the rib of the fifth vertebra, reticulating pattern of dermal ridges on the skull roofing bones, simple subparallel ridges on the posterior process of the cleithrum (perhaps one exception), relatively short pectoral spine (length, excluding base, contained in standard length more than five times), and nine pelvic rays.

Perhaps *Astephus* is unique in having the ventral surface of the supraethmoid cornua dorsal to the level of the ventral surface of the vomer.

Type Species.– *Astephus antiquus* (Leidy), 1873a, p. 99 (here designated).

Description.– The abundant and well-preserved remains of various species of *Astephus* permit a fairly detailed description of the anatomy of this genus.

Supraethmoid cornua robust and widely separated; median cleft shallow and broad; ventral edges of cornua do not extend downward to level of vomer (USNM 18104). Snout very broad; dorsal width of supraethmoid very broad. Skull roof slightly arched. Skull broad at epiphyseal bar. Anterior and posterior cranial fontanelles broadly open. Supraoccipital process narrow (at least in *A. antiquus*), long, and contacts an unreduced supraneural. No scars of muscle origin on supraoccipital and frontals; bones of skull roof sculptured with reticulating ridges, grooves, and pits, arranged more longitudinally along margin of posterior cranial fontanelle. Sphenotic extends to level of anterior margin of epiphyseal bar; sphenotic margin distinctly convex. Posttemporal bone large, platelike, sutured to pterotic and supraoccipital; not divided into separate laminar and laterosensory parts.

Pterotic wing angular, without deep pits. Nasal bone a wide tube. Number of supraorbital sensory canal pores and infraorbital bones indeterminate. Infraorbital canal exits from skull roof through sphenotic (AMNH 6387, PU 18850). First infraorbital or lachrymal tetraradiate (USNM 8122, AMNH 6388); its anterior process long and slender. Lateral-ethmoid wing long and slender, apparently not strongly curved downward. Posterodorsal margin of lateral-ethmoid wing not truncated for muscle origin. Foramen for superficial ophthalmic branches of fifth and seventh cranial nerves not expanded. Vomer t-shaped as in modern ictalurids, but bears transverse band of close-set villiform teeth. Parasphenoid incorporated into cranial floor, its stem below orbit narrow, its ascending wings straight and nearly horizontal below trigeminofacialis foramen and along pterosphenoid suture. Adductor arcus palatini muscle scar curved dorsally away from ventral edge of parasphenoid. Frontals with large descending wings (USNM 18104). Single trigeminofacialis foramen; prootic and pterosphenoid contact present. Orbitosphenoid shelves very broad. Prootic-exoccipital contact partly sutural, prootic-basioccipital contact synchondral. Optic foramen small.

Lower jaw moderately large, total number of mandibular pores indeterminate but first pore remote from symphysis. No symphyseal process on dentary, and anteroventral crest present but tapered near symphysis. Posterior or articular edge of coronoid process shallowly inclined; no strong articular process.

Premaxilla rectangular and well ossified, with distinct dorsolateral groove. No mesial process on premaxilla, form of sublateral premaxillary process indeterminate. Premaxillary teeth close set, villiform, and nearly uniform in size. Maxillae small and edentulous (YPM 844). Palatines rodlike, single headed, moderately long (YPM 844).

Cranial facet of hyomandibular short, included in hyomandibular depth about two times (UMMP V57961, V57962, USNM 8122). Anterior process of hyomandibular flattened and directed anterodorsally but articulates with small shelves on pterosphenoid (USNM 18104, MCZ 8500). Opercular facet near midpoint of hyomandibular. Hyomandibular-metapterygoid suture long, hyomandibular-quadrate suture present. Scar of A_3 bundle of adductor mandibulae present, and levator arcus palatini crest long but weakly developed. Dorsal edge of adductor crest at the level of the opercular facet. Levator operculi crest weak and adductor hyomandibularis process low and rounded. Lower end of facial canal separated from mandibularis nerve foramen; groove between facial canal and symplectic canal shallow or absent. Symplectic canal incorporated into preopercle.

Preopercle concave and expanded behind sensory canal, its upper limb extends above level of adductor crest. At least one suprapreopercle developed; presence of subpreopercle indeterminate.

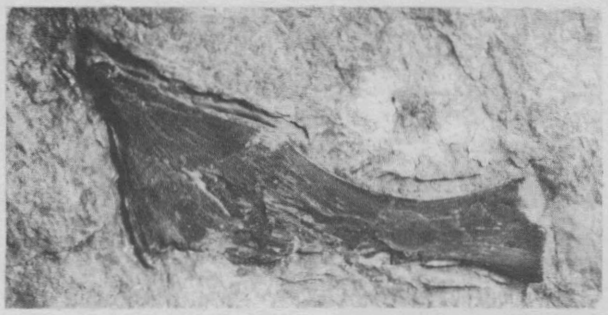
Quadrate-metapterygoid suture short, with little cartilage. Dorsal edge of metapterygoid convex, anterior precess developed. Endopterygoid present, but its size indeterminate.

Cartilage persists dorsally in epihyal-ceratohyal contact. Ceratohyal compressed, with no dorsal keel; epihyal with no ventral expansion; no ceratohyal-hypohyal sutures; dorsal hypohyal unreduced. Urohyal trapezoidal in form with subequally developed vertical and horizontal laminae.

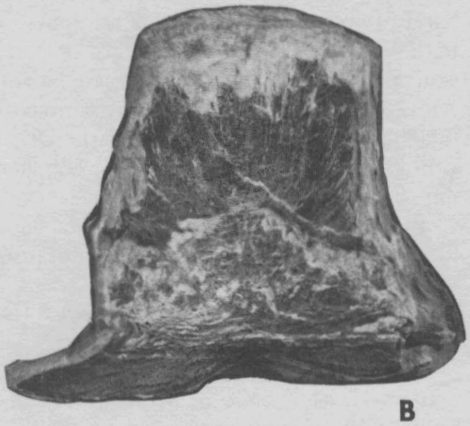
Opercle form normal, its dorsal edge straight and not markedly flattened. Interopercle shallow, with no posteroventral expansion.

First centrum with pair of pits dorsally; ventral ridges well developed. Fifth centrum strongly sutured to complex centrum and superficial ossification well developed. Aortic groove open. Anterior limb of fourth transverse process moderately expanded, basal recess for tripus broad and deep. Posterior limb separated from anterior by deep, smooth concavity. Third and fourth neural arches and spines well developed, joined by vertical lamina.

PLATE I



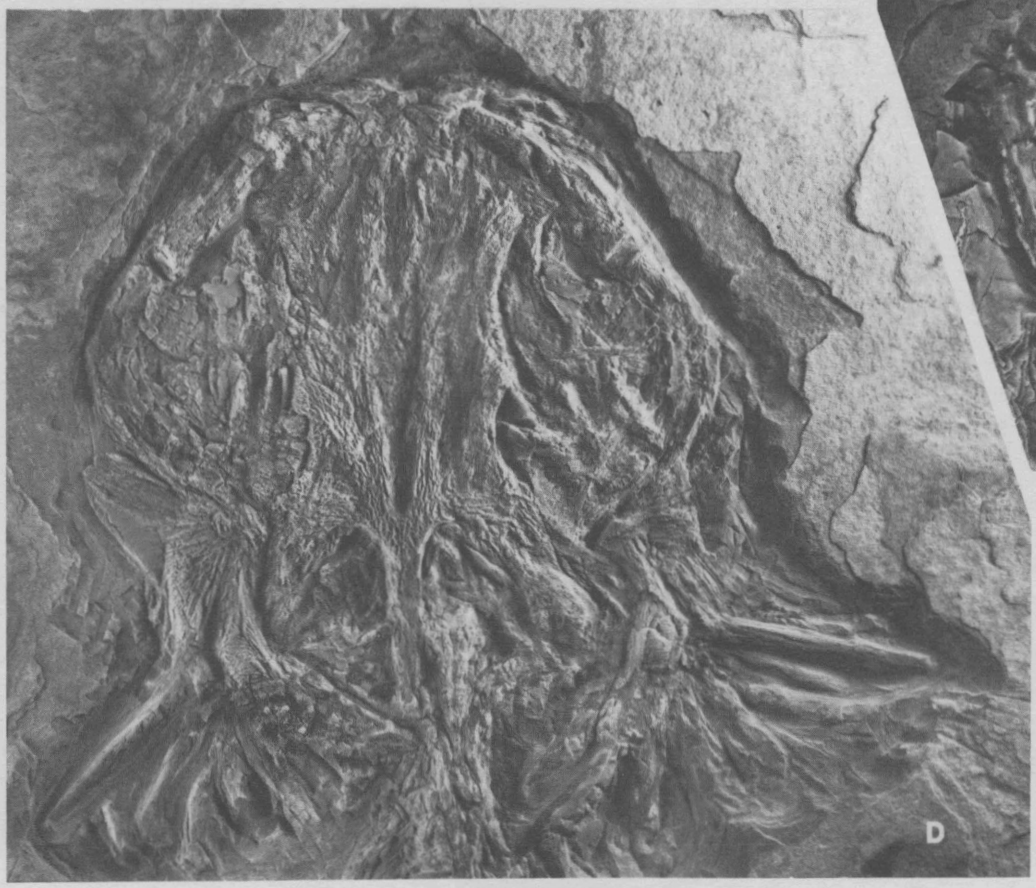
A



B

C

E



D

F

Precaudal vertebrae 17 or 18, caudal vertebrae 24, or 25 (USNM 8122, UNSM 70107). Hypural formula PH; 1;2;3;4;5;6, hypurapophysis and secondary hypurapophysis well developed. Caudal fin forked, with pointed lobes; principal rays 8 in upper, and 9 in lower lobe.

First dorsal basal and spine well developed; second dorsal basal well developed, facets for second spine horizontal. Second, or defensive, dorsal spine slightly shorter than pectoral spine; spine usually ornamented with median row of regularly spaced anterior dentations and occasionally a few weakly developed posterior dentations. At least 5 dorsal soft rays. Anal rays about 26, basals about 24 (UNSM 70107). Eastman (1917) thought USNM 8122 possessed about 15 anal rays, but the anal fin of this individual is distorted and some of the anterior rays appear to have been lost in preparation.

Pectoral soft rays 10 (AMNH 6388), pectoral radials unfused. Posterior process of cleithrum long and sculptured with subparallel ridges and grooves, no tubercles. Cleithral symphysis short. Coracoid symphyseal sutures 5 to 7. Coracoid ventral keel short, secondary keel present. Extensor fossa of coracoid short, broad and shallow.

Supracleithrum with completely ossified transcapular ligament; no pterotic process.

Pectoral spine with sharp tip; anterior distal serrae weakly developed or absent; anterior ridge weakly to moderately developed, anterior dentations weak, numerous, irregularly spaced; posterior dentations weak and numerous; dentation halves often irregularly spaced, and erect, but all arise from posterior groove.

Pelvic girdle with moderate lateral process and no lamina lateral to anterolateral process; no ossified ischiac process. Pelvic splint large, pelvic rays 9 (AMNH 6387, YPM 844, UNSM 70107).

Astephus antiquus (Leidy)

(Fig. 1 C-E; Pl. I A-F, Pl. II A, D, E, Pl. III, Pl. VII F)

Pimelodus antiquus.– Leidy, 1873a, p. 99 (original description; Bridger Formation, junction of Big Sandy and Green River, Wyoming). Leidy, 1873b (characters).

Rhineastes arcuatus.– Cope, 1873, p. 641 (original description; Bridger Formation, Wyoming). Cope, 1884 (characters). Hay, 1929, p. 727 (list of previous references).

Ameiurus primaevus.– Eastman, 1917, p. 293 (original description; almost certainly Green River Shales, Wyoming).

Diagnosis.– A species of *Astephus* that differs from the other known species of the genus in the combination of the following characters: (1) supraethmoid cornua moderately broad and robust, (2) supraethmoid cleft very shallow, (3) margin of frontal bone above orbit straight or slightly concave, (4) no distinct depression or groove along frontal-sphenotic suture, (5) supraoccipital process slender and long, (6) vomerine tooth patch slender at the midline.

Holotype.– USNM 2179, right pectoral spine, and dentary bone.

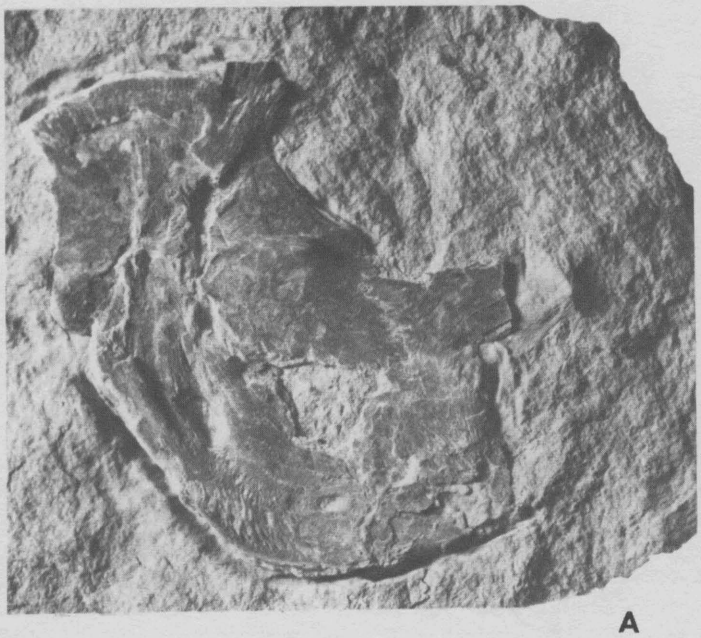
Horizon and Type Locality.– Bridger Formation, middle Eocene. Junction of Big Sandy and Green River, Sweetwater County, Wyoming.

Material, Localities, and Horizons.– Green River Formation: AMNH 6387, partial anterior part of fish, Powder Springs, Utah. Green River Formation, Laney Shale Member: USNM 8122, nearly complete fish, no data (Eastman's type of *Amiurus primaevus*); AMNH 6388, complete anterior part of fish, 1 mi S of Green River, Sweetwater County, Wyoming; AMNH 9499, complete neurocranium, "Fish Cut," on Union Pacific Railroad bed, W of Green River, Sweetwater County, Wyoming; YPM 844, nearly complete fish, no data; USNM 167588, partial neurocranium, Hams Fork, about 20 mi above Granger Station, Wyoming; PF 6399, basioccipital and vertebra, "Mystery Gulch," NE¼, SE¼, Sec. 30, T. 30 N, R. 105 W, Sublette County, Wyoming; PF 6400, pectoral spines and miscellaneous bones, "Scale Canyon," NW¼, Sec. 30, T. 30 N, R. 105 W, Sublette County, Wyoming; UW 979, two pectoral spines, from Morrow Creek Member of Green River Formation (McGrew, 1959).

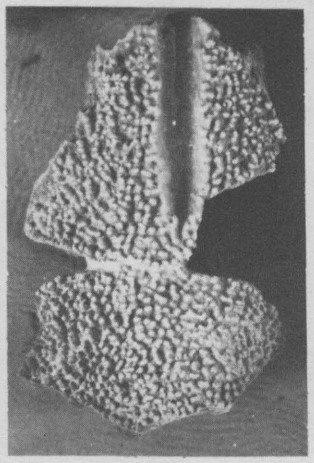
Bridger formation: USNM 3985, complete pectoral spine (Cope's type of *Rhineastes arcuatus*), USNM 167-589, vertebrae, Weberian complex fragments, and basioccipitals; USNM 167590, pectoral spines and miscellaneous bones, junction of Big Sandy and Green River, Sweetwater County, Wyoming; UMMP V59687 neurocranium, V57961-V57963, suspensoria, V57964-V57971 neurocrania, V57972 two supraethmoid bones, V57973 dorsal spine and second dorsal basal, V57974 hyoid bar, V57975-V57977 cleithra, V57978 supracleithra, V57979-V57980 pectoral spines, V57981 opercle, V57982 Weberian complexes, V57983 miscellaneous bones, junction of Big Sandy and Green River, Sweetwater County, Wyoming; USNM 3983, pectoral spines and miscellaneous bones, Fort Bridger, Wyoming; UW 3275, pectoral spines, Lombard Buttes, NE¼, Sec. 25, T. 22 N, R. 110 W, Sweet-

Plate I. (A) *Astephus antiquus*, mesial view of left hyoid bar (UMMP V57974), 35 mm in length. (B) *Astephus antiquus*, dorsal view of supraethmoid (UMMP V57972), 19 mm in length at midline. (C) *Astephus antiquus*, dorsolateral view of partial right shoulder girdle with spine base in place (UMMP V57976), anterior at bottom, 44 mm in width. (D) *Astephus antiquus*, dorsal view of anterior part of fish (USNM 8122), 71 mm in skull length. (E) *Astephus antiquus*, pelvic girdle and nine fin rays (YPM 844), 31 mm in length. (F) *Astephus antiquus*, ventral view of fragmentary supraethmoid and vomer (UMMP V57072), 15 mm in length at midline.

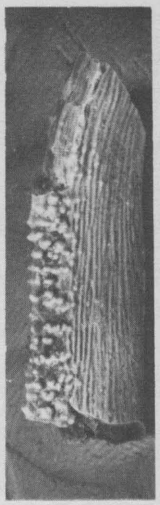
PLATE II



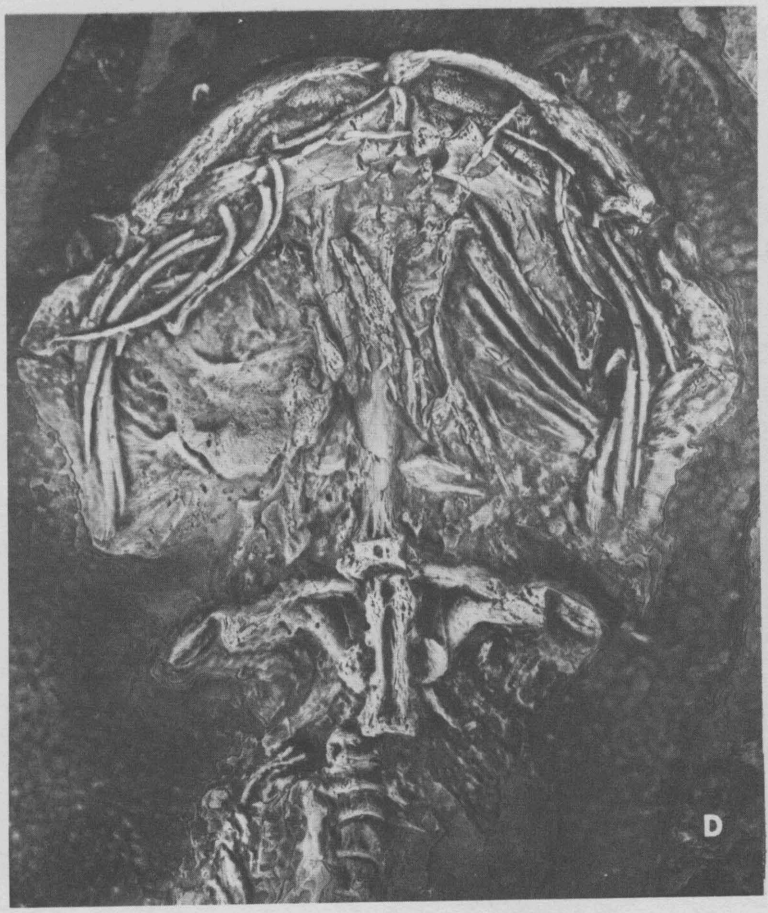
A



B



C



D

E

water County, Lower Bridger A; UW 3276, pectoral spines, Sublette County, Wyoming, Early Bridger; PF 640, pectoral spine, SE¼, NE¼, Sec. 25, T. 30 N, R. 105 W, Sublette County, Wyoming, Lower Bridger; UW 990, pectoral spine, Locality 3 (McGrew, 1959), Tabernacle Butte, Sublette County, Wyoming, Upper Bridger; PF 6402, pectoral spines, "Fish Hill," SW¼, Sec. 5, T. 29 N, R. 105 W, Sublette County, Wyoming, Lower Bridger; PF 6403, pectoral spines, NE¼, Sec. 19, T. 29 N, R. 105 W, Sublette County, Wyoming, Lower Bridger; PF 6404, pectoral spines, "Jeans Quarry," S½, Sec. 8, T. 25 N, R. 105 W, Sublette County, Wyoming, Lower Bridger. Wyoming, no data: USNM 3981, pectoral spines; USNM 3982, pectoral spine, opercle, dentary, supracleithrum.

Description and Remarks.– The previous discussions of the anatomy of the genus *Astephus* are based largely on the numerous specimens referred to this species, and no more details need be added here.

Cope (1884) and Hay (1901) pointed out that the name *Pimelodus antiquus* Leidy (1873a) predates *Rhineastes arcuatus* Cope (1873) but they treated the former as a *nomen nudum*. Later in 1873 Leidy published a complete description of *P. antiquus*. In addition to the binomen, Leidy's original description includes only a general statement on the presence of siluriform remains at the type locality and he estimated the size of the individual from which the material came. This reference to size constitutes a valid descriptive character (Carl Hubbs, pers. comm.), and therefore, *Pimelodus antiquus* is regarded here as the oldest valid name for the species.

Astephus calvus (Cope)

(Pl. IV C, D, Pl. V B)

Rhineastes calvus.– Cope, 1873, p. 640 (original description, Bridger Formation, Mammoth Buttes, South Bitter Creek, Wyoming). Hay, 1929, p. 727 (list of previous references).

Diagnosis.– A species of *Astephus* that differs from other known species of the genus in the combination of the following characters: (1) very widely separated and slender supraethmoid cornua; (2) supraethmoid cleft shallow; (3) margin of frontal bone above the orbit convex; (4) distinct, oval-shaped depressions across the fronto-sphenotic suture; (5) supraoccipital process broad at least at base; and (6) vomerine tooth patch wide at midline.

Holotype.– USNM 3980, partial neurocranium.

Horizon and Type Locality.– Bridger Formation, middle Eocene. Mammoth Buttes, South Bitter Creek, Sweetwater County, Wyoming.

Material, Localities, and Horizons.– MCZ 8500, complete neurocranium and anterior vertebrae, 5 mi N of Opal, Lincoln County, Wyoming, Bridger A Formation.

Description and Remarks.– As far as known *A. calvus* is similar to *A. antiquus* in all features except those mentioned in the diagnosis. The postcranial anatomy of this form is unknown. The two specimens of *A. calvus* are larger than the known individuals of *A. antiquus*; the approximate dorsomedian skull length of MCZ 8500, measured to the base of the supraoccipital process, is 87 mm, whereas the largest known skull of *A. antiquus* (UMMP V59687) is approximately 59 mm long.

Astephus resimus, new species

(Pl. IV A, B)

Diagnosis.– A species of *Astephus* that differs from the other known species of the genus in the combination of the following characters: (1) supraethmoid cornua moderately broad and robust; (2) supraethmoid cleft relatively deep; (3) margin of frontal bone above the orbit probably convex; (4) distinct oval-shaped depressions across fronto-sphenotic suture, continued posteriorly as shallow grooves onto anterolateral corners of supraoccipital; (5) supraoccipital process broad at least at base, (6) vomerine tooth patch slender at midline.

Holotype.– USNM 18104, nearly complete neurocranium. Length of skull from tip of supraethmoid to end of posterior cranial fontanelle 79.2 mm, minimum dorsal supraethmoid width 13.8 mm, skull width at epiphyseal bar (approx.) 45.0 mm, skull width at pterotics (approx.) 44.0 mm.

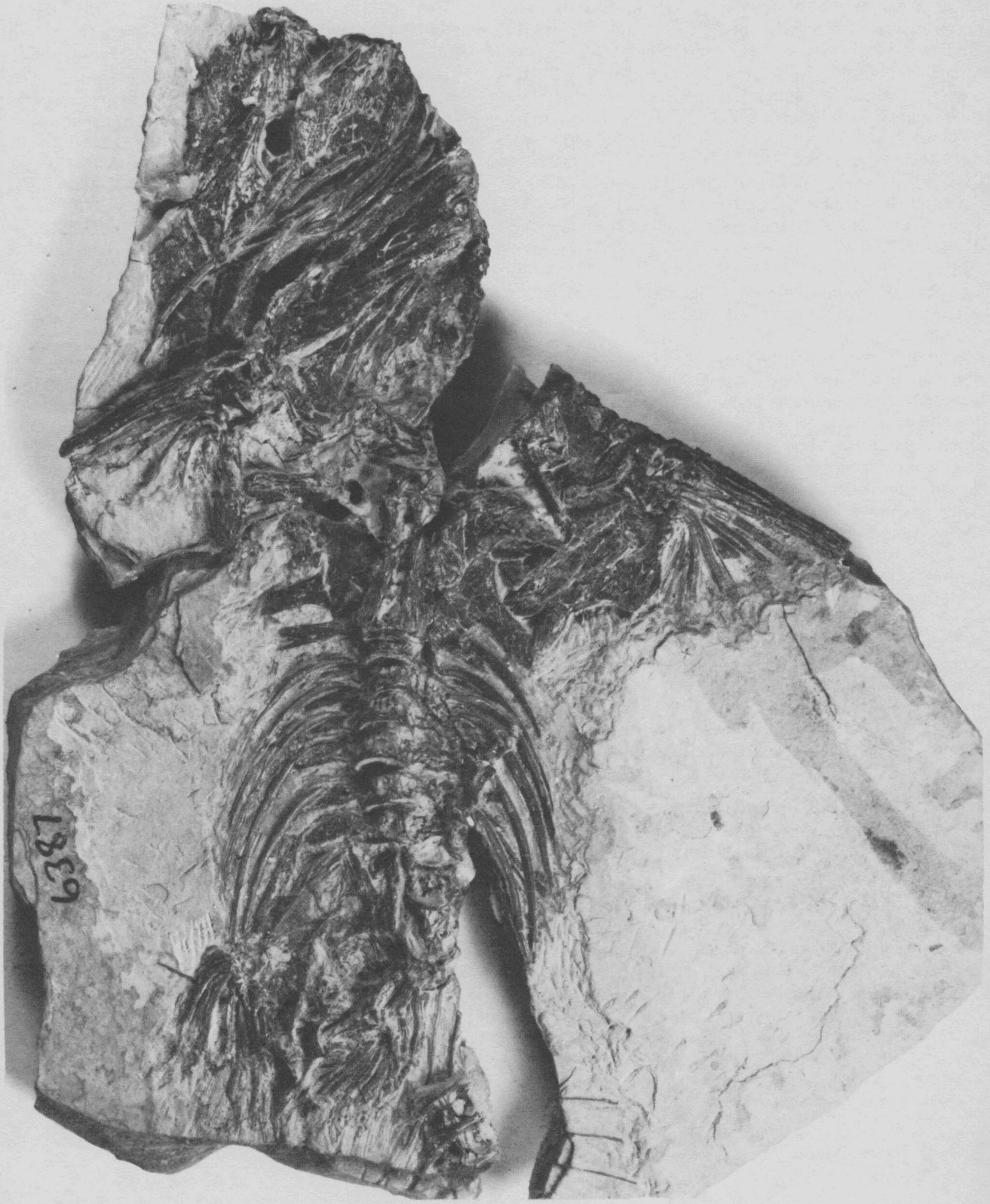
Horizon and Type Locality.– Bridger B Formation, middle Eocene. Pinnacle Rock between Little America and Twin Buttes, Bridger Basin, Sweetwater County, Wyoming. Collected by C. L. Gazin, 1947.

Description and Remarks.– The type and only known specimen of *A. resimus* is a nearly complete and uncrushed neurocranium. The relative lack of distortion of the specimen has permitted clarification of a number of anatomical features of the genus *Astephus* that were mentioned above. The postcranial anatomy of this species is unknown.

A. resimus and *A. calvus* share a number of features of the skull roof that are not present in *A. antiquus*, e.g., a convex frontal margin, depressions at the fronto-sphenotic suture, a massive supraethmoid, and broad supraoccipital process. These similarities may indicate a close relation-

Plate II. (A) *Astephus antiquus*, lateral view of right suspensorium (hyomandibular, preopercle, quadrate, metapterygoid) (UMMP V57961), 35 mm in depth. (B) *Rhineastes peltatus*, dorsal view of fragmentary supraoccipital bone, (USNM 3984), anterior at top, 28 mm in length. (C) *Rhineastes peltatus*, anterolateral view of fragmentary dorsal spine (USNM 3984), 24 mm in length. (D) *Astephus antiquus*, ventral view of anterior part of fish (YPM 844), 55 mm in skull length. (E) *Astephus antiquus*, dorsal view of posterior part of skull roof (UMMP V57966), 32 mm in maximum width (across the pterotics).

PLATE III



ship between *resimus* and *calvus*.

The name, *resimus*, "with turned-up nose," refers to the peculiar dorsal position of the supraethmoid cornua relative to the vomer.

Astephus, Indeterminate Species

The following specimens are referable to the genus *Astephus*, but being known only from fragmentary or poorly preserved material their assignment to species or description of new taxa is not possible.

1) *Material, Localities, and Horizons*.– Cedar Point Quarries, Big Horn County, Wyoming, SW¼, Sec. 23, T. 55 N, R. 96 W. Collected by R.V. Witter and party, 1950. Polecat Bench Formation, late Paleocene. PU 17140, partial skull (Pl. XI B).

This constitutes the only Paleocene record for the Siluriformes in North America. (Casier, 1960, reported *Arius* sp. from Paleocene deposits in the Congo.)

This individual possesses the ridges and pits on the surface of the posterior skull roof that are typical of *Astephus*. In form the skull is broad and apparently quite depressed. The base of the supraoccipital process is broad as in *A. calvus* and *A. resimus*, and the cranial fontanelles are widely open. On the ventral surface of the skull, the parasphenoid, orbitosphenoid and hyomandibular facet are identical in form to other species of *Astephus*. A fragment of the premaxillary tooth patch, which is typically siluriform in structure, is applied to the supraethmoid. The latter bone is badly broken but it appears that the cornua are widely separated and stout. The approximate length of this skull is 155 mm, larger than any other known specimen of *Astephus*.

2) *Material, Localities, and Horizons*.– 4¼ mi S of Church Buttes, W of oil well road, Bridger Basin, Wyoming. Collected by C.L. Gazin, 1947. Bridger B Formation, middle Eocene. USNM 18103, fragmentary remains of cleithra, hyoid arch and dentary.

3) *Material, Localities, and Horizons*.– Grizzly Buttes, Wyoming. Collected by L. S. Quackenbush, 1903. Bridger Formation, middle Eocene. AMNH 6060, partial skull, hyoid arch, lower jaw and shoulder girdle (Fig. 1 F).

Remarks.– In this specimen and USNM 18103 the structure of the posterior process of the cleithrum is well preserved. It has the typical ridged but non-tuberculated ornamentation of *Astephus*. Based on their large size alone it may be that these individuals represent either *A. calvus* or *A. resimus*.

4) *Material, Localities, and Horizons*.– Piceance Creek Basin, Rio Blanco County, Colorado, Sec. 34, T. 2 S, R. 100 W. Collected by D. A. Brobst and J. D. Tucker, 1967. "Pipeline Section," Green River Formation, middle Eocene. USNM 25024, partial skull and shoulder girdle.

5) *Material, Localities, and Horizons*.– Gulch southwest of Fairview, Utah, T. 14 S, R. 4 E, Wasatch Formation, early Eocene. USNM 18124, supraoccipital bone (Pl. V C).

Remarks.– The enormous supraoccipital process of this specimen may be unique among the known species of *Astephus*, or this could represent a large individual of *A. resimus* or *A. calvus*. Complete supraoccipital processes of the latter species are unknown.

6) *Material, Localities, and Horizon*.– Slim Buttes, Harding County, South Dakota, T. 16 N, R. 8 E, Slim Buttes Formation, late Eocene. SDSM 6948, 2 pectoral spines (Fig. 1 G).

Remarks.– These spines were reported by Bjork (1967). They are here referred to *Astephus* on the basis of the weakly developed ornamentation. The anterior ridge is present but not prominent, anterior dentations are absent, and posterior dentations are absent from the basal portion of the shaft.

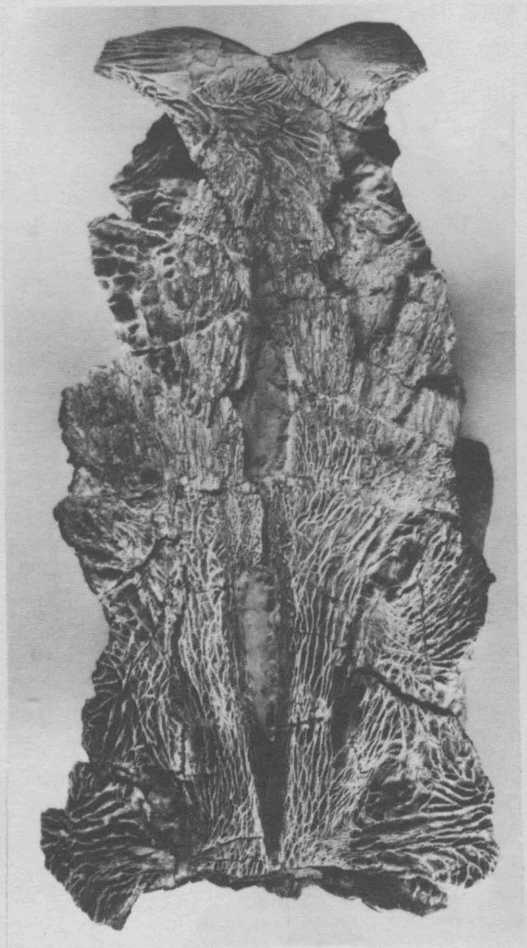
7) *Material, Localities, and Horizons*.– Cypress Hills Formation, lower Oligocene, Saskatchewan. UMMP V57992, V57993, pectoral spines, V57994, dorsal spines, V57991, basioccipital, V57995, cleithra from Hanson Ranch, cliffs surrounding Calf Creek, about 3 mi NW of Eastend, Saskatchewan; NMC 17552, pectoral and dorsal spines; UC 54240 (part), pectoral and dorsal spines, University of California locality V5923, Hunter Quarry.

Remarks.– This material is referred to the genus *Astephus* on the basis of pectoral spine (Pl. VII J) and basioccipital structure. The ornamentation of the pectoral spine is closest to that of *A. antiquus* except that the anterior dentations are slightly less well developed. The basioccipital is slightly concave on the midline just anterior to the median pit as in *A. antiquus*, and the facet for the attachment of the transcapular ligament are well-developed.

The dorsal spines (Pl. VII J) from the Cypress Hills deposits are referred to this form on the basis of relative abundance. They are unique in having the basal condyles directed more anteroventrally than in any other catfish examined. These dorsal spines also have a moderately deep posterior groove, small, numerous posterior dentations, and anterior dentations. The fragments of cleithra are also referred to this form on the basis of relative abundance, but these are unlike the cleithra of other species of *Astephus* in having the posterior process ornamented with reticulating ridges and tubercles. This pattern of ornamentation is also unlike that developed in modern ictalur-

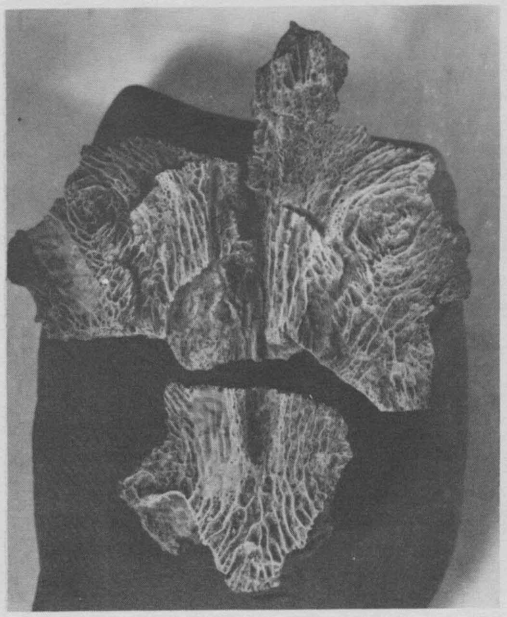
Plate III. *Astephus antiquus*, ventral view of Weberian complex, precaudal vertebrae, and pelvic fins (AMNH 6387), length of figured part of specimen 71 mm.

PLATE IV

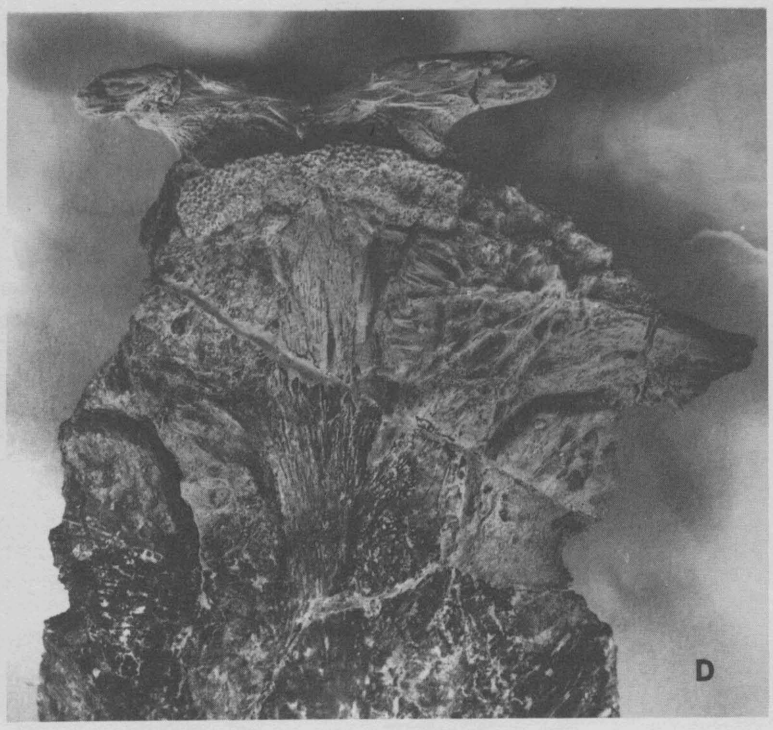


A

B



C



D

ids in which tubercles tend to be formed on subparallel ridges.

Three species of catfishes were described by Cope (1891) from the Cypress Hills Oligocene deposits. Of these, *Rhineastes rhaeas* was questionably referred to the genus *Rhineastes*, and the other two were questionably referred to *Ictalurus (Amiurus): A. cancellatus* and *A. maconnelli*. The material on which the descriptions were based includes vertebral centra only.

Vertebral centra of large catfishes are fairly common fossils in the Cypress Hills deposits. It is questionable, however, whether these bones can be used to distinguish catfish species. Cope's "diagnostic" characters for these species, e.g. pits, ridges, and striae, have broken down on comparison with additional material, and comparisons among Recent skeletons show few, or no consistent interspecific differences in post-Weberian centra. The unusual character of Cope's type material, however, is the large size of the centra. In vertical diameter the holotypes of the above mentioned "species" measure respectively, 31 mm, 24 mm, and 40 mm. On size alone it is possible that these centra represent a single species.

In addition, based on the pectoral spines it appears that there are two kinds of catfishes in the Cypress Hills fauna. Of these, the most common form, as indicated above, is *Astephus* sp. (which would have been *Rhineastes* to Cope), but this is a small species. The second species is represented by a series of small to large spines. Again on the basis of size these spines possibly belong to the same form represented by the large vertebrae. On the basis of spine structure this large species is referred to the genus (and subgenus) *Ictalurus* (see below).

Genus *Hypsidoris* Lundberg and Case

Hypsidoris.– Lundberg and Case, 1970, p. 452.

Diagnosis.– A genus of ictalurid catfishes that differs from living members of the family in the possession of villiform vomerine teeth and a distinct though small rib on the fifth vertebra. The posterior part of the skull roof is not excavated laterally for the origin of the adductor mandibulae muscles.

Hypsidoris differs from other fossil North American catfishes in the slender supraethmoid, two patches of vomerine teeth, and reduced development of the rib of the fifth vertebra.

The great length of the dorsal and pectoral spines of *Hypsidoris* is exceptional among fossil and Recent ictalurids. In *Hypsidoris* their lengths (excluding bases) are contained less than 5 times in the standard length. *Hypsidoris* has 7 (or 6) pelvic rays whereas other ictalurids have from 8 to 10. In addition, it is probable that *Hypsidoris* has a toothed maxilla, a condition known elsewhere in the Siluriformes only in *Diplomystes*.

Type Species.– *Hypsidoris farsonensis* Lundberg and Case, 1970, p. 452, by original designation.

Hypsidoris farsonensis Lundberg and Case

(Fig. 2 A-C; Pl. VI A-C)

Hypsidoris farsonensis.– Lundberg and Case, 1970, p. 452 (original description; Laney Shale Member, Green River Formation, Sweetwater County, near Farson, Wyoming).

Diagnosis.– As for genus.

Holotype.– PU 20570a and b, impression of complete fish (a, dorsal surface; b, ventral surface).

Horizon and Type Locality.– Laney Shale Member of the Green River Formation, middle Eocene. 3 mi E of Big Sandy Reservoir, Sweetwater County, near Farson, Wyoming. T. 27 N, R. 105 W.

Material.– As listed by Lundberg and Case (1970).

Description and Remarks.– The following points can be added to the description of the anatomy of *H. farsonensis* given by Lundberg and Case (1970).

1) The dermal ornamentation of the skull roof consists of strong reticulating ridges that are irregularly raised into tubercles. Near the midline on the supraoccipital the ridges tend to be oriented longitudinally.

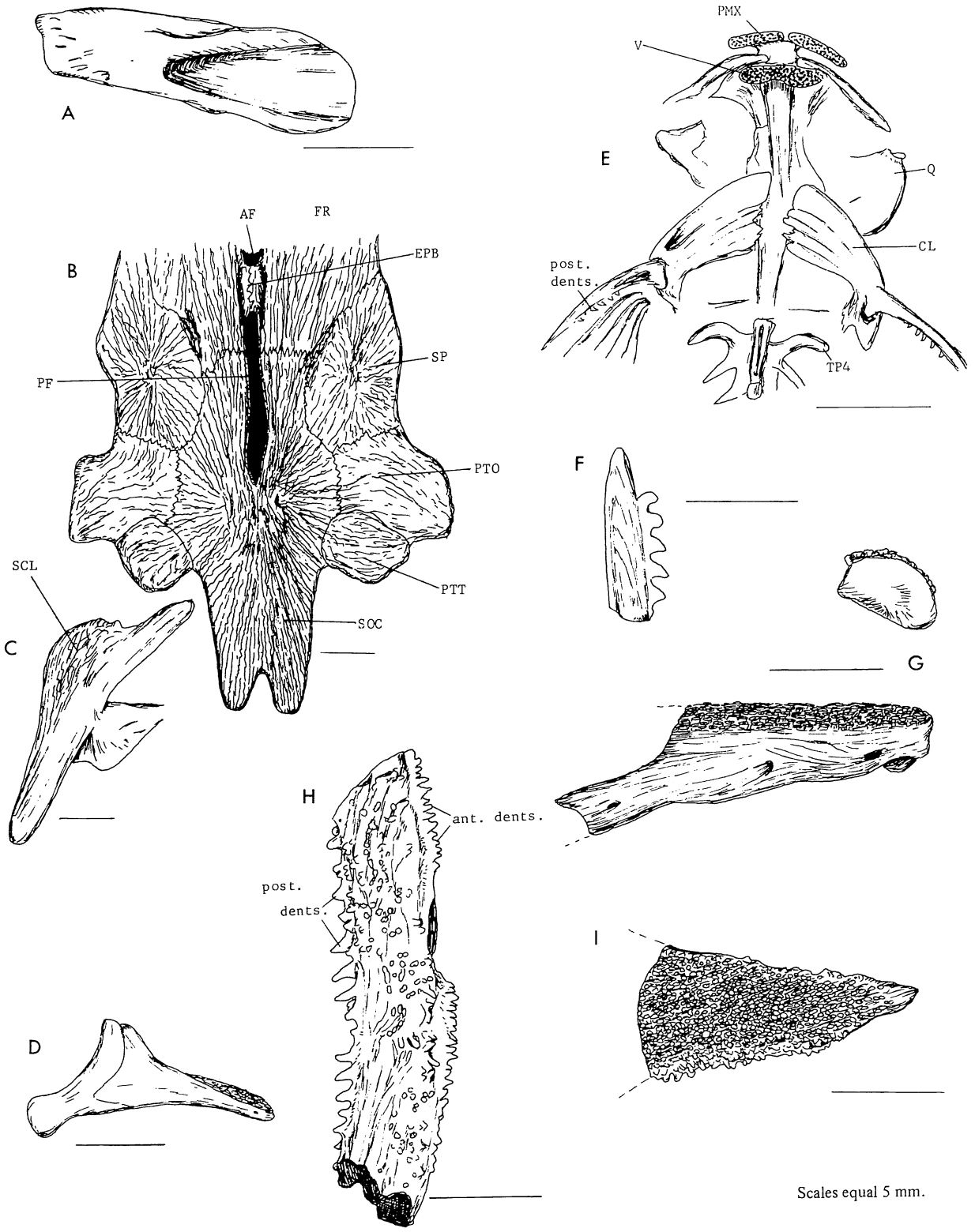
2) There are deep grooves on the skull on either side of, and parallel to, the posterior cranial fontanelle for the exposed part of the parietal branch of the supraorbital canal. These extend from the posterior edge of the frontals, along the frontosphenotic suture, onto the anterolateral corners of the supraoccipital. Unlike the condition in *Astephus* these grooves are not expanded into depressions anteriorly.

3) The premaxilla has no clear indication of a sublateral posterior projection, but on the dorsolateral surface of the bone there is a distinct trough that narrows mesially. This is similar to the grooved premaxilla in extant ictalurids although it is longer in the fossils. In modern ictalurids and probably in *H. farsonensis* the palatine condyles of the maxilla are seated in this groove.

4) Additional preparation of UMMP V57142 has uncovered more of the right maxilla and it appears that maxillary teeth are present. The teeth are similar in form to those on the premaxillae, vomer, and dentaries. The re-

Plate IV. (A) *Astephus resimus*, dorsal view of skull roof (USNM 18104, Holotype), 77 mm in length. (B) *Astephus resimus*, ventral view of anterior part of skull (USNM 18104, Holotype), length of figured part of specimen 29 mm. (C) *Astephus calvus*, dorsal view of fragmentary posterior part of skull roof (USNM 3980, Holotype), combined length of fragments 51 mm. (D) *Astephus calvus*, ventral view of anterior part of skull (MCZ 8500), length of figured part of specimen 43 mm.

FIGURE 2



Scales equal 5 mm.

mainder of the structure of the maxilla, as indicated in the original description, is essentially like that of catfishes that have an edentulous maxilla – the dorsal palatine condyle is large, the ventral palatine condyle is short, and distal to the palatine condyles the maxilla is fairly deep but there is no constricted neck and distal expansion. In addition, judging from the position of the head of the maxilla relative to the premaxilla and the dorsolateral groove of the premaxilla, it is probable that the maxilla articulated over the premaxilla. In *Diplomystes*, on the other hand, the ventral palatine condyle is long and directed mesially behind the premaxilla, the dorsal palatine condyle is small and the distal portion of the maxilla is expanded.

The palatine of *H. farsonensis* appears to have a mesiolateral articulation with the lateral ethmoid, and the palatine is rod-like and not distinctly double-headed. In *Diplomystes* the palatine is flattened anteriorly and greatly expanded to form two condyles separated by a distinct notch.

Thus, the structure of the upper jaw of *H. farsonensis* is intermediate between *Diplomystes* and all other catfishes.

Indeterminate Early Cenozic Genera

1) *Material, Localities, and Horizon*.– UMMP V59720, impression of skull and anterior vertebrae, and shoulder girdle; V57984, impression of articular and angular bone; V59718, impression of skull. All material from outcrops of Laney Shale Member of Green River Formation, about 3 mi E of Big Sandy Reservoir, T. 27 N, R. 105 W, Sublette County, Wyoming.

Remarks.– This material almost certainly represents an undescribed species and probably a new genus. Formal description is withheld until more suitable material becomes available. With the specimens at hand the diagnostic features of the skull roof and pectoral spines are not preserved.

This form is, however, unique among known fossil and recent North American catfishes in the extremely elevated coronoid process and short lower jaw (Fig. 2 D). In addition, from V59720 it appears that: (1) the supraethmoid cornua are slender and widely separated; (2) the skull roof is at least partially sculptured with ridges, tuberculations and pits; (3) the vomer bears a broad patch of close-set viliform teeth; (4) the premaxillae are short, and without sublateral posterior processes; (5) the hyomandibular is short and broad and has no clear traces of levator arcus palatini or A_3 crests; (6) the meatpterygoid has a broad suture with the hyomandibular; (7) the fifth vertebra is strongly sutured to the complex centrum; and (8) the coracoids are broadly sutured to each other on the midline, and the ventral coracoid keel is long.

2) *Material, Localities, and Horizons*.– UMMP V576-71, latex peel of impression of nearly complete fish (Fig. 2 E-G), collected near Rock Springs, Wyoming, Green River Formation?; AMNH uncat., pectoral spine and dentary, and UW 3295, pectoral spines, Tabernacle Butte, center, Sec. 31, T. 29 N, R. 105 W, Sublette County, Wyoming. Bridger Formation, middle Eocene.

Remarks.– This material may possibly represent an undescribed species related to *Hypsidoris farsonensis*, but is not complete enough to warrant formal description.

In UMMP V57671: (1) the premaxillae are short and moderately broad; (2) the vomer bears a broad patch of teeth that is indented posteriorly on the midline, thus suggesting the double patch of *H. farsonensis*; (3) the fifth vertebra is sutured to the complex centrum; (4) the transverse process of the fifth vertebra appears to bear a short rib as in *Hypsidoris*; (5) there are 42 vertebrae; (6) the coracoids are broadly sutured on the midline; (7) the pectoral spines are short, unlike those of *H. farsonensis* (their length, excluding base, included in standard length about 7 times); and (8) the pectoral-spine shaft is quite smooth, and the posterior dentations are moderately strong, regularly spaced, and uniformly retrorse (Fig. 2 E-F).

On the basis of pectoral-spine morphology, the Tabernacle Butte material appears to represent the same species as UMMP V57671. If so, the following characters can be added to the above list: (1) the anterior ridge of the pectoral spine is well developed but bears weakly developed or no anterior dentations; and (2) the dentary (Fig. 2 G) bears a ventrolateral crest as in most ictalurids. This crest is short and does not reach the mandibular symphysis.

3) *Material, Localities, and Horizon*.– UMMP V56360, basipterygium; V56361, supraethmoid; V56362, cleithrum; all material from Ochoco Pass locality, road cut on U.S. Highway 26, 13.5 mi W of Mitchell, Wheeler County, Oregon. W½, Sec. 17, T. 12 S, R. 20 E. Clarno Formation, late Eocene or early Oligocene.

Remarks.– The fossil fishes, including the catfish, from the Ochoco Pass locality were described in detail by Cavender (1968, figs. 3B, 4I). The catfish is similar to *Astephus* in the structure of the supraethmoid and cleithrum. It is strikingly different from all known fossil and modern

Fig. 2. (A) *Hypsidoris farsonensis*, UMMP V59708, premaxilla, dorsal view. (B) Same, temporal region of skull, dorsal view. (C) Same, supracleithrum. (D) Indeterminate genus and species, UMMP V59720, dentary. (E) Indeterminate genus and species of Eocene catfish, UMMP V57671, ventral view of anterior part of fish. (F) Indeterminate genus and species of Eocene catfish, UW 3295, tip of pectoral spine. (G) Indeterminate genus and species of Eocene catfish, AMNH uncatalogued, dentary, lateral and symphyseal views. (H) Indeterminate genus and species from Big Sheep Creek, Montana, UMMP V57987, pectoral spine. (I) Same, posterior process of cleithrum.

FIGURE 3

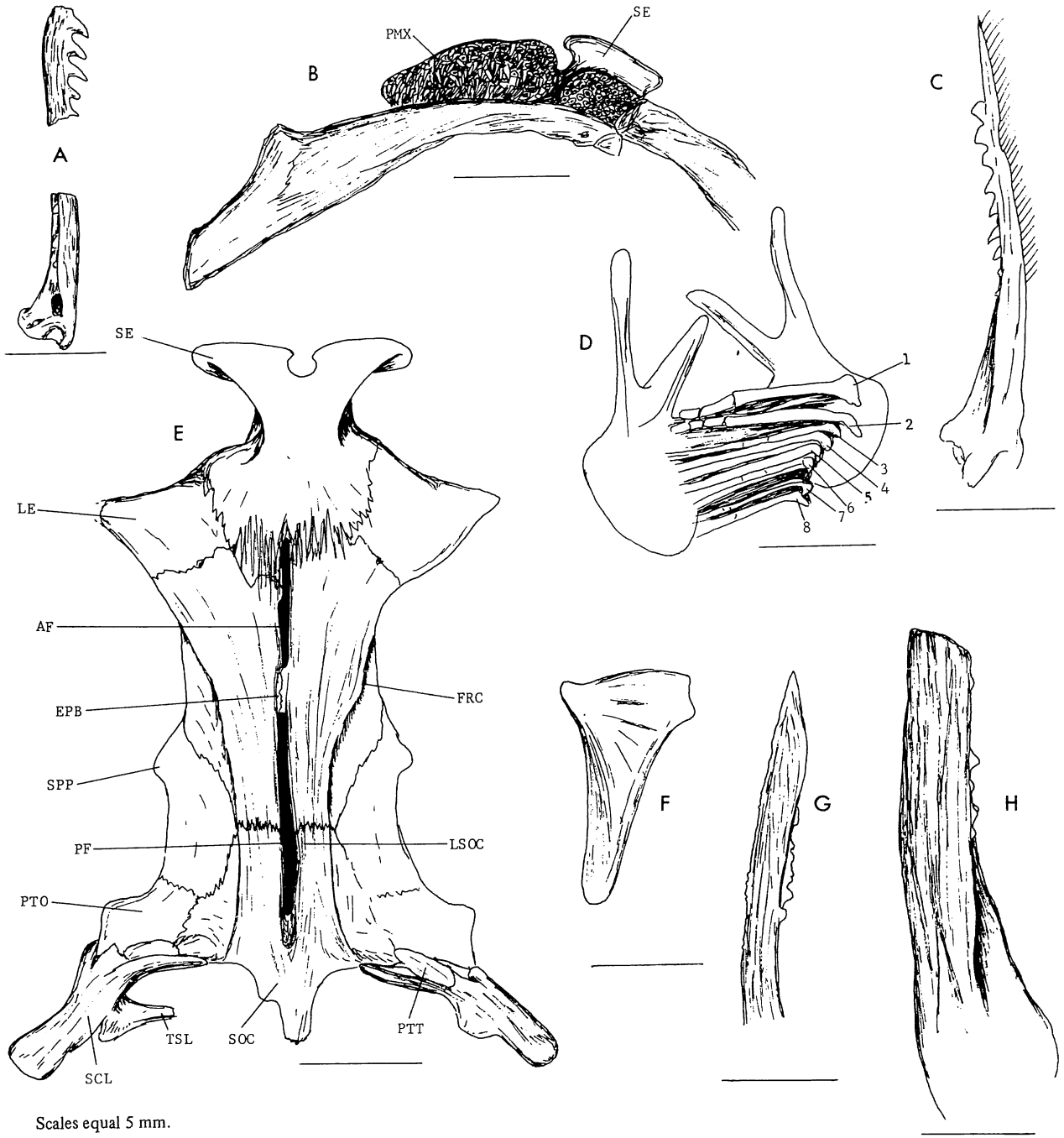


Fig. 3. (A) *Ictalurus rhaeas*, UMMP V57989, pectoral spine fragments. (B) *Ictalurus pectinatus*, USNM 4080, ventral view of supraethmoid and jaws. (C) Same, pectoral spine. (D) *Ictalurus pectinatus*, AMNH 8090, pelvic fins and girdles. (E) *Ictalurus macgrewi*, UW 3297, skull. (F) Same, opercle. (G) Same, pectoral spine. (H) *Ictalurus macgrewi*, UW 3298, pectoral spine.

ictalurids, however, in the possession of an ossified ischiac process from the posterior edge of the basipterygium. This feature is considered primitive for catfishes (Lundberg and Case, 1970), and on this basis the Ochoco Pass

catfish should perhaps not be included in the Ictaluridae. Until more is known of the anatomy of this form there can be little speculation on its systematic position. It must be emphasized, however, that if this form does not turn out to be an ariid, or a relict of a preictalurid line, it will represent some third phyletic line of catfishes in the fresh waters of North America.

4) *Material, Localities, and Horizon.*— UMMP V57986, 24 incomplete pectoral spines (Fig. 2 H, I); V57987, four partial cleithra (Fig. 2 H, I); V57988, one partial premaxilla. All material from the "Big Sheep Creek" locality, S of Grant, Beaverhead County, Montana. The age of the deposits is uncertain, but it is probably early Miocene or late Oligocene (Ted Cavender, pers. comm.).

Remarks.— A striking feature of the pectoral spines of this catfish is the possession of sharp, irregularly spaced tubercles that are developed on the ridges of the pectoral-spine shaft. These tubercles are present on both sides of the spine but are larger on the dorsal surface. Also, the anterior dentations are unique in being conical rather than compressed. These dentations are well developed, sometimes multifid, and set on a strong anterior ridge. There are no well-developed anterior distal serrae. The posterior dentations are slender, moderately strong, evenly spaced and retrorse, and single cusped. The posterior groove is deep.

The posterior process of the cleithrum is covered with fine, close-set tubercles that are arranged in subparallel rows distally. The premaxillary fragment is ventrally covered with the typical small, villiform tooth bases.

The ornamentation of the pectoral spine of this catfish is a most peculiar feature. Among other North American catfishes, there is a fossil species of *Ictalurus* from the lower Pliocene of Nebraska that has a tuberculated spine shaft, but in that form the anterior dentations are strongly compressed rather than conical (Pl. VII A). In a single individual of *Ictalurus (Amiurus) platycephalus* (UMMZ 186245-S, 3) a few tubercles, similar to those of the fossils, are present on the shaft ridges anteriorly. Of all of the catfishes examined, however, the condition of the fossil is most closely approached by *Pelteobagrus nudiceps*, a bagrid from Japan.

It is probable that these fossils represent a new species, and perhaps a new genus of catfishes. I believe, however, that description should be delayed at least until the age of the material is more firmly established. Also, with the material available it is impossible to speculate on the possible relationships of this form.

Genus *Ictalurus* Rafinesque

Subgenus *Ictalurus* Rafinesque

Ictalurus rhaeas (Cope)

(Fig. 3 A; Pl. VII G, H)

Rhineastes rhaeas.— Cope, 1891, p. 3 (original description; Cypress Hills Formation, middle lower Oligocene, Cypress Hills, Saskatchewan, Canada). Gardiner, 1966, p. 80-81 (references).

Ameiurus cancellatus.— Cope, 1891, p. 4 (original description; Cypress Hills Formation, middle lower Oligocene, Cypress Hills, Saskatchewan, Canada). Gardiner, 1966, p. 81 (references).

Ameiurus maconnellii.— Cope, 1891, p. 5 (original description; middle lower Oligocene, Cypress Hills, Saskatchewan, Canada). Gardiner, 1966, p. 81-82 (references).

Diagnosis.— A large species of *Ictalurus* (subgenus *Ictalurus*) that differs from other members of its subgenus in having the pectoral spine shaft of large individuals ornamented with prominent, but narrow, subparallel ridges and deep grooves. In other features of the pectoral spine this species most closely resembles *Ictalurus furcatus.*

Holotype.— NMC 6209, vertebral centrum.

Horizon and Type Locality.— Bone Coulee (N branch of Frenchman River), T. 7 and 9, R. 21 and 22, W of 3rd Median. Cypress Hills Formation, middle lower Oligocene. Cypress Hills, Saskatchewan, Canada.

Material.— UMMP V57989, pectoral spines; V57990 vertebral centra. UC 54240 (part), pectoral spines. NMC 17553, pectoral spine; NMC uncatalogued, centra.

Description and Remarks.— As previously discussed the characters used by Cope to diagnose three forms of catfishes from the Cypress Hills fauna break down with additional comparisons. All three of Cope's names are considered to be synonyms here, and *Ictalurus rhaeas* with page precedence is selected as the name of the species.

Placement of this form in the subgenus *Ictalurus* is based on pectoral spine anatomy. The small spines are usually quite worn but apparently the spine shafts are finely striate, and the anterior ridge is prominent and shows traces of regularly spaced anterior dentations. The posterior dentations in small individuals are uniformly spaced, evenly retrorse, and single cusped. The bases of the proximal dentations arise from the posterior groove. In larger individuals the posterior dentations become erect and multifid, the anterior ridge becomes more prominent, and the anterior dentations become stronger and fused. The spine shaft of the large spines is uniquely sculptured with fine but prominent ridges and grooves. In other species of the subgenus *Ictalurus* the spine-shaft ridges are broader and the intervening grooves shallower. In the overall pattern of anterior and posterior dentations the spines of *I. rhaeas* are most like those of *I. furcatus*, but certainly more of the anatomy of this fossil must be known before any statement on relationship can be made.

Ictalurus lambda Hubbs and Hibbard

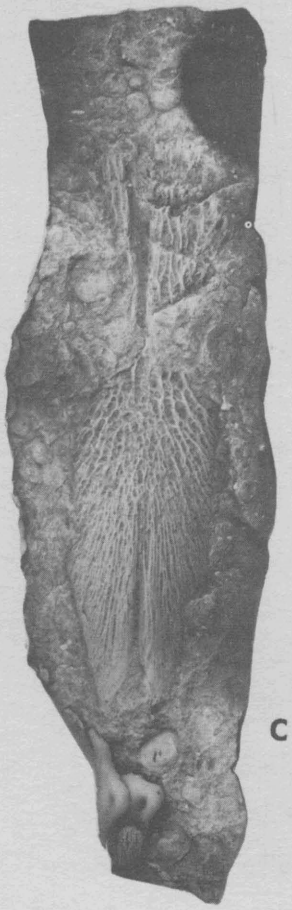
(Pl. VII E, Pl. VIII D-G)

Ictalurus lambda.— Hubbs and Hibbard, 1951, p. 9 (or-

PLATE V

A

B



C

iginal description; Ogallala Formation, Trego County, Kansas). Smith, 1961, p. 925. Smith, 1962, p. 510. Wilson, 1968, p. 86. Voorhies, 1969, p. 14.

Diagnosis.– A catfish of the *furcatus* group of the subgenus *Ictalurus* which, as far as is known, differs from *Ictalurus furcatus* in the following features only: (1) presence of tubercles on the posterior process of the cleithrum; and (2) slightly stronger anterior dentations on the pectoral spine.

Holotype.– UK 6887, partial left pectoral spine.

Horizon and Type Locality.– Lower Pliocene, Ogallala Group, Trego County, Kansas. SW¼, Sec. 15, T. 11 S, R. 22 W.

Material, Localities, and Horizons.– UK 6888, partial pectoral spine (paratype). UMMP V55595, pectoral spine; V55614, maxilla; V55617, pectoral spine, from University of Michigan locality, UM-K6-59, NW of Ogallah, Kansas, 2350-2550 ft S, 75 ft E of the NW corner, Sec. 22, T. 11 S, R. 22 W, Ogallala Formation.

UC 37188, pectoral spines, from University of California locality V4142, Box Butte County, Nebraska.

TMM 31081-1284 (part), pectoral spines; 31081-1127, pectoral spines; 31081-1059, articular bone, from Lapara Creek locality, SE of Narmana, Bee County, Texas. Lower Pliocene or upper Miocene (Quinn, 1955).

UW 3277, pectoral spines; 3278, pectoral spines; 3279, ceratohyals and epihyals; 3280, hyomandibulars, preopercle and quadrate; 3281, dentaries; 3282, lower jaws; 3283, premaxilla; 3284, shoulder girdles; 3285, supracleithra; 3286, lateral ethmoid; 3287, dorsal spines; 3288, Weberian complex fragment; 3289, partial neurocranium. From Verdigre Quarry, SW part of Knox County, Nebraska, NW ¼, Sec. 16, T. 29 N, R. 7 W. Valentine Formation, lower Pliocene part of section.

UF 17470, pectoral spines, dentary, articular, supraethmoid, supracleithrum, coracoid, cleithrum; UF 17471, supraethmoid, pectoral and dorsal spines, from McGehee Fauna locality, near Newberry, Alachua County, Florida. Alachua Formation, middle Pliocene.

Description and Remarks.– Based on two large but broken pectoral spines, Hubbs and Hibbard (1951) named and described *Ictalurus lambda* from the lower Pliocene Ogallala Formation. Additional comparisons of fossil and Recent material indicate that the characters of the spines of large individuals of *I. lambda* fall within the limits of variation of *I. furcatus.*

The large spines from the Lapara Creek locality, McGehee Farm locality and the Verdigre Quarry are quite similar to the material from the Ogallala, and all of these are Miocene-Pliocene or lower Pliocene in age. I therefore consider the fossils to be conspecific.

In most features the fossils are identical to modern *I. furcatus*, but the fossil cleithra and small pectoral spines are consistently more strongly ornamented. In *I. furcatus* the posterior process of the cleithrum is always ornamented with subparallel ridges and grooves but tubercles are not present. In addition, the anterior dentations of the pectoral spines are lost early in development. In *lambda* the large cleithra bear moderately developed tubercles, and the anterior dentations are retained in larger individuals.

Although the differences are slight, they appear to be consistently present. Thus, *I. lambda* may be regarded as specifically distinct. Similar interspecific differences in ornamentation are found in the subgenus *Amiurus.*

The lack of tubercles on the posterior cleithral process was thought to be a primitive feature for ictalurids because this condition is found in Eocene ictalurids and numerous Recent catfish groups. The presence of the tubercles in *I. lambda* suggests that the condition in *I. furcatus* is a reversal rather than a retention of a primitive character.

Zoogeographically, the McGehee Farm fossils are a significant find since *Ictalurus furcatus*, the modern representative of *I. lambda*, does not live in the drainages east of the Alabama River system (Smith-Vaniz, 1968). Hirschfeld and Webb (1968) referred the McGehee catfish remains to the Ariidae, but on the basis of pectoral spine, pectoral girdle, and supraethmoid morphology there is little doubt that the material represents *I. lambda.* The McGehee deposits are believed to be estuarine and the fossil fishes associated with the catfish are primarily marine acanthopterygians. *Ictalurus furcatus* is known to enter estuarine waters of low salinity.

Ictalurus furcatus (Lesueur)

Material, Localities, and Horizons.– Damp Cave local fauna, and Centipede Cave local fauna, rock shelter along Rio Grande, near Langtry, Val Verde County, Texas late Pleistocene. Material not examined. Lundelius (1963) reported remains of *Ictalurus furcatus.*

Ictalurus punctatus (Rafinesque)

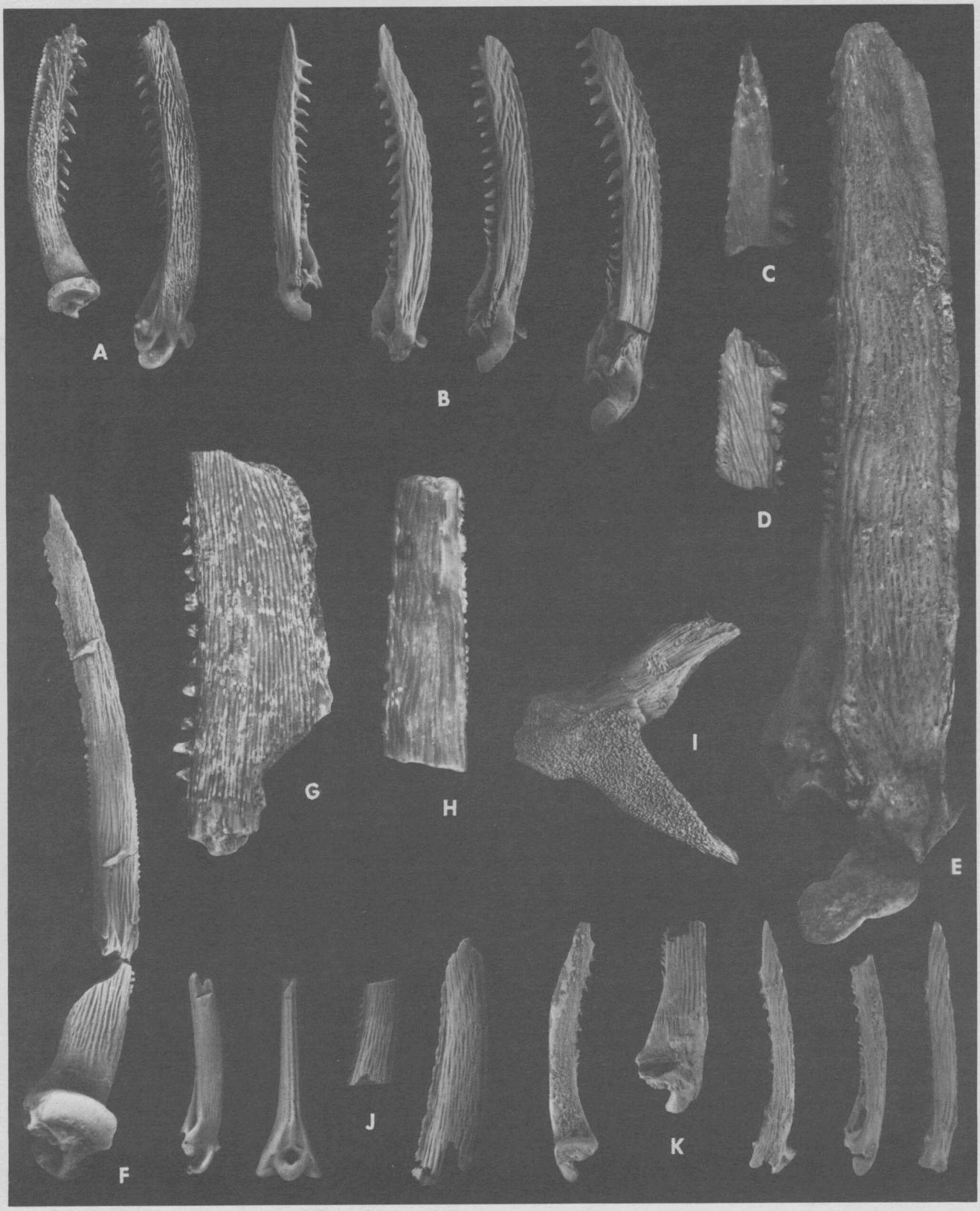
(Pl. VIII B, Pl. X D, E)

Middle Miocene Records: Material and Localities.– Flint Hill fossil site, Jim Ross Ranch W of Martin, in the center SW¼, Sec. 31, T. 37 N, R. 38 W, Bennett County, South Dakota. Flint Hill fauna, lower middle Miocene (Hemingfordian). UMMP V26595, partial neuro-

Plate V. (A) *Ictalurus leidyi*, dorsal view of skull roof (F:AM 10509), 56.5 mm in length. (B) *Astephus calvus*, dorsal view of skull roof and Weberian complex (MCZ 8500), length of figured part of specimen 128 mm. (C) *Astephus* sp., dorsal view of fragmentary supraoccipital (USNM 18124), 64 mm in length.

PLATE VI

PLATE VII



cranium; V32419, pectoral spines; V32436 (part), pectoral and dorsal spines, cleithrum. F:AM 10639, pectoral spines. UC 37257 (part), pectoral spine, cleithra; 39465, anterior part of neurocranium; 39466, pectoral spines; 39467, supraethmoid; 39703, pectoral spine; 77681, pectoral spine; 77682, pectoral spine; 77684, partial dentary. SDSM 63599 (part), pectoral spine, articular, cleithrum. Uncatalogued material at University of Notre Dame, cleithra, pectoral and dorsal spines, supraethmoids, dentaries, articulars, basioccipital.

Long Quarry, Antelope Draw, Sioux County, Nebraska. Sheep Creek Formation, late middle Miocene. F:AM 10541-10555, 10557-10561, 10570, pectoral spines; 10556, 10562, dentaries; 10569, articulars; 10563-10568, partial skulls.

Ginn Quarry, NE¼ of NW¼, Sec. 24, T. 31 N, R. 47 W, Dawes County, Nebraska. Sheep Creek equivalent, middle Miocene. F:AM 10535, pectoral spine.

Miscellaneous localities in Sioux County, Nebraska, Sheep Creek beds. AMNH 2910, partial neurocranium; 2919 (part), partial Weberian complex, partial neurocranium; 2914 (part), cleithrum, supraethmoids, opercle, partial hyoid arch, hyomandibulars, preopercles, quadrates; 2916, pectoral spine, cleithrum, coracoid, partial Weberian complex, supraoccipital, lower jaws; 2909, partial cranium and Weberian complex; 2912, hyoid arch, hyomandibular, preopercle, quadrate, two partial skulls; 2911, neurocranium; 2915, partial neurocranium; 2905 and 2904, lower jaws; 2908, two partial neurocrania; 2906, pectoral spines; 2903, lower jaws. This Sheep Creek material was compared to *Ictalurus punctatus* by Matthew (1918).

Potter Quarry, Sand Canyon region, S½, Sec. 19, T. 30 N, R. 47 W, Dawes County, Nebraska. Upper Marsland = Runningwater Formation, middle Miocene. F:AM 10539, pectoral spine.

"B" Quarry, middle of NE¼, Sec. 30, T. 31 N, R. 47 W, Dawes County, Nebraska. Upper Marsland = Runningwater Formation, middle Miocene. F:AM 10532, pectoral spine.

"A" Quarry, NW¼, Sec. 24, T. 31 N, R. 47 W, Dawes County, Nebraska. Upper Marsland = Runningwater Formation, middle Miocene. F:AM 10533, pectoral spines.

Late Miocene Records: Material and Localities.– West Sinclair Draw Quarry No. 7, Horizon A, Sioux County, Nebraska. Lowermost part of Lower Snake Creek beds, early late Miocene. F:AM 10571 pectoral spine.

West Sinclair Draw, Sioux County, Nebraska. Lower Snake Creek, late Miocene. F:AM 10572, lower jaw.

New Surface Quarry, East Sinclair Draw, Sioux County, Nebraska. Lower Snake Creek, late Miocene. F:AM 10583, articular; 10587, 10588, lower jaws.

Quarry No. 2, East Sinclair Draw, Sioux County, Nebraska. Lower Snake Creek, late Miocene. F:AM 10589, partial neurocranium.

Humbug Quarry, Ranch House Draw, Sioux County, Nebraska. Lower Snake Creek, late Miocene. F:AM 10590, partial neurocranium; 10591-10595, lower jaws.

Echo Quarry, Antelope Draw, Sioux County, Nebraska. Lower Snake Creek, late Miocene. F:AM 10578, partial neurocranium.

Boulder Quarry, NE face of Olcott Hill, Sioux County, Nebraska. Lower Snake Creek, late Miocene. F:AM 10598, supraethmoid.

Douglas Quarry, Sinclair Draw, Sioux County, Nebraska. Lower Snake Creek, late Miocene. F:AM 10599, partial neurocranium.

Mill Quarry, Antelope Draw, Sioux County, Nebraska. Lower Snake Creek (latest fauna in type area), late Miocene. F:AM 10597, partial neurocranium.

Miscellaneous localities in Sioux County, Nebraska, Snake Creek beds. AMNH 2921 (part), pectoral spine; 2920, supraethmoid, hyoid arch, hyomandibular, preopercle, quadrate, pectoral spine; 2932 and 2933, partial neurocranium; 2934, supraoccipital; 2922 (part), supraethmoid; 2923, cleithrum, dorsal spine.

Early to Middle Pliocene Records: Material and Localities.– Nenzel Quarry, on Niobrara River, S of Nenzel, Cherry County, Nebraska. Valentine Formation, Crookston Bridge Member, early Pliocene. F:AM 10630,pectoral spine; 10631, cleithrum.

Railroad Quarry A, S side of Niobrara River, SE of Valentine, Cherry County, Nebraska. Valentine Formation, Crookston Bridge Member, early Pliocene. F:AM 10617, partial neurocranium; 10618, nearly complete skeleton.

University of California locality V-3218, on the quarter section line, between the NW and SW quarters of Sec. 24, T. 34 N, R. 26 W; Cherry County, Nebraska. Valentine Formation, Crookston Bridge Member, late Miocene or early Pliocene. The material examined is listed by Estes and Tihen (1964). The dentary bone figured by these authors (UC 31985c, fig. 1a) represents *I. punctatus*, and there are numerous pectoral spines of this species in the collection.

Norden Bridge locality, Sec. 33, T. 33 N, R. 23 W, Brown County, Nebraska. Lower Valentine Formation, Crookston Bridge Member, late Miocene or early Pliocene. UMMP V37117, cleithrum supraethmoid, articular and dentary. This material was referred tentatively to *I. punc-*

Plate VI. (A) *Hypsidoris farsonensis*, blow-up of B to show details of upper and lower jaws, and palatine. (B) *Hypsidoris farsonensis*, anterolateral view of skull (UMMP V57142), length of figured part of specimen 49 mm. (C) *Hypsidoris farsonensis*, ventral view of anterior part of fish (AMNH 6888), length of figured part of specimen 56 mm.

tatus by Smith (1962). *Ictalurus punctatus* is represented in the Norden Bridge locality material along with remains of an extinct channel catfish relative (see below). As the latter is known with certainty only from pectoral spines, firm identification of other bones is impossible.

East side of Nebraska Highway 12, SW¼, Sec. 22, T. 33 N, R. 27 W, Cherry County, Nebraska. Valentine Formation, near top of Crookston Bridge Member, late Miocene or early Pliocene. UMMP V57998, pectoral and dorsal spine.

Egelhoff local fauna, SE corner, NE¼, SW¼, Sec. 29, T. 33 N, R. 23 W, Keya Paha County, Nebraska. Valentine Formation, Crookston Bridge Member, late Miocene or early Pliocene. UMMP V57356, lower jaw, V57361 (part), dentary, articular, sphenotic, coracoid, ceratohyal, V56258 (part), pectoral spines, cleithrum, dentary, frontal, supraethmoid, hyoid arch.

Burge Quarry, about .5 mi NW of Burge Post Office on the Snake River, NE¼, SE¼, Sec. 15, T. 32 N, R. 30 W, Cherry County, Nebraska. Valentine Formation, Burge Member, early Pliocene. F:AM 10619, nearly complete skull; UMMP V56405 (part), pectoral spine.

Lucht Quarry, on Bone Creek, center of N side of Sec. 10, T. 21 N, R. 31 W, Brown County, Nebraska. Valentine Formation, Burge Member, early Pliocene. F:AM 10625, cleithrum; 10626, pectoral spine.

University of California locality V-3314, E½, SE¼, Sec. 5, T. 31 N, R. 30 W, Cherry County, Nebraska, Burge Sands, Ogallala Group, early Pliocene. UC 77683, pectoral spine.

Magle Ranch, NE of rapids in Niobrara River, Cherry County, Nebraska. Burge Member, early Pliocene. F:AM 10607, pectoral spines.

Whiteface Quarry, NW¼, Sec. 27, T. 32 N, R. 30 W, on Snake River, Cherry County, Nebraska. Valentine Formation, Burge Member, early Pliocene. F:AM 10622, lower jaw and cleithrum.

Fairfield Creek, Brown County, Nebraska. Valentine Formation, early Pliocene. F:AM 10601, partial lower jaw.

Plum Creek, N side, 2 mi above Horse Thief Canyon, Brown County, Nebraska. Valentine Formation, early Pliocene. F:AM 10602, articular.

Wessington Springs local fauna, Wessington Springs, in Sec. 12, T. 107 N, R. 65 W, Jerauld County, South Dakota. Beds equivalent to the Valentine Formation, early Pliocene. SDSM 6214 (part), pectoral spines. This material was reported by Green (1965) as *Ictalurus* sp.

Wolf Creek fauna, SDSM loc. V521, SW¼, SE¼, Sec. 16, T. 35 N, R. 43 W, Shannon County, South Dakota. Ogallala Group, Wolf Creek fauna, lower Pliocene (Green, 1956). SDSM 53161, pectoral spine.

Gordon Roadcut, about 10¾ mi W of Gordon, Sheridan County, Nebraska. Ash Hollow Formation (?), early Pliocene. F:AM 10611, pectoral spines and cleithrum; 10613, pectoral and dorsal spines, dentaries, articulars, quadrate, preopercle, hyomandibulars, supraethmoids, premaxillae; 10614, dentary, articular, premaxilla.

Pratt Quarry, on Plum Creek, N of Johnstown, Brown County, Nebraska. Beds equivalent to Ash Hollow Formation or Xmas Quarry, late lower or early middle Pliocene. F:AM 10632, pectoral spine; 10633, pectoral spine, supraethmoid, quadrates, preopercles; 10634, cleithrum.

Bear Creek Quarry, SE¼, Sec. 25, T. 34 N, R. 35 W, Cherry County, Nebraska. Ash Hollow Formation, lower part, above Caprock Member, early Pliocene. F:AM 10620, partial neurocranium.

Pleistocene Records: Material and Localities.— Gilliland local fauna, Burnett Ranch, 7 mi W of Vera, Knox County, Texas. Seymour Formation, late Kansan, Pleistocene. UMMP V45858, pectoral spine; V45859, Weberian centrum; V45860, lower jaw. Reported as *I. punctatus* by Hibbard and Dalquest (1966).

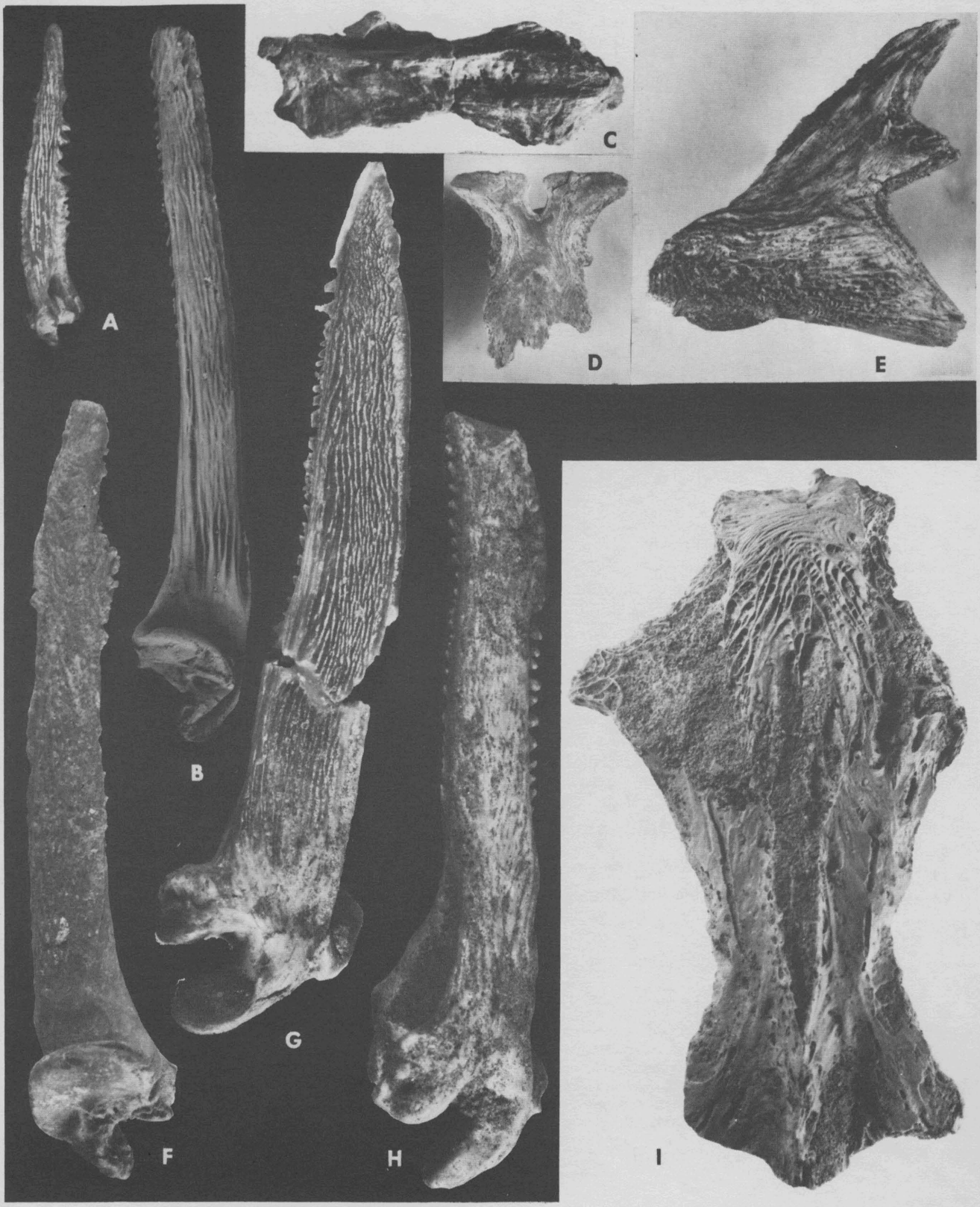
Cudahy fauna. University of Michigan locality UM-T1-58, E of catchpens in SW¼, SE¼, Sec. 110 of Block C of the Houston and Texas Central Railroad Company Survey, on the O. L. Patterson ranch, Knox County, Texas. Cudahy fauna, Vera faunule, late Kansan, Pleistocene. V46912, articular. This material was referred to *I. punctatus* by Getz and Hibbard (1965) and Hibbard and Dalquest (1965).

Berends local fauna, SE¼, Sec. 6, T. 5 N, R. 28 E.C.M., near Gate Ash Pit, 4½ mi N and about 1 mi W of Gate, Beaver County, Oklahoma. Deposits equivalent to lower part of Kingsdown Formation, Illinoian. UMMP V31156, pectoral spine. This spine was correctly referred to *Ictalurus punctatus* by Smith (1954).

Mt. Scott local fauna, UM-K2-59 locality, Big Springs Ranch, SE¼, Sec. 18, T. 32 S, R. 28 W, Meade County, Kansas. Illinoian. UMMP V45571, dorsal basal. This

Plate VII. (A) *Ictalurus echinatus*, pectoral spines, left in dorsal view (UW 3291), 25 mm in length; right in ventral view (UW 3290, Holotype), 30.7 mm in length. (B) *Ictalurus vespertinus*, four pectoral spines (UMMP V50367), 26 mm, 30 mm, 30 mm, 36 mm in length respectively from left to right. (C, D) *Ictalurus peregrinus*, pectoral spine fragments (UO 28038), C, 19 mm, D, 15 mm in length. (E) *Ictalurus lambda*, ventral view of right pectoral spine (UW 3277), specimen 81 mm in length. (F) *Astephus antiquus*, dorsal view of left pectoral spine (USNM 2149, Holotype), 62 mm in length. (G, H) *Ictalurus rhaeas*, pectoral spine fragments (NMC 17553), left 35 mm in length, right 26 mm in length. (I) *Ictalurus echinatus*, lateral view of fragmentary cleithrum (UW 3292), 23 mm in length. (J) *Astephus* sp., second from left, dorsal spine (UC 54240), 18 mm in length; three pectoral spines, 17 mm (UC 54240) (far left), 10 mm (UMMP 57992) and 22 mm (UMMP V57992) (on right) in length. (K) *Ictalurus leidyi*, five pectoral spines (F:AM 10524), 22 mm, 12 mm, 22 mm, 19 mm, 22 mm in length respectively from left to right.

PLATE VIII



bone was correctly referred to *Ictalurus punctatus* by Smith (1963).

Butler Spring local fauna, XI Ranch, SE¼, Sec. 32, T. 34 S, R. 29 W, Meade County, Kansas. Illinoian. UMMP V34858, cleithra, pectoral spines, supracleithrum, dorsal spine. I agree with Smith's (1958) identification of this material as *Ictalurus punctatus.*

Don Beds, near Toronto, Ontario, Canada. Toronto Formation, Sangamon. Uncatalogued pectoral spines examined.

Ichtucknee River fauna, 2.5 mi above bridge on Route 5A, 10 mi E of Branford, 6.5 mi NW of Fort White, Columbia County, Florida. Wisconsinan. F:AM 10641, pectoral spines and cleithrum; F:AM 10643, pectoral spines; F:AM 10647, pectoral spine; F:AM 10649, articular; 10651, coracoid, pectoral spines.

Moore Pit local fauna. T-2, Terrace, Trinity River, Dallas, Dallas County, Texas, late Pleistocene. SMUMP 60457-60460, as described in Uyeno and Miller (1962). Uyeno and Miller correctly identified this material as *Ictalurus punctatus.*

Wilson Ford fauna, E side of Fall River, SE¼, NE¼, Sec. 18, T. 29 S, R. 14 E, Wilson County, Kansas. Late Pleistocene (Hibbard, pers. comm.). UMMP V33489, partial skull and pectoral girdle.

Remarks.— Hay (1924) described *Ictalurus decorus* from a pectoral spine from the Garvin Gully fauna of Texas (not examined), and Smith (1961) referred the middle Miocene Flint Hill catfish remains listed above to that species. Through comparison of additional fossil material to a large series of Recent skeletons of *I. punctatus*, it is concluded that there is no morphological basis for recognizing *I. decorus* as specifically distinct from *I. punctatus.* Where they are known the character states of the Flint Hill catfish fall well within the limits of variation of modern *I. punctatus*. In his description of the University of Michigan material Smith (1961) pointed out that the neurocranium (UMMP V26595) is peculiar in having the "proatlas centrum" detached from the basioccipital. This is almost certainly an abnormality, as all ostariophysans examined (and probably most teleosts) have this centrum (the first centrum) completely incorporated into the basioccipital. The catfish basioccipital in Notre Dame collection has a normal structure.

Ictalurus dugesi (Bean)

Material, Localities, and Horizon.— Lake Zacoalco and Lake Chapala, Jalisco, Mexico. Pleistocene beach deposits. The material described by Alvarez (1966) was not reexamined here.

Ictalurus echinatus, new species

(Pl. VII A, I)

Ictalurus cf. *punctatus.*— Smith, 1962, p. 507.

Diagnosis.— A species of *Ictalurus*, subgenus *Ictalurus*, that differs from the other members of its subgenus, and all other living ictalurids, in having numerous, small tubercles developed on the ridges of the pectoral spine shaft.

The catfish from the Miocene (?), Big Sheep Creek locality near Grant, Montana, also has these tubercles developed. *Ictalurus echinatus* differs from this form in having compressed, rather than conical, anterior dentations that are restricted to the margin of the anterior ridge (Fig. 2 H, I).

Holotype.— UW 3290, nearly complete right pectoral spine; maximum length 30.7 mm, depth of base 9.0 mm, depth of shaft 3.1 mm, width of shaft (excluding posterior dentations), 3.2 mm.

Horizon and Type Locality.— Verdigre Quarry on the E bank of an unnamed tributary of Verdigre Creek, in the NW¼, SE¼, Sec. 16, T. 29 N, R. 7 W, approximately 7.5 mi S and 5.5 mi W of the town of Verdigre, Knox County, Nebraska. Valentine Formation, late Miocene or early Pliocene.

Material.— UW 3291, pectoral spines; and 3292, cleithra, from the type locality.

UMMP V42186 (part), pectoral spines, from Sec. 33, T. 33 N, R. 23 W, Brown County, Nebraska. Valentine Formation, Crookston Bridge Member, early Pliocene. This material was reported as *Ictalurus* cf. *punctatus* by Smith (1962).

F:AM 10608, cleithrum, from Turkey Creek, N side of Niobrara River, Keya Paha County, Nebraska. Valentine Formation, Crookston Bridge Member.

Description and Remarks.— *Ictalurus echinatus* is known only from pectoral spines and cleithra, but the ornamentation of these bones is unique compared to living North American catfishes.

The posterior process of the cleithrum is long, robust, and entirely covered with evenly spaced and uniformly developed tubercles. None of the individuals at hand have a dorsolateral groove such as is present on the process in many modern ictalurids, especially bullheads (*Amiurus*).

Plate VIII. (A) *Ictalurus peregrinus*, ventral view of left pectoral spine (UO 28035, Holotype), 28.3 mm in length. (B) *Ictalurus punctatus*, dorsal view of left pectoral spine (F:AM 10643), 65 mm in length. (C) *Ictalurus* sp., dorsolateral view of incomplete skull (UMMP V14591), 52 mm in length. (D) *Ictalurus lambda*, dorsal view of partial supraethmoid (UF 17471), 25 mm in width across the cornua. (E) *Ictalurus lambda*, lateral view of partial cleithrum (UW 3284), 47 mm in length. (F) *Ictalurus lambda*, dorsal view of right pectoral spine (UF 17471), 69 mm in length. (G) *Ictalurus lambda*, ventral view of right pectoral spine (UW 3277), specimen 78 mm in length. (H) *Pylodictis olivaris*, ventral view of right pectoral spine (F:AM 10547), 68 mm in length. (I) *Ictalurus vespertinus*, dorsal view of partial skull (UMMP V57999), specimen 85 mm in length.

PLATE IX

The pectoral spines are moderately large, well-ossified, and sharp. Anterior distal serrae are hardly developed, but the anterior ridge is prominent, especially near the tip. Moderately strong and regularly spaced anterior dentations are developed on the margin of the anterior ridge. Because the dentations are restricted to the margin they appear to be compressed. The posterior dentations are strong, uniformly spaced and retrorse. The dentation halves are almost without exception perfectly aligned so that the dentations are single cusped. Basally, the dentations arise from the posterior groove only. In addition to these features the subparallel ridges that cover the surface of the spine shaft bear numerous small tubercles. Among the fossil catfishes examined these tubercles have been found only in the unnamed catfish from the Miocene (?) Big Sheep Creek locality. In the latter, however, the tubercles tend to be more prominent and the anterior dentations are stronger and more conical in form. Among the living ictalurids examined a few tubercles are developed on the spines of a single specimen of *I. (Amiurus) platycephalus*.

Ictalurus echinatus is tentatively referred to the subgenus *Ictalurus* on the basis of the long posterior cleithral process (shortened in other groups), and the position of origin of the proximal posterior dentations from the posterior groove (from the dorsal half of the shaft in other ictalurids). Admittedly, these are primitive features, but until more is known about the anatomy of this form, there is little else that can be said about its systematic position. It can be pointed out, however, that the specializations of the shoulder girdle and pectoral spine of *Amiurus* and *Pylodictis* are known to have evolved before the lower Pliocene. *Ictalurus echinatus* should have possessed these specializations if it were related to either *Amiurus* or *Pylodictis*.

The adjective *echinatus* refers to the "prickly" ornamentation of the spines.

Subgenus *Ictalurus*, Indeterminate Species

The following records of the subgenus *Ictalurus* are based on pectoral spines of very small individuals. The spines of the young of these species are too similar to permit identification, but it is probable that they are either *Ictalurus punctatus, I. lambda,* or *I. furcatus*.

Material, Localities, and Horizons.— Mission local fauna, NW¼, NE¼, Sec. 35, T. 40 N, R. 28 W, Melette County, South Dakota. Lower Pliocene (Macdonald, 1960). SDSM 6866.

Laverne local fauna. Sec. 5, T. 3 N, R. 28 E.C.M., Beaver County, Oklahoma. Laverne Formation. Laverne local fauna, lower Pliocene (Hibbard, 1951). UMMP V422-01, cleithrum; UMMP V42208, pectoral spine. Reported by Smith (1962) as *Ictalurus* sp.

Clear Creek local fauna, Clear Creek, Denton County, Texas. Middle Wisconsinan, Pleistocene (Hibbard, pers. comm.). Material as listed in Uyeno (1963), not examined.

Ben Franklin local fauna, Sulphur River, at bridge on highway 38, Ben Franklin, Delta County, Texas. Late Wisconsinan, Pleistocene. Material as listed in Uyeno (1963), not examined.

Subgenus *Amiurus* Gill

Ictalurus pectinatus (Cope)

(Fig. 3 B-D; Pl. IX B, C)

Rhineastes pectinatus.— Cope, 1874, p. 49 (original description; Florissant lake beds, Oligocene, Florissant, Colorado). Hay, 1929, p. 727 (list of previous references).

Diagnosis.— An extinct species of ictalurid catfish that differs from all other members of the family by the following combination of features: (1) supraethmoid cornua broad with mesial processes and separated by a narrow, rounded cleft; (2) lower jaw large, with well-developed anteroventral crest on dentary that extends to symphysis; (3) premaxilla broad; (4) moderately broad and shallow basal recess between anterior limb of the fourth transverse process and complex centrum; (5) short ventral coracoid keel; (6) posteroventrally expanded interopercle; and (7) origin of proximal posterior dentations from posterior groove. Of these character states, the first four are thought to be relatively advanced whereas the last three are believed to be primitive.

Holotype.— USNM 4086, impression of ventral surface of articulated skull, pectoral girdle, and anterior vertebrae.

Horizon and Type Locality.— Near Florissant, South Park, Colorado. Florissant lake beds, middle Oligocene (Keroher et al., 1966).

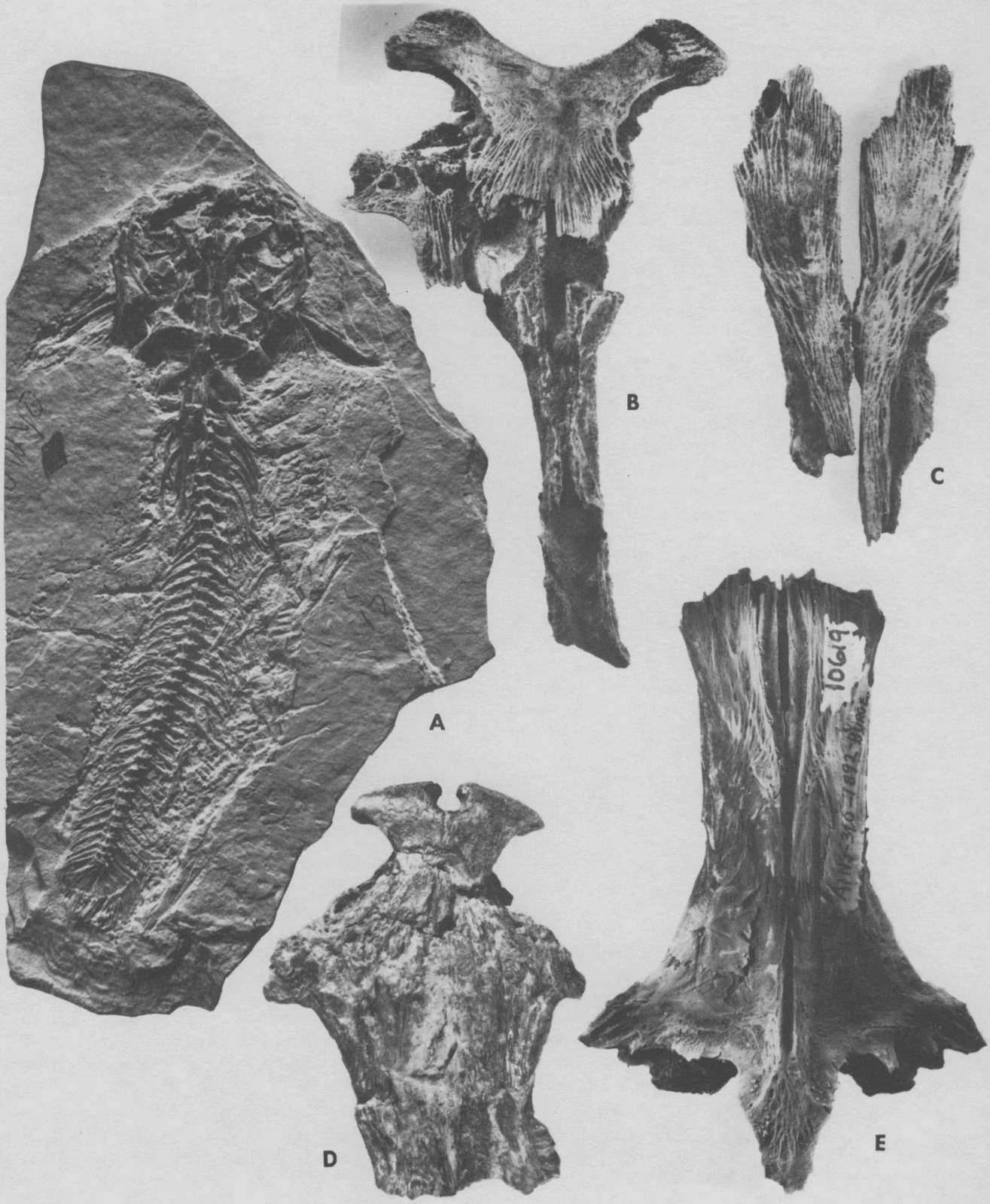
Material.— AMNH 8070, impression of ventral surface of articulated anterior part of fish to level of pelvic fins, from the Florissant lake beds.

Description and Remarks.— The two known specimens of *Ictalurus pectinatus* are impressions of the ventral surface of the anterior parts and have been studied through latex peels.

The supraethmoid cornua are not widely separated and they bear mesial processes; the median cleft is small and rounded. The width across the cornua is contained in

Plate IX. (A) *Ictalurus vespertinus*, dorsal view of partial skull (UMMP V57999), specimen 59 mm in length. (B) *Ictalurus pectinatus*, ventral view of anterior part of fish (AMNH 8070), length of figured part of specimen 87 mm. (C) *Ictalurus pectinatus*, ventral view of anterior part of fish (USNM 4086, Holotype), length of figured part of specimen 65 mm.

PLATE X



the skull length about 2.5 times. The parasphenoid stem is tapered posteriorly below the orbit, and the orbitosphenoid bears at least moderately broad horizontal shelves. A few sutures are developed between the prootic and exoccipital, but none are seen between the prootic and basioccipital. The lower jaw is somewhat enlarged and the dentary bears a prominent anteroventral crest that extends to the symphysis. There are no enlarged symphyseal or articular processes on the lower jaw. The premaxilla is broad and its sublateral process is not expanded. The jaw teeth are numerous and close set. The epihyal-ceratohyal is compressed and bears at least a small dorsal keel. The urohyal is trapezoidal in form and the vertical lamina is slightly longer than the horizontal. The interopercle in USNM 4086 is displaced and seen in external view; its surface is sculptured with pits, and in form it is relatively short and deep.

The ventral ridges of the first centrum are well developed. The fifth centrum is strongly sutured to the complex centrum and the superficial ossification is well developed. There is no extension of the superficial ossification onto the sixth centrum. The anterior limb of the fourth transverse process is at least moderately expanded distally, and the basal recess for the tripus is broad. The first rib appears to be associated with the sixth centrum.

The posterior process of the cleithrum is rather short and its external surface bears at least a few tubercles. The cleithral symphysis is short. There are 7 coracoid sutures, the ventral coracoid keel is short, and the secondary coracoid keel is present. The extensor fossa appears to be long and narrow but this feature is difficult to assess in ventral view. The transcapular ligament is completely ossified.

The tip of the pectoral spine is sharp. The ornamentation of the anterior edge of the spine is not visible, but the posterior dentations are strong, uniformly spaced and retrorse. The dentation halves are aligned, and the proximal dentations arise from the posterior groove, rather than from the dorsal half of the spine shaft.

There is a strong lateral process on the pelvic girdle and no lamina is developed between it and the anterolateral process. A pelvic splint and 8 soft rays are present in the pelvic fin.

Cope (1874) referred this species to *Rhineastes (Astephus)* on the basis of the pitted surface of the interopercle. That feature, however, is not diagnostic of *Astephus* and the bone usually bears some pits in modern ictalurids. This is the earliest certain record of an ictalurid with a modern form of the supraethmoid bone. I consider *Ictalurus pectinatus* to be a member of the subgenus *Amiurus* because of the combination of advanced features listed in the diagnosis above. Especially important are the broad snout and premaxillae, and the anteroventral crest of the dentary. The other unique features of *Amiurus* are indeterminate in the specimens at hand. The short ventral coracoid keel is a primitive feature shared with other species *Amiurus*. It is notable that the proximal posterior dentations of the pectoral spine arise from the posterior groove. This is a primitive feature that is found in living ictalurids in the subgenus *Ictalurus*. All other known species of *Amiurus* have these proximal dentations attached to the dorsal half of the spine shaft.

Thus, based on the available evidence, *Ictalurus (Amiurus) pectinatus* is considered to lie near the base of the *Amiurus* lineage. It appears to bear a sister group relationship to the other known members of the subgenus, and it represents a stage in the evolution of the bullheads before the origin of the characteristic position of the pectoral spine dentations.

Ictalurus serracanthus Yerger and Relyea

Yerger and Relyea (1968, p. 379) reported pectoral spines of this living species in Pleistocene deposits in the Suwannee drainage, Florida. The material has not been reexamined.

Ictalurus catus (Linnaeus)

Material, Localities, and Horizons.– Vero Beach, Sec. 35, T. 32 S, R. 39 E, Indian River County, Florida. Bed 3 of Vero deposits. Wisconsinan, Pleistocene, probably less than 3550 years B.P. (Weigel, 1963). AMNH 2935 (part), pectoral spine.

Remarks.– This spine is most similar to that of the modern white catfish, *Ictalurus (Amiurus) catus.*

Ictalurus brunneus (Jordan)

Yerger and Relyea (1968, p. 380) tentatively referred pectoral spines from Pleistocene deposits in the Suwannee drainage, Florida, to *I. brunneus*. At present this species does not live in the Suwannee River but it does occur in the Apalachicola and St. Johns systems. The material has not been reexamined.

Ictalurus macgrewi, new species

(Fig. 3 E-H; Pl. X A)

Diagnosis.– A species of *Ictalurus*, subgenus *Amiurus*,

Plate X. (A) *Ictalurus macgrewi*, dorsal view of complete fish (UW 3297, Holotype), 125.0 mm in standard length. (B, C) *Pylodictis olivaris*, dorsal views of two parts of a broken skull (F:AM 10580), length of left part 115 mm. (D) *Ictalurus punctatus*, dorsal view of anterior part of skull roof (UC 39465), 73 mm in length. (E) *Ictalurus punctatus*, dorsal view of posterior part of skull roof (F:AM 10619), 88 mm in length.

that differs from other members of its subgenus in the following combination of features: (1) supraoccipital process moderately long and slender, not marked by deep pits; (2) longitudinal crests on supraoccipital broad, low and completely ornamented with fine ridges; (3) transverse crests on supraoccipital nearly vertical; (4) pterotic surface smooth; (5) mesial processes developed on supraethmoid cornua; (6) width across supraethmoid cornua contained in skull length about 2.5 times; (7) minimum dorsal width of supraethmoid moderate, contained about 8 times in skull length; (8) foramen between lateral ethmoid and frontal for superficial ophthalmic nerves not enlarged; (9) lateral ethmoid wing short and robust; (10) head length contained in standard length about 4.5 times; (11) premaxilla moderately broad, covered with close-set, nearly straight, villiform teeth; (12) palatine short; (13) ventral edge of metapterygoid strongly curved; (14) horizontal and vertical laminae of urohyal about equal in length; (15) opercle narrow; (16) fourth neural spine short; (17) total vertebrae 42, 17 precaudal, 25 caudal; (18) about 16 anal rays; (19) posterior process of cleithrum ornamented at least basally with tubercles; (20) anterior dentations of pectoral spine weakly developed and irregularly spaced; and (21) posterior dentations of pectoral spine weakly developed, irregularly spaced and erect.

Holotype.— UW 3297, complete fish in dorsal view; standard length (approx.) 125.0 mm, dorsomedian skull length 33.3 mm, width across supraethmoid cornua 10.3 mm, minimum dorsal width of supraethmoid 3.5 mm, width of skull at epiphyseal bar 8.5 mm.

Horizon and Type Locality.— Banks of Horse Creek, Sec. 3, T. 17 N, R. 66 W, Laramie County, Wyoming. Beds of middle Miocene age (Paul McGrew, pers. comm.).

Material.— UW 3298, partial skull, pectoral girdle and anterior vertebrae in ventral view, from the type locality.

Description and Remarks.— Only two individuals of *Ictalurus macgrewi* are known, and of these the holotype is a rather small individual and the referred specimen is poorly preserved. The following description is based largely on the holotype and it must be pointed out that since this is a juvenile, features of the skull roof involving muscle crests might change with increasing size.

As judged solely from the holotype the most peculiar feature of *I. macgrewi* is the small head, which, as measured from snout tip to the rear edge of the opercle, is contained in the standard length about 4.5 times. Most other bullheads have the head contained in the standard length about 3.0 to 3.5 times, but in at least *I. serracanthus* this value is about 4.0 or slightly more. This is apparently a highly variable measurement in ictalurid catfishes, for example, head length in *Noturus gilberti* varies from 3.5 to 4.5 (Taylor, 1969).

The snout is relatively broad but the minimum dorsal width of the supraethmoid is moderate, as *I. serracanthus* and *I. nebulosus*. The cornua bear mesial processes and the median cleft is oval or rounded. The skull roof is slightly depressed and moderately broad; it is not constricted at the level of the epiphyseal bar as in *I. natalis*. The anterior fontanelle is open, and the posterior is slightly narrowed. The supraoccipital process is moderately long and slender. The longitudinal crests on the supraoccipital are broad and low, and completely covered with fine ridges. No deep pits are developed on the superficial parts of the longitudinal crests or supraoccipital process. The transverse crests on the rear margin of the supraoccipital appear to be oriented vertically, but there has been some distortion in this region. The upper limb of the supracleithrum, however, is sharply truncated, indicating that there was some forward expansion of the epaxial musculature. The crests of muscle origin on the frontal meet the margin of the skull roof anterior to the level of the epiphyseal bar, and there is a dorsolateral trough on the bone anterior to the point of exit of the infraorbital canal. The sphenotic process is prominent. The posttemporal is divided into separate laterosensory and laminar components. The wing of the pterotic is angular and its surface is not pitted. The lateral ethmoid wing is short and robust; its posterior margin is entire, and the foramen between the frontal and lateral ethmoid for the superficial ophthalmic nerves is not enlarged.

The lower jaw is long and wide, and there are almost certainly 6 mandibular sensory pores, the first of which is remote from the mandibular symphysis. The anteroventral crest of the dentary is well developed and extends to the symphysis. There are no symphyseal or articular processes on the mandible, and the posterior edge of the coronoid processes is steeply inclined. The premaxilla is moderately broad and the sublateral processes are not enlarged. The teeth are uniformly developed and close set.

The muscle crests on the hyomandibular are well developed and have the form typical of most bullheads. The lower end of the facial canal is nearly superimposed on the mandibularis notch, and there is a shallow groove between it and the symplectic canal. The upper limb of the preopercle is shortened, the bone is expanded behind the sensory canal and slightly concave. The metapterygoid appears to be moderately elongated and its ventral margin is curved. The endopterygoid is not visible on either specimen. The hyoid bar is like that in other species of *Amiurus*, with a strong dorsal keel on the dorsal edge of the ceratohyal. The vertical and horizontal laminae of the urohyal are subequal in length. The opercle is narrower than in other bullheads; its dorsal border is not flattened or concave. The interopercle is shallow and elongate.

The ventral ridges of the first centrum are well developed. The fifth and complex centra are strongly sutured and the superficial ossification is well developed but does not extend onto the sixth centrum. The basal recess of

the anterior limb of the fourth transverse process is broad. The fourth neural spine is somewhat shortened, and the vertical lamina is small. The nuchal plates of the first and second dorsal basals are slender. The first dorsal spine is well developed, and the second, or defensive, spine is long (slightly shorter than the pectoral spines). There are 42 total vertebrae in the holotype; 17 precaudal, and 25 caudal. The caudal skeleton does not differ from that in other bullheads. The anal fin contains about 16 rays, but the fin is distorted and this count may be an underestimate.

The posterior process of the cleithrum is poorly preserved but appears to have been slightly shortened and tubercles are present at least basally. The cleithral symphysis is short. There are 7 or 8 coracoid sutures, the coracoid ventral keel is short, and the secondary keel is moderately developed. The form of the extensor fossa is difficult to reconstruct in ventral view, but it appears to be long. The transcapular ligament of the supracleithrum is completely ossified and the subpterotic process is present.

The tip of the pectoral spine is sharp. Anterior distal serrae are hardly or not developed. The anterior ridge is weak, and the anterior dentations are small and irregularly spaced. The posterior dentations are weakly developed and erect; the dentation halves are imperfectly aligned distally, and the proximal dentations arise from the dorsal half of the spine shaft. The pelvic fin appears to contain 8 rays and the lateral process of the pelvic girdle is well developed but there is no lateral lamina.

I. macgrewi possesses the derived features (where known) of the subgenus *Amiurus*, e.g., extension of the levator arcus palatini origin anterior to the infraorbital canal exit, a steeply inclined posterior edge of the coronoid process, a prominent anteroventral crest on the dentary, a broad supraethmoid cornua and premaxilla, and a keeled ceratohyal. Three features of this fossil fall outside of the known range of variation of other bullheads. These are the small head (discussed above), the narrow opercle, and the short fourth neural spine. All of these features are more similar to conditions in *Noturus*. In *Noturus*, however, the angle between the anterior and dorsal edges of the opercle is much greater than 90°, whereas in this fossil, and most other ictalurids this angle is nearly 90°. Furthermore, the short fourth neural spine is found in flat-headed bullheads, and *I. serracanthus*. *Ictalurus macgrewi* does not possess any of the characteristic specializations of the skull roof, suspensorium, or caudal skeleton that are unique to *Noturus*. In addition, within *Amiurus* there is some evidence that suggests that *I. macgrewi* is cladistically closer to the *natalis* group *(I. natalis, I. melas* and *I. nebulosus)* than to the *catus* group *(I. catus, I. serracanthus, I. brunneus)*. The lateral ethmoid wing in *I. macgrewi* is quite short and robust, and the palatine bone is very short. These are derived features which are shared with the *natalis* group, but other advanced features of that group are apparently absent, e.g., the foramen for the superficial ophthalmic nerves is not enlarged, pits are not developed on the pterotic wing, and the metapterygoid is apparently not shortened. *Ictalurus macgrewi* does not possess any of the derived features peculiar to the *catus* group. The rather primitive form of the longitudinal crests on the supraoccipital in the holotype may simply be a juvenile character, and occasional specimens of *I. nebulosus* have similar conditions. Thus it is concluded here that *I. macgrewi* shares a most recent common ancestry with the *natalis* group of *Amiurus*. From this common ancestor the fossil appears to have diverged in the development of a relatively small head, narrow opercle, short fourth neural spine, and reduction of the ornamentation of the pectoral spine. In overall structure the pectoral spine of *I. macgrewi* is most similar to the weakly ornamented condition in *I. melas* and *I. leidyi*. Other fossil evidence (e.g., *I. sawrockensis*) strongly suggests that the weakly ornamented spine has evolved independently in *melas*.

This species is named for Paul O. McGrew of the University of Wyoming who called the fossils to my attention, and who has generously assisted in making other fossil catfishes available for study. In forming the zoological name for this species I have followed the recommendation of the International Code of Zoological Nomenclature (Appendix D, 21).

Ictalurus lavetti, new species

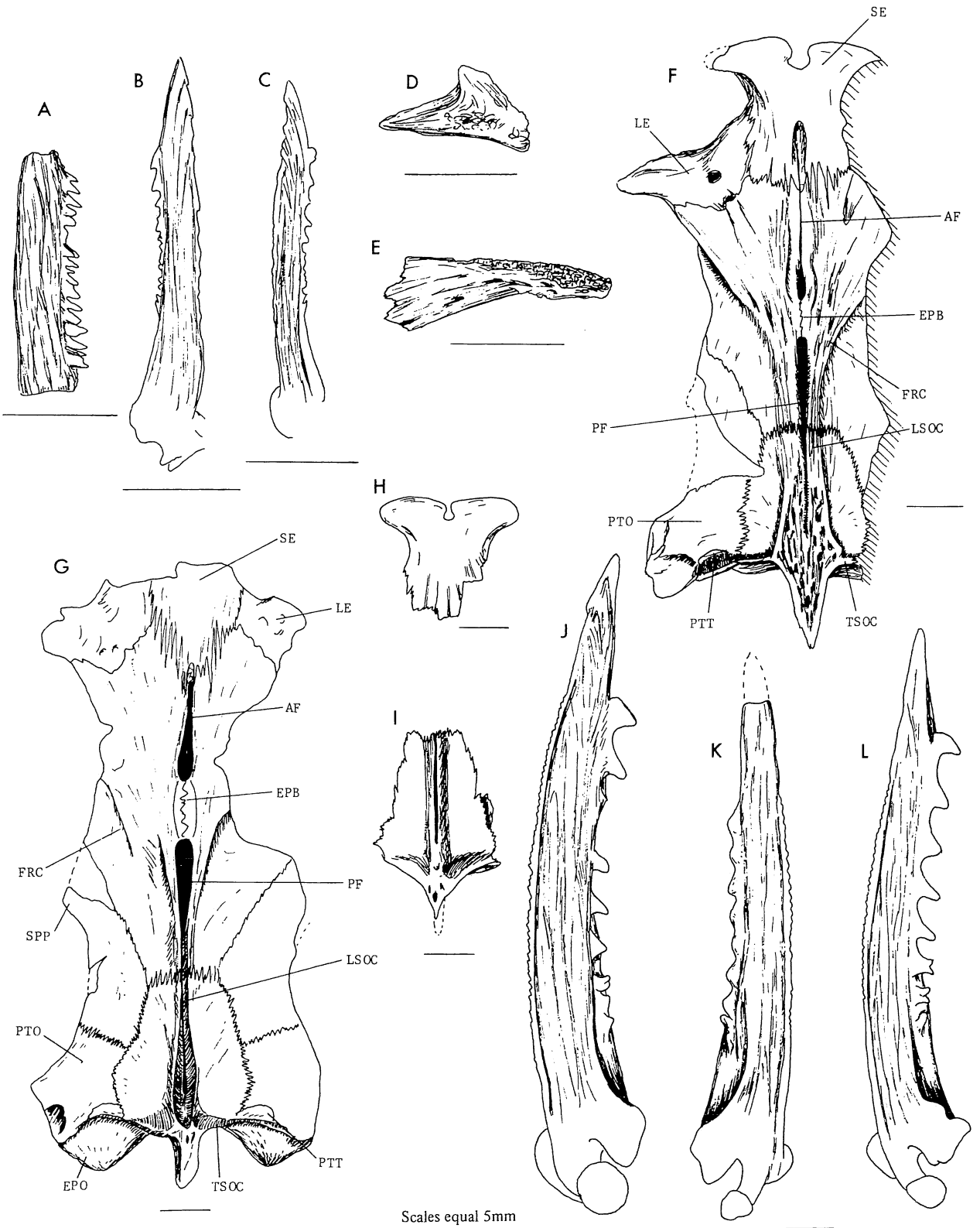
(Fig. 4 A-E; Pl. XI A)

Ictalurus cf. *nebulosus*.– Smith, 1962, p. 512.

Ictalurus sp.– Wilson, 1968.

Diagnosis.– A species of *Ictalurus*, subgenus *Amiurus*, that is distinguished from other members of the subgenus by the following combination of characters: (1) supraoccipital process very short, slender, with a few deep pits present basally; (2) longitudinal crests on the supraoccipital high, appressed on the midline, thus closing the posterior cranial fontanelle; (3) transverse crests on supraoccipital vertical and expanded posteromesially onto the base of the supraoccipital process; (4) mesial processes developed on supraethmoid cornua; (5) width across supraethmoid cornua contained in skull length about 2.3 times; (6) supraethmoid broad dorsally, contained in skull length about 6 times; (7) foramen for superficial ophthalmic nerves not enlarged; (8) lateral ethmoid wing short, robust, and sharply truncated posteriorly; (9) nasal bone broad and flattened; (10) skull quite narrow at level of epiphyseal bar; (11) epiphyseal bar in anterior half of skull; (12) premaxilla broad uniformly covered with close-set, villiform teeth; (13) palatine short; (14) anteroventral crest of dentary very deep, first mandibular sensory pore remote from symphysis; (15) total vertebrae 41, 18 precaudal, 23

FIGURE 4


A
B
C
D
E
F
SE
LE
AF
EPB
FRC
PF
LSOC
PTO
PTT
TSOC
G
SE
LE
AF
EPB
FRC
PF
SPP
LSOC
PTO
EPO
TSOC
PTT
H
I
J
K
L
Scales equal 5mm

caudal; (16) about 18 anal rays; (17) posterior process of cleithrum moderately long, ornamented with a few irregular tubercles basally; (18) anterior distal serrae of pectoral spine well developed and sharp; (19) anterior dentations weak and somewhat irregularly spaced; (20) posterior dentations numerous and moderately strong, strongly retrorse in young to erect in large individuals, and usually irregularly spaced.

Holotype.– USNM 22455, complete fish, skull in dorsal view; width across supraethmoid cornua 34.2 mm, minimum dorsal supraethmoid width 13.0 mm, skull width at epiphyseal bar 18.0 mm, lower jaw length 57.0 mm, dorsomedian skull length 90.0 mm (approx.), standard skull length 74.0 mm (approx.), standard length 320 mm (approx.).

Horizon and Type Locality.– Sec. 7, T. 11 S, R. 37 W, Old Vincent Ranch, 22 mi NE of Wallace, Logan County, Kansas. Diatomaceous marl beds in middle Pliocene part of Ogallala Group.

Material.– UMMP V55597-55607, pectoral spines; V55608, V55610, dentaries; V55611-55613, V55615, V55618-V55620, V55622-V55624, pectoral spines; V55625 (part), miscellaneous bones including dentaries, articulars, premaxillae, cleithra, coracoids, pectoral and dorsal spines, preopercles, supraethmoid, supraoccipital, ceratohyal, supracleithra, frontals and maxilla; MSU VP450 (part), pectoral spines, from University of Michigan locality UM-K6-59, NW of Ogallah, Trego County, Kansas, 2350-2550 ft S, and 75 ft E of the NW corner, Sec. 22, T. 11 S, R. 22 W. From Wakeeney local fauna, Ogallala Group, middle or late early Pliocene (Clarendonian) (Wilson, 1968).

UMMP V56160, pectoral spine, from University of Kansas locality 29, 2450 ft S and 10 ft W of the NE corner, Sec. 21, T. 11 S, R. 22 W. Horizon as above.

F:AM 10621, partial skull; from Hollow Horn Bear Quarry, Rosebud Indian Reservation, Little White River, NE¼, Sec. 28, T. 37 N, R. 32 W, Todd County, South Dakota. Basal Ash Hollow Formation, early Pliocene. (Tentative identification).

Description and Remarks.– The catfish remains from the Logan County diatomite beds and the Wakeeney local fauna represent markedly different-sized individuals but are thought to belong to a single species because of their similarity to the modern *Ictalurus natalis* and their geographical and temporal proximity. In addition, some of the larger spines of MSU VP450 closely resemble the holotype in the structure of the posterior dentations. The following description is based largely on the holotype. Some of the characters were previously reported by Smith (1962).

The snout and supraethmoid are broad. The cornua bear mesial processes and the median cleft is deep and rounded. The skull roof is slightly depressed, and it is quite narrow at the level of the epiphyseal bar, similar to the condition in *I. natalis*. The epiphyseal bar is placed in the anterior half of the skull roof, i.e., the distance from the tip of the snout to the anterior edge of the epiphyseal bar is much less than the distance from the bar to the base of the supraoccipital process. The anterior cranial fontanelle is open, but the posterior fontanelle is nearly closed by the appression of the longitudinal crests. These crests are quite high and together they form a sharp median crest on the supraoccipital. The supraoccipital process is short and narrow. A few pits are developed at the base of the supraoccipital process but otherwise the bone is not ornamented. The transverse crests of the supraoccipital are enlarged posteromesially and they extend onto the base of the process. Behind the transverse crests the upper limb of the supracleithrum is sharply truncated. The crests on the frontal meet the margin of the skull roof anterior to the level of the epiphyseal bar. The lateral ethmoid wing is short and sharply truncated posterodorsally, reflecting a marked forward extension of the levator arcus palatini origin. The foramen for the superficial ophthalmic nerves is not enlarged. The nasal bone is very broad and flattened. The sphenotic process is moderately large. The pterotic wing is angular and a few ridges are developed on its surface distally.

The lower jaw is large, with the anteroventral crest very strongly developed. The first mandibular sensory pore is remote from the symphysis. There are no large symphyseal or articular processes and the posterior edge of the coronoid process is steeply inclined.

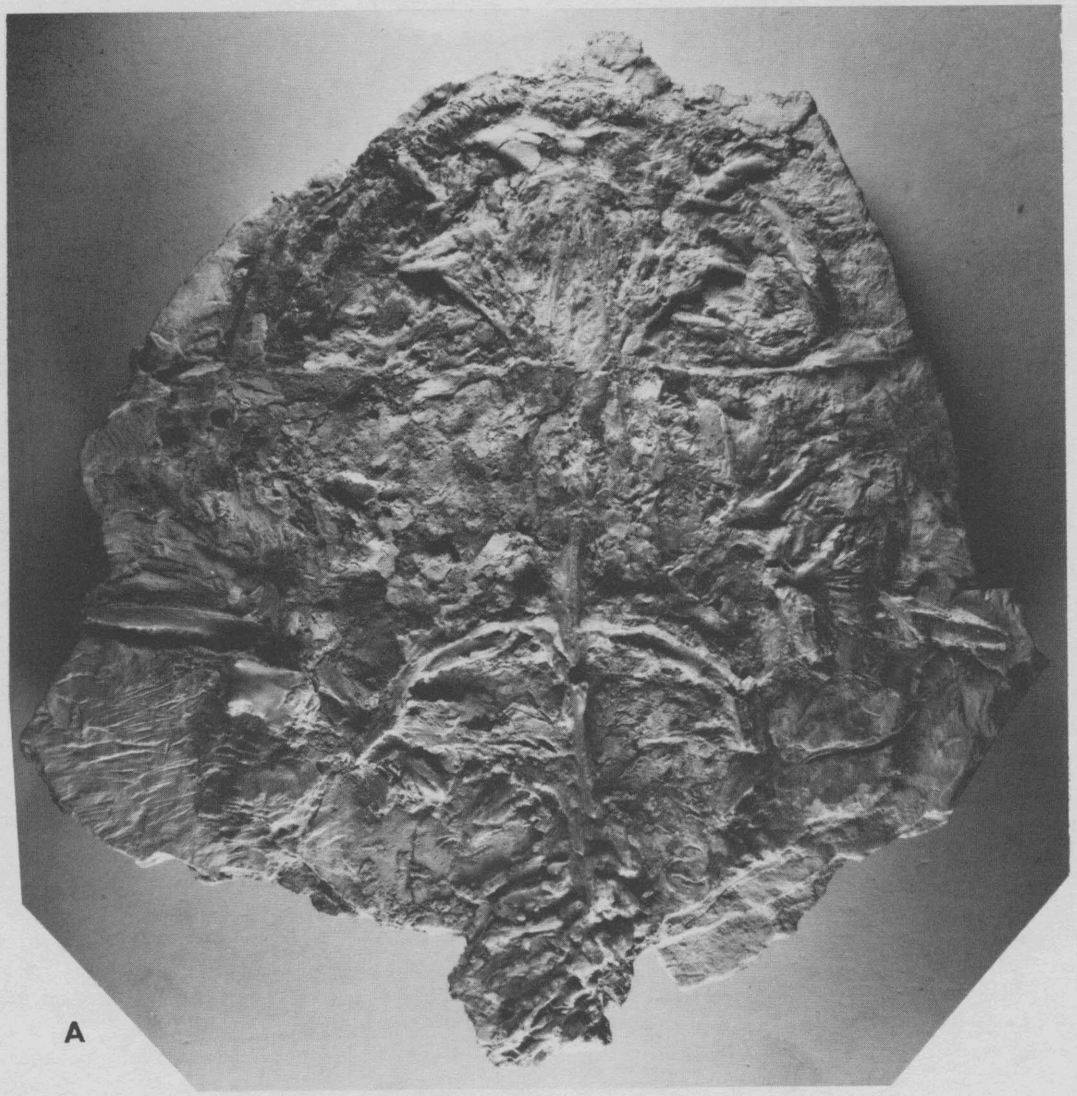
The premaxillae are moderately broad and uniformly covered with close-set teeth. The sublateral process of the premaxilla is not enlarged but the posteromesial process is prominent.

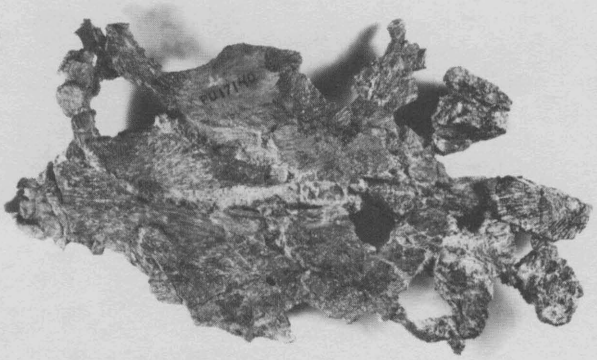
The hyomandibular muscle crests are prominent. The lower end of the facial canal is separated from the mandibularis notch. The upper limb of the preopercle is short, and the bone is concave and expanded behind the sensory canal. The form of the metapterygoid is indeterminate, but the endopterygoid appears to be large. The opercle is broad and its dorsal border is not markedly flattened.

There are 41 total vertebrae, of which 18 are precaudal

Fig. 4. (A) *Ictalurus lavetti*, MSU 450, pectoral spine. (B) *Ictalurus lavetti*, UMMP V55615, pectoral spine. (C) *Ictalurus lavetti*, UMMP V55598, pectoral spine. (D) *Ictalurus lavetti*, UMMP V55625, posterior process of cleithrum. (E) *Ictalurus lavetti*, UMMP V55610, dentary. (F) *Ictalurus leidyi*, F:AM 10509, skull. (G) *Ictalurus sawrockensis*, UMMP V57959, dorsal view of skull. (H) *Ictalurus sawrockensis*, UMMP V37101, supraethmoid. (I) *Ictalurus sawrockensis*, UMMP V57167, supraoccipital. (J) *Ictalurus sawrockensis*, UMMP V45381, Rexroad local fauna, pectoral spine. (K) *Ictalurus sawrockensis*, UMMP V37067, Sawrock Canyon local fauna, pectoral spine. (L) *Ictalurus sawrockensis*, UMMP V57375, Sand Draw local fauna, pectoral spine.

PLATE XI





and 23 are caudal. The caudal skeleton does not differ from that in other bullheads but there appear to be 8+10 principal caudal rays rather than the usual 8+9. Occasional variation such as this has been observed in *I. natalis*. The caudal fin is slightly emarginate. The anal fin contains about 18 rays and basals.

The posterior process of the cleithrum is moderately long, and irregular tubercles are developed basally. The ventral keel of the coracoid is short, and there appear to be about 6 coracoid sutures.

The pectoral spine is well ossified and its tip is sharp. In the holotype the anterior distal serrae are obsolescent (almost certainly an age change) but in the smaller spines there are usually 3 or 4 well-developed and sharp serrae. The anterior ridge is not prominent and the anterior dentations are weak and usually irregularly spaced. The posterior dentations are moderately strong, retrorse to erect, and generally multifid. A prominent lateral process is developed on the pelvic girdle and there is no lateral lamina. The pelvic fin contains 8 rays.

Ictalurus lavetti possesses the advanced features (where known) of the subgenus *Amiurus* and the *natalis* group. On the basis of anal ray count and pectoral spine structure Smith (1962) referred the holotype to *I. nebulosus*. The number of anal rays, 18, however, is not diagnostic for *I. nebulosus*, and I interpret the pectoral spine structure differently. In the holotype, which is a rather large individual, the posterior dentations are more numerous, erect and less strongly developed than in Recent *I. nebulosus* of comparable size.

In other parts of its anatomy *I. lavetti* appears to be closest to *I. natalis*. The fossil is not known to have any of the derived features peculiar to *I. nebulosus*, but it does share the following specializations with *I. natalis*: (1) skull roof constricted at epiphyseal bar; (2) anterior position of epiphyseal bar; (3) high longitudinal crests on supraoccipital that are nearly appressed on midline; (4) posteromesial expansion of transverse crests onto the base of narrowed supraoccipital process; (5) sharply truncated posterior edge of lateral ethmoid wing; (6) broad snout and supraethmoid; (7) enlarged anteroventral crest on dentary; and (8) increased number of anterior distal serrae on pectoral spine.

Ictalurus lavetti is, however, less advanced than *I. natalis* in lacking the following derived features of the latter: (1) enlarged foramen for superficial ophthalmic nerves (this is not a constant feature of modern *I. natalis*); (2) secondary slight reduction of the levator arcus palatini crest (prominent in *lavetti*); (3) first mandibular sensory pore placed close to the symphysis (remote in *lavetti*); (4) relatively high number (26-28) of caudal vertebrae (23 in *lavetti*) and (5) relatively high number (26-30) of anal fin rays (about 18 can be counted in the holotype of *lavetti*, but some of the anterior rays are not visible).

The only feature of *I. lavetti* that might be considered derived relative to *I. natalis* is the slightly more prominent and irregularly spaced posterior dentations of the pectoral spine. Otherwise, there are no known features of the fossil that exclude it from an evolutionary position near the line leading to modern *I. natalis*.

This species is named for C. Lavett Smith who pioneered much of the recent work on late Cenozoic fossil fishes at the University of Michigan.

Ictalurus natalis (Lesueur)

Material, Localities, and Horizons.— Easley Ranch local fauna. Easley Ranch, Monument Creek, Foard County, Texas. Early Wisconsinan, Pleistocene (Taylor, 1965). SMUMP 7154, miscellaneous bones as listed in Lundberg (1967, p. 454).

Ingleside Pit, 1 mi E of Ingleside, San Patricio County, Texas. Late Wisconsinan, Pleistocene. TBEG and UMMP numbers as listed in Swift (1968b, p. 66).

Vero Beach, center SE¼, Sec. 35, T. 32 S, R. 39 E, Indian River County, Florida. Late Wisconsinan, Pleistocene (Weigel, 1963). AMNH 2935 (part), pectoral spines.

Ictalurus leidyi, new species

(Fig. 4 F; Pl. V A, Pl. VII K)

Diagnosis.— A species of *Ictalurus* subgenus *Amiurus*, that is distinguished from other members of the subgenus by the following combination of characters: (1) supraoccipital process moderately long, tapered, and ornamented with ridges, grooves and small pits; (2) longitudinal crests on supraoccipital moderately high, angular, rather broad and extensively ornamented posteriorly; (3) posterior cranial fontanelle constricted but not closed; (4) transverse crests on supraoccipital nearly vertical, not expanded onto base of supraoccipital process; (5) supraethmoid cornua with mesial processes; (6) width across supraethmoid cornua contained in skull length about 3 times; (7) dorsal width of supraethmoid contained in skull length about 5 to 6 times; (8) foramen for superficial ophthalmic nerves often enlarged; (9) lateral ethmoid wing not truncated posteriorly; (10) skull roof not constricted at epiphyseal bar; (11) premaxilla broad, covered with evenly spaced close-set villiform teeth; (12) palatine short; (13) anteroventral crest of dentary moderately deep, first mandibular sensory pore remote from symphysis; (14) posterior process of cleithrum moderately long, ornamented with irregularly spaced tubercles; (15) anterior distal serrae of pect-

Plate XI. (A) *Ictalurus lavetti*, dorsal view of anterior part of fish (USNM 22455), 90.0 mm in length. (B) *Astephus*, indeterminate species, dorsal view of fragmentary skull (anterior to left) (the vertebra has disappeared) (PU 17140), length of skull 155 mm.

oral spine few in number and weakly developed; (16) anterior dentations generally weak to moderately developed and irregularly spaced; (17) posterior dentations weak to moderately strong, usually erect to slightly retrorse, multifid and irregularly spaced.

Holotype.– F:AM 10509, nearly complete skull in dorsal view; width across supraethmoid cornua 16.2 mm, minimum dorsal supraethmoid width 8.1 mm, skull width at epiphyseal bar 17.3 mm, dorsomedian skull length 56.5 mm (approx.), standard skull length 48.0 mm (approx.).

Horizon and Type Locality.– Observation Quarry, NW ¼, SE¼, Sec. 4, T. 31 N, R. 47 W, Dawes County, Nebraska. Beds equivalent to early Lower Snake Creek, early late Miocene.

Material.– F:AM 10504, partial skull, hyomandibular pectoral spines; 10505, miscellaneous bones include partial skulls, jaws, shoulder girdles, and pectoral spines; 10506, complete skull; 10507, partial skulls and spines; 10508, partial skull, spine and pectoral girdle; 10510, partial skulls, and spines; 10511, pectoral spines; 10512, Weberian complex, hyomandibulars, preopercle, spine; 10513, cleithra, hyomandibulars, spines; 10514, pectoral and dorsal spines, cleithral fragment; 10515, partial skull, cleithrum, spine; 10516, epihyal, cleithra, spines; 10517, partial skull; 10518, supraethmoids, frontal, cleithra, spines; 10519, articulars; 10520, cleithrum and articulars; 10521, spines, cleithra, coracoid, supraoccipital, frontal, preopercle; 10522, interopercle, spines, articulars, basioccipital, parasphenoid; 10523, miscellaneous bones include dentaries, articulars, quadrates, supraethmoid, basioccipitals and Weberian centra, ceratohyals, cleithra, pectoral spines; 10524, miscellaneous bones include palatine, cleithra, pectoral spines, supraethmoid, hyoid bar; 10525, miscellaneous bones; 10526, pectoral spine; 10527, 10528, miscellaneous bones include premaxillae, palatine, dentaries, articulars, quadrates, hyomandibulars, metapterygoid, supraethmoids, frontals, supraoccipitals, orbitosphenoid, basioccipitals, Weberian centra, ceratohyals, urohyals, dorsal spines, pectoral spines, coracoids, cleithra; 10529, basioccipital; 10530, miscellaneous bones include ceratohyals, pectoral spines, articulars, dorsal basal, cleithra, metapterygoid, hyomandibulars, coracoids, supraethmoids; 10531; cleithrum and pectoral spine. All of the above from the type locality.

UMMP V57361 (part), ceratohyal, dentary, supraoccipital, pectoral spine, cleithra; V56528 (part), supraoccipital, lateral ethmoid, cleithra, dentary, Weberian complex fragment; V57357, pectoral spines; Egelhoff local fauna, Keya Paha County, Nebraska. Valentine Formation, Crookston Bridge Member, lower Pliocene (Skinner et al., 1968).

F:AM 10606, pectoral spine, from Magle Ranch. NE of rapids in the Niobrara River, Cherry County, Nebraska. Valentine Formation. Burge Member, early Pliocene. (Identification tentative.)

F:AM 10536, 10538, pectoral spines from Gallup Gulch Quarry, SE¼, SW¼, Sec. 24, T. 33 N, R. 38 W, Cherry County, Nebraska. Ash Hollow Formation, lower Pliocene. (Identification tentative.)

F:AM 10638, pectoral spine from June Quarry on Plum Creek, 4.5 mi N of Johnstown, Brown County, Nebraska. Valentine Formation, Burge Member, early Pliocene.

F:AM 10610, pectoral spines; 10612, pectoral spines and dentary fragment from roadcut about 10¾ mi W of Gordon, Sheridan County, Nebraska. ? Ash Hollow Formation, early Pliocene. (Identification tentative.)

UC 31985a, pectoral spine (fig. 1c, Estes and Tihen, 1964), UC locality V3218, on the quarter section line between the NW and SW quarters of Sec. 24, T. 34 N, R. 26 W, Cherry County, Nebraska.

UW 3293, pectoral spines, Verdigre Quarry on the E bank of an unnamed tributary to Verdigre Creek, in the NW¼ of Sec. 16, T. 29 N, R. 7 W, approximately 7.5 mi S and 5.5 mi W of the town of Verdigre, Knox County, Nebraska. Valentine Formation, lower Pliocene (Voorhies, 1969). (Identification tentative.)

F:AM 10603, pectoral spines, cleithra, dorsal spines, from Kat Quarry, Cherry County, Nebraska. Middle part of Ash Hollow Formation, early Pliocene.

Description and Remarks.– *Ictalurus leidyi* is known from a few articulated neurocrania and numerous disassociated bones. The following description is based largely on the material from Observation Quarry.

The snout and suparethmoid are broad. The cornua bear mesial processes and the median cleft is rounded. The skull is somewhat depressed as in most other bullheads, and it is broad at the level of the epiphyseal bar. The anterior cranial fontanelle is constricted or closed anteriorly. The posterior fontanelle is narrowed but never closed. The longitudinal crests on the supraoccipital are high, and, near the base of the supraoccipital process, they are quite broad and covered with ridges, grooves and pits. This ornamentation is continued posteriorly onto the moderately long and tapered supraoccipital process. The transverse crests are oriented vertically and do not extend onto the base of the supraoccipital process. The frontal crests meet the margin of the skull roof anterior to the epiphyseal bar. The trough for the levator arcus palatini muscle extends anterior to the exit of the infraorbital canal, but does not reach the lateral ethmoid wing. The latter is short and directed horizontally. The foramen for the superficial ophthalmic nerves, between the lateral ethmoid and frontal, is often enlarged. The sphenotic extends anteriorly to the epiphyseal bar, and its lateral process is large. The posttemporal bone is divided into separate laminar and laterosensory components, and the pterotic wing is angular with deep pits developed distally.

The parasphenoid stem is tapered below the orbit and its ascending wings are not twisted mesially. The horizontal shelves of the orbitosphenoid are broad, and the descending wings of the frontal are large. Contact between the prootic and pterotic appears to be variable as in most modern ictalurids. A few sutures are developed between the prootic and exoccipital, and the prootic-basioccipital contact is synchondral. The optic foramen is small.

The anteroventral crest of the dentary is moderately strong and the coronoid process is steeply inclined posteriorly. The first mandibular sensory pore is remote from the symphysis. There are no large symphyseal or articular processes on the mandible.

The premaxilla is moderately broad, and its sublateral process is not enlarged. There is a weakly developed posteromesial process near the symphysis. Uniformly spaced teeth cover the premaxilla.

The levator arcus palatini and A_3 crests on the hyomandibular are prominent. The levator operculi crest is a low ridge, and the adductor hyomandibularis process is prominent but not elongated. The lower end of the facial canal is slightly separated from the mandibularis notch and joined to the symplectic canal by a shallow groove. The metapterygoid is rather slender and its ventral margin is slightly curved. The relative size of the endopterygoid is unknown. The ceratohyal bears a strongly developed dorsal keel.

The fifth centrum is tightly sutured to the Weberian centrum. The superficial ossification is well developed but lacks posterior extensions onto the sixth centrum. The vertical lamina of the Weberian complex is small. The nuchal plates of the dorsal fin basals are moderately well developed, and the dorsal spine is long.

The posterior cleithral process is moderately long and consistently ornamented with irregularly spaced tubercles. Seven or 8 coracoid sutures are developed, and the ventral keel is short. The secondary coracoid keel is well developed. The coracoid extensor fossa appears to be rather short and narrow.

The pectoral spine is well ossified and bears a sharp tip. A few anterior distal serrae are usually present but these are not especially prominent. The anterior dentations are weak to moderately developed and irregularly spaced. The anterior ridge is rather weak. The halves of the posterior dentations are usually imperfectly aligned so that the dentations are multifid. Proximally, the dentations arise from the dorsal half of the spine shaft. The posterior dentations are generally weakly developed and erect. The pectoral spines of *I. leidyi* closely resemble those of *I. melas*, hence the tentative records in the preceding materials list where spines only were available for examination although the latter species does not appear with certainty until late Kansan.

In overall anatomy *I. leidyi* appears to be a member of the *natalis* group, and most closely related to *melas* and *nebulosus*. *Ictalurus leidyi* possesses the advanced osteological features (where known) of the subgenus *Amiurus*, and of the *natalis* group. In addition, it shares with *melas* and *nebulosus*, vertically oriented, transverse muscle crests on the supraoccipital, and deep pits on the pterotic wing and sometimes on the supraoccipital. *Ictalurus leidyi* has reduced ornamentation of the pectoral spine and a broad snout and supraethmoid, as in *melas*. These have been considered derived conditions but *leidyi* is apparently more primitive than either *nebulosus* or *melas* in having unreduced jaw dentition, a more elongate metapterygoid, and an unreduced secondary coracoid keel. In addition the consistently broad and extensively ornamented longitudinal supraoccipital crests are apparently a primitive feature, but rare individuals of *nebulosus* have similarly developed crests. One feature of *I. leidyi* that appears to be derived relative to other bullheads is the constricted anterior cranial fontanelle. This is a constant feature of the fossils from the type locality, but again the condition is occasionally developed in modern *melas* and *nebulosus*.

The most reasonable conclusion on the cladistic position of *I. leidyi* is that it lies near the common ancestor of both *I. melas* and *I. nebulosus*. It appears that the similarities between the fossil and *I. melas* in snout width and pectoral spine morphology were independently developed, unless they are the primitive states for this section of the subgenus.

The fossil species is named for the North American vertebrate paleontologist, Joseph Leidy (1823-1891).

Ictalurus nebulosus (Lesueur)

Material, Localities, and Horizons.– Ichtucknee River fauna, 2.5 mi above bridge on Route 5A, 10 mi E of Branford, 6.5 mi NW of Fort White, Columbia County, Florida. Wisconsinan, Pleistocene. F:AM 10640, pectoral spine; 10642, pectoral spine and cleithra; 10644, pectoral spines; 10645, pectoral and dorsal spines, cleithra; 10646, pectoral spines; 10648, pectoral spines, cleithra, supracleithrum; 10650, cleithrum and coracoid.

Durham Cave, near Riegelsville, Bucks County, Pennsylvania. Late Pleistocene, reported by Leidy (1889). The material has not been reexamined.

Ictalurus sawrockensis Smith

(Fig. 4 G-L)

Ictalurus sawrockensis.– Smith, 1962, p. 514 (original description; Sawrock Canyon local fauna, upper Pliocene, Kansas). Smith and Lundberg, 1972 (redescription, synonymy).

Ictalurus benderensis.– Smith, 1962, p. 527 (original description; Bender local fauna, upper Pliocene, Kansas).

Diagnosis.– A species of the subgenus *Amiurus* (bull-

heads) of *Ictalurus* distinguished from other members of its subgenus by the combination of the following features: (1) supraoccipital process moderately long and slender, with a deeply pitted surface in adults; (2) longitudinal crests on supraoccipital rather narrow in adults, without broad ornamented area at base of supraoccipital process; (3) transverse crests of supraoccipital vertically oriented and not expanded onto base of supraoccipital process; (4) mesial processes developed on supraethmoid cornua; (5) snout and supraethmoid broad (dimensions relative to skull length indeterminate but apparently close to that of *I. melas* and *I. leidyi*); (6) foramen for superficial opthalmic nerves slightly enlarged; (7) lateral ethmoid wing short and horizontal, posterodorsal margin entire; (8) dorsal surface of pterotic with deep pits; (9) premaxilla broad, uniformly covered with close-set, villiform teeth; (10) palatine bones short; (11) anteroventral crest of dentary moderately deep, first mandibular pore remote from symphysis; (12) metapterygoid short and deep, its ventral edge slightly curved; (13) vertical lamina of urohyal usually slightly longer than horizontal lamina; (14) posterior process of cleithrum moderately long, with weakly developed or no tubercles; (15) anterior distal serrae of pectoral spine weakly developed; (16) anterior dentations moderately strong and regularly spaced along most of the length of the spine shaft; (17) posterior dentations moderate in strength, often multifid, erect to slightly retrorse, and generally regularly spaced distally.

Holotype.— UMMP V37066, left pectoral spine, 12.6 mm in length.

Horizon and Type Locality.— West side of Sec. 36, T. 34 S, R. 31 W, Seward County, Kansas. Sawrock Canyon local fauna, XI Member of lower part of the Rexroad Formation, upper Pliocene (Smith, 1962).

Material.— Listed in Smith and Lundberg (1972).

Remarks.— C. L. Smith (1962) described two bullhead catfishes from the upper Pliocene Rexroad Formation of Kansas: *Ictalurus sawrockensis* and *I. benderensis*, from the Sawrock Canyon local fauna, and from the Benders and Rexroad local faunas, respectively. Based on additional comparisons to both living and fossil ictalurids it has become apparent that the characters used by Smith tend to be highly variable within species. Only a single species of bullhead is represented in the Rexroad Formation. Smith and Lundberg (1972) selected *Ictalurus sawrockensis*, with page precedence, as the name of this species (Smith, 1962, p. 514-515, fig. 6). The bullhead remains from the Sand Draw, Dixon and Wathena local faunas are referable to this species.

A full redescription of material referable to *I. sawrockensis* was given by Lundberg (1970) and Smith and Lundberg (1972). It was concluded that *I. sawrockensis* is an extinct species of *Amiurus* close to, or perhaps even on, the line leading to the modern black bullhead, *I. melas*.

Ictalurus melas (Rafinesque)

Material, Localities, and Horizons.— Cudahy fauna, Vera faunule. Patterson Ranch, SW corner of N½, Sec. 101 of Block C of Houston and Texas Central Railroad Company Survey, and Jones Ranch, SW¼, Sec. 110, of Block C, Knox County, Texas. Seymour Formation, Cudahy fauna, late Kansan, Pleistocene (Getz and Hibbard, 1965). UMMP V39649, pectoral spine; V39790, V45707, V45708, V45826, V46904, miscellaneous bones including dentaries, hyomandibulars, metapterygoid, supraoccipital, cleithra, coracoids, pectoral spines.

Cudahy fauna. Gate Ash Pit, NW¼, NW¼, Sec. 8, T. 5 N, R. 28 E.C.M., Beaver County, Oklahoma. Crooked Creek Formation, below Type O Perlette Ash, late Kansan. UMMP V28122, pectoral spine.

Gate Ash Pit, above Type O Perlette Ash. Locality as above. UMMP V24771, V24772, pectoral spines.

Berends local fauna. SE¼, Sec. 6, T. 5 N, R. 28 E.C.M., near Gate Ash Pit, Beaver County, Oklahoma. Deposits comparable to lower part of Kingsdown Formation, Berends fauna, Illinoian, Pleistocene (Smith, 1954). Material listed by Smith (1954, p. 285-286).

Doby Springs local fauna. N½, SW¼, Sec. 10, T. 27 N, R. 24 W, Harper County, Oklahoma. Illinoian, Pleistocene. Material listed by Smith (1958, p. 178).

Butler Spring local fauna. XI Ranch, SE¼, Sec. 32, T. 34 S, R. 29 W, Meade County, Kansas. Late Illinoian, Pleistocene (Hibbard and Taylor, 1960). Material listed by Smith (1958, p. 179).

Mt. Scott local fauna. Big Springs Ranch, SE¼, Sec. 14, T. 32 S, R. 29 W; SE¼, Sec. 18, T. 32 S, R. 28 W; SW¼, SW¼, Sec. 13, T. 32 S, R. 29 W, Meade County, Kansas. Basal Kingsdown Formation, Mt. Scott local fauna, late Illinoian, Pleistocene (Hibbard and Taylor, 1960). Material listed by Smith (1963, p. 281).

Rezabek local fauna. Rezabek gravel pit in Sec. 20, T. 13 S, R. 11 W, Lincoln County, Kansas. Illinoian, Pleistocene (Hibbard, 1943). Material UMMP V47642, pectoral spines and cleithra.

Rice County, Kansas. Illinoian, Pleistocene. Material UMMP V57997, pectoral spine.

Sandahl local fauna. Sandahl Gravel Pit, SE¼, SW¼, Sec. 29, T. 18 S, R. 4 W, McPherson County, Kansas. McPherson Formation, Illinoian, Pleistocene (Semken, 1966). Material UMMP V50488 (part), pectoral spine; V50457, V50458 (part), pectoral spines.

Jinglebob local fauna. SW¼, Sec. 32, T. 33 S, R. 29 W, Meade County, Kansas. Late Sangamon, Pleistocene (Hibbard and Taylor, 1960). Material UMMP V56811, pectoral spine.

Clear Creek local fauna. Terrace above Clear Creek, at Trietsch Pit, 4 mi above Elm Fork of Trinity River, Denton County, Texas. Middle Wisconsinan, Pleistocene (Hib-

bard, pers. comm.). Material listed by Uyeno (1963).

Ben Franklin local fauna. Sulphur River, at bridge on Highway 38, Ben Franklin, Delta County, Texas. Late Wisconsinan, Pleistocene. Material listed by Uyeno (1963).

Jones local fauna. University of Kansas locality 13, Sec. 8, T. 33, S, R. 27 W, Meade County, Kansas. Vanham Formation, Wisconsinan, Pleistocene (Hibbard et al., 1965). Material UMMP V56495, pectoral spine.

Ingleside Pit. One mi E of Ingleside, San Patricio County, Texas. Wisconsinan, Pleistocene. Material listed in Swift (1968b, p. 65).

Quitaque local fauna. Terrace on Quitaque Creek in NE corner of Motley County, Texas. Wisconsinan, Pleistocene (Dalquest, 1964). Midwestern University, uncatalogued specimen, complete skull, pectoral girdle and anterior vertebrae.

Ree Heights. Sec. 22, T. 111 N, R. 70 W, Hand County, South Dakota. Wisconsinan, Pleistocene. Material listed in Ossian (1973, p. 110, pl. 3).

Ictalurus peregrinus, new species

(Fig. 5 A-E; Pl. VII C, D, Pl. VIII A)

Diagnosis.– A species of *Ictalurus*, subgenus *Amiurus*, that differs from the other members of the subgenus by the combination of the following features: (1) supraoccipital process long, slender, ornamented with deep pits and prominent ridges; (2) longitudinal crests on supraoccipital moderately high, narrow, angular or sharp, and nearly appressed on midline; (3) transverse crests on supraoccipital vertically oriented, not greatly expanded onto base of supraoccipital process; (4) basioccipital in large individuals develops a midventral groove posterior to median pit; (5) supraethmoid cornua very broad, mesial processes present; (6) premaxilla moderately broad, symphysis rather long, sublateral process not enlarged, uniformly covered with close-set teeth; (7) anteroventral crest of dentary moderately strong, first mandibular sensory pore remote from symphysis; (8) palatine short; (9) posterior process of cleithrum moderately long, ornamented basally and ventrally with prominent, irregularly spaced tubercles; (10) anterior distal serrae of pectoral spine absent or few and weakly developed; (11) anterior dentations of pectoral spine strongly developed and generally regularly spaced; and (12) posterior dentations of pectoral spine strongly developed, generally irregularly spaced and irregularly oriented distally, often multifid.

Holotype.– UO 28035, left pectoral spine 28.3 mm in length.

Horizon and Type Locality.– Sec. 14, T. 21 S, R. 37 E, Malheur County, Oregon. Upper member of the Juntura Formation, Black Butte local fauna (Shotwell and Russell, 1963).

Material.– UO 28036, pectoral spines; 28037, miscellaneous bones; 28038, pectoral spines; 28039, dentaries and dorsal spine; 28040, pectoral and dorsal spines; 28041, pectoral spines; UMMP V58003, miscellaneous bones; all from the type locality.

Description and Remarks.– *Ictalurus (Amiurus) peregrinus* is the second extinct species now known to occur outside of the present range of the Ictaluridae. The remains of this form include disarticulated, and, for the most part broken, cranial and pectoral elements.

The structure of the snout is known only from a fragmentary supraethmoid, but the bone appears to be very broad as in *I. vespertinus* (see below), and mesial processes are developed on the cornua. The supraoccipital process is long but narrow and tapered. The longitudinal crests on the supraoccipital are narrow, angular, and nearly appressed on the midline so that the posterior cranial fontanelle is constricted. The surface of the supraoccipital process is ornamented with ridges and deep pits, and these extend slightly onto the crests. The transverse crests are oriented vertically and not broadly expanded onto the base of the supraoccipital process. The basioccipital exhibits an unusual growth pattern, with the development of a midventral groove posterior to the median pit in large individuals. This gives rise to a deeply indented cranial facet for articulation with the first centrum.

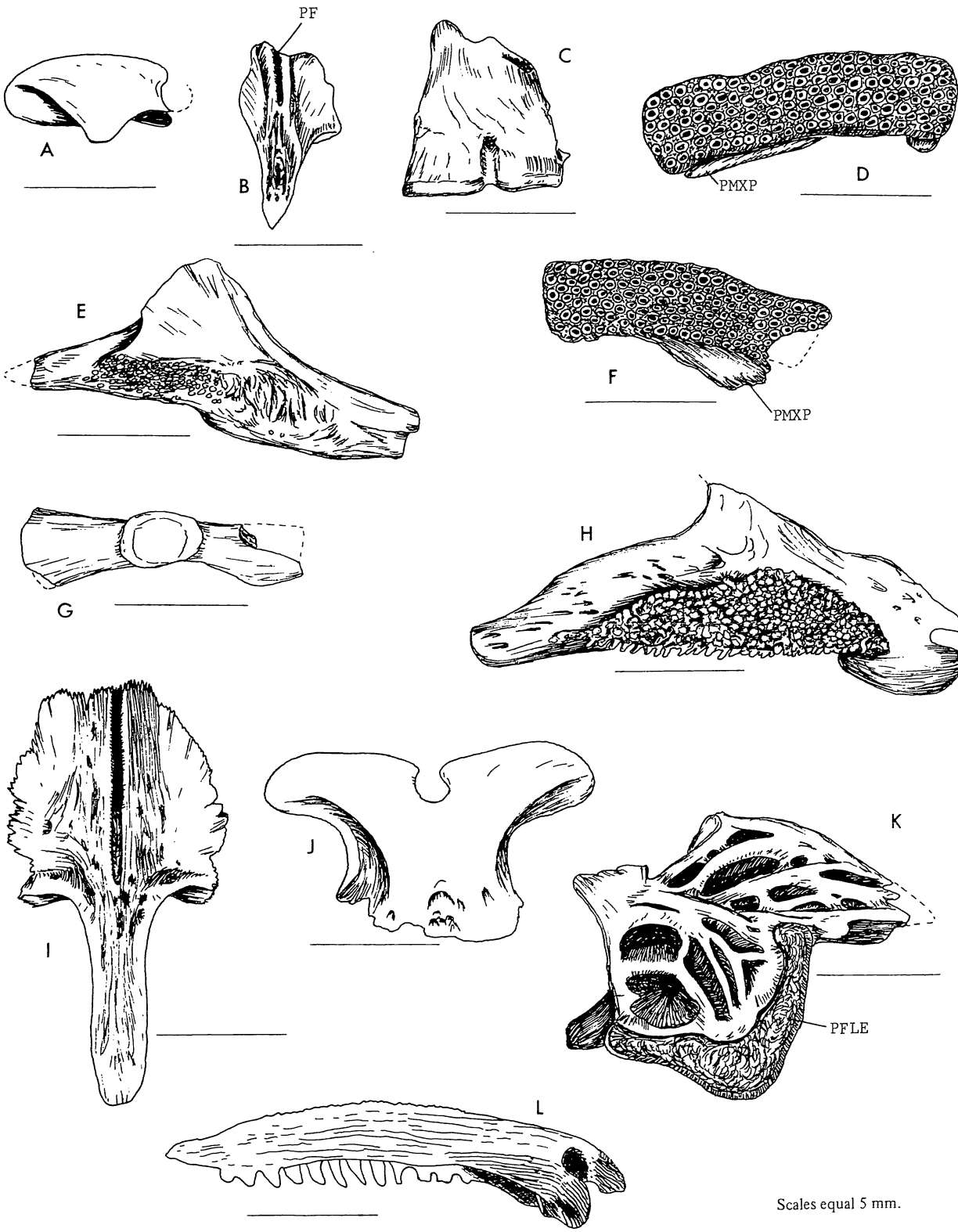
The premaxillae are moderately wide and somewhat elongated. The sublateral process is not enlarged, and a small posteromesial process is generally present near the symphysis. The premaxillary tooth patch is unreduced. Fragmentary remains of the dentary indicate a relatively large lower jaw with a broad band of teeth. The anteroventral crest of the dentary is moderately strong and the first mandibular sensory pore is remote from the symphysis. No prominent symphyseal or articular porcesses are developed. The posterior edge of the coronoid process is steeply inclined. The palatine bone is short.

The muscle crests on the hyomandibular are prominent. The abductor hyomandibularis process is not elongated. The dorsal edge of the opercle is flattened for insertion of the levator operculi. The dorsal spine is long and slender, and small posterior dentations are generally present.

The posterior process of the cleithrum is moderately long and slender. Strong, irregularly spaced tubercles are developed on the basal and ventral parts of the process. The anterior distal serrae of the pectoral spine are obsolescent, but the anterior dentations are strong and regularly spaced. The dorsal and ventral halves of the strong posterior dentations are often not perfectly aligned so that the dentations appear multifid and irregularly spaced.

In addition to possessing the advanced osteological features of *Amiurus, I. peregrinus* shares derived states with some or all members of the *natalis* group, e.g., vertically oriented transverse crests on the supraoccipital, and an ex-

FIGURE 5



tremely short palatine bone. The broad supraethmoid and rather wide band of teeth on the dentary in *I. peregrinus* are derived features shared with *I. vespertinus*, and the grooved basioccipital is found only in these two forms. In most other features *peregrinus* and *vespertinus* are nearly identical. The only characters separating these forms are those of pectoral-spine ornamentation. In *vespertinus* (Fig. 5 F-L) the posterior dentations of the pectoral spine have a primitive form in being regularly spaced and unicuspid distally, whereas in *peregrinus* these dentations tend to be multifid and irregularly spaced. In overall structure the pectoral spine of *peregrinus* appears to be quite advanced and most like that of *I. nebulosus*. Otherwise, the fossil does not have any derived features peculiar to *nebulosus*. Thus, on the basis of the similarities in basioccipital, snout and jaw structure the closest relative of *I. peregrinus* is thought to be *I. vespertinus*.

The name *peregrinus*, foreign or exotic, is a Latin adjective referring to the occurrence of this species outside of the Recent range of *Ictalurus*.

Ictalurus vespertinus Miller and Smith

(Fig. 5 F-L; Pl. VII B, Pl. VIII I, Pl. IX A)

Ictalurus vespertinus.– Miller and Smith, 1967, p. 15 (original description; Glenns Ferry Formation, Owyhee County, Idaho). Late Pliocene.

Amiurus sp.– Cope, 1883, p. 161.

Ictalurus.– Miller, 1959, p. 194.

Ictalurus (?).– Uyeno and Miller, 1962, p. 340. Uyeno and Miller, 1963, p. 16.

Ictalurus sp.– Miller, 1965, p. 573, 576, 577. Taylor, 1966, p. 74.

Diagnosis.– A species of *Ictalurus*, subgenus *Amiurus*, that is distinguished from other members of the subgenus by the combination of the following features: (1) supraoccipital process moderately long, narrow and tapered, ornamented with prominent ridges, grooves, and deep pits; (2) longitudinal crests of supraoccipital moderately high, narrow, rounded or sharp and appressed at midline so that the posterior cranial fontanelle is nearly closed; (3) transverse crests of supraoccipital vertically oriented, not expanded onto base of supraoccipital process; (4) snout and supraethmoid very broad, cornua with mesial processes; (5) pterotic surface with few or no pits; (6) basioccipital in large individuals develops a midventral groove posterior to median pit; (7) dorsal surface of supraethmoid and lateral ethmoid with unique spongy texture; (8) lateral ethmoid wing short and horizontal, its posterodorsal margin slightly truncated; (9) foramen for superficial ophthalmic nerves not enlarged; (10) premaxilla moderately broad, symphysis rather long, sublateral process not enlarged, uniformly covered with close-set teeth; (11) dentary large, with a moderately prominent anteroventral crest and broad band of teeth, first mandibular sensory pore remote symphysis; (12) palatine short; (13) posterior process of cleithrum long and slender, ornamented basally and ventrally with prominent, irregularly spaced tubercles; (14) anterior distal serrae of pectoral spine absent or few weakly developed; (15) anterior dentations of pectoral spine moderately strong and usually irregularly spaced; and (16) posterior dentations of pectoral spine strongly developed, generally regularly spaced, unicuspid, and evenly retrorse distally.

Holotype.– UMMP V55561, right lower jaw; measurements given in Miller and Smith (1967).

Horizon and Type Locality.– University of Michigan locality UM-IDA-9-62, roadcuts on state highway 45 about 1.5 mi SE of Fossil Butte, Sec. 16, T. 4 S, R. 1 W. Glenns Ferry Formation, lacustrine facies, late Pliocene.

Material.– UMMP V57999, two partial skulls. Little Valley about 14 mi SW of Bruneau, Idaho. Chalk Hills Formation, middle Pliocene (Malde and Powers, 1962).

UO 28042, pectoral spines, dorsal spines, and lateral ethmoid, from UO locality 2380; 28043, spines, dentaries, premaxillae, from UO locality 2516. Both localities in Mitchell Butte Quadrangle, Malheur County, Oregon, in the NE¼, Sec. 33, T. 19 S, R. 43 E. Chalk Butte Formation, middle Pliocene (Shotwell, pers. comm.).

UC 74663, pectoral spine; 74690, pectoral and dorsal spines; locality V6419, Rome, Malheur County, Oregon. Rome Beds, middle Pliocene.

UMMP V53631, pectoral spines; V53637, dorsal spines; from NE¼, Sec. 32, T. 7 S, R. 13 E, 1440 ft W and 1350 ft S of NE corner, Sec. 32, Twin Falls County, Idaho. Glenns Ferry Formation, late Pliocene.

UMMP V53246, cleithra; V53248, pectoral spines; SW ¼, Sec. 32, T. 7 S, R. 13 E, 2200 ft N and 2200 ft E of SW corner, Sec. 32, Twin Falls County, Idaho. Glenns Ferry Formation, late Pliocene.

UMMP V34443, miscellaneous bones; V45302, dorsal spines; V50367, V50368, pectoral spines; V50369, dorsal spines; V50376, articulars; V50380, cleithra; V50381, first dorsal spines; V50385 (part), dentaries and articulars; V53143 (part), palatines; V53144 (part), basioccipitals and Weberian centra; V53145, supraoccipitals; V53146,

Fig. 5. (A) *Ictalurus peregrinus*, UO 38037, supraethmoid. (B) Same, supraoccipital. (C) Same, basioccipital. (D) Same, premaxilla. (E) Same, posterior process of cleithrum. (F) *Ictalurus vespertinus*, UMMP V53166, premaxilla. (G) *Ictalurus vespertinus*, UMMP V53143, palatine. (H) *Ictalurus vespertinus*, UMMP V50380, posterior process of cleithrum. (I) *Ictalurus vespertinus*, UMMP V58001, supraoccipital. (J) *Ictalurus vespertinus*, UMMP V53146, supraethmoid. (K) *Ictalurus vespertinus*, UO 28042, lateral ethmoid. (L) *Ictalurus vespertinus*, UMMP V58994, right pectoral spine.

supraethmoids; V53148, quadrates; V53150, parasphenoid; V53151, first dorsal spines; V53152, dorsal spines; V53153, articulars; V53154, cleithra; V53155, pectoral spines; V53166 (part), premaxillae and dentaries; V53435, cleithra; V55040, pectoral spines; V55041, miscellaneous bones; USNM 22345, pectoral spine. SW¼, Sec. 28, T. 7 S, R. 13 E, 350 ft E, 2100 ft N of SW corner of Sec. 28 (USGS Cenozoic locality 20765), Twin Falls County, Idaho. Glenns Ferry Formation, late Pliocene.

UMMP V50605, pectoral spines and cleithrum. NW¼, SW¼, Sec. 28, Twin Falls County, Idaho. Glenns Ferry Formation, late Pliocene.

UMMP V54386, dentary; V54391, pectoral spines; V54392, dorsal spines; SW¼, Sec. 28, T. 7 S, R. 13 E, 100 ft E and 1650 ft N of SE corner Sec. 28, Twin Falls County, Idaho. Glenns Ferry Formation, late Pliocene.

UMMP V54709, pectoral spines. SW¼, Sec. 28, T. 7 S, R. 13 E, 225 ft N and 475 ft E of SW corner of Sec. 28, Twin Falls County, Idaho. Glenns Ferry Formation, late Pliocene.

UMMP V50036, pectoral spines and cleithra; V52779, supraoccipital; V52781, dorsal basals; V52782, first dorsal spines; V52788, cleithra; V52803, pectoral spines; USNM 22332, pectoral spine. NE¼, Sec. 20, T. 7 S, R. 13 E, 1100-1150 ft W, 650-775 ft S of NE corner, Sec. 20 (USGS locality 19216), Twin Falls County, Idaho. Glenns Ferry Formation, late Pliocene.

UMMP V53437, pectoral spines. SE¼, NE¼, Sec. 17, T. 7 S, R. 13 E, 100 ft W and 2000 ft S of NE corner of Sec. 17, Twin Falls County, Idaho. Glenns Ferry Formation, late Pliocene.

UMMP V53525 (part), coracoid and miscellaneous bones. Gidley's Horse Quarry, NW¼, Sec. 16, T. 7 S, R. 13 E, 1275-1725 ft E and 675 ft S of NW corner of Sec. 16, Twin Falls County, Idaho. Glenns Ferry Formation, late Pliocene.

UMMP V53340, pectoral spines. N½, NE¼, Sec. 5, T. 8 S, R. 13 E, Twin Falls County, Idaho. Glenns Ferry Formation, late Pliocene.

USNM 167591, partial skull. From SW¼, Sec. 2, T. 8 S, R. 9 E (USGS Cenozoic locality 20099), Owyhee County, Idaho. Glenns Ferry Formation, late Pliocene.

UMMP V45162, pectoral spine and cleithrum; V45176 (part), dentaries. S½, SW¼, Sec. 1, T. 6 S, R. 8 E, Owyhee County, Idaho. Sand Point local fauna, Glenns Ferry Formation, late Pliocene.

UMMP V58000, pectoral spines, cleithra, supraoccipital; V58001, partial skull. Roadcut on state highway 78, 1.4 mi W of Oreana turnoff, Owyhee County, Idaho. Glenns Ferry Formation, late Pliocene.

UMMP V45216, V49616, V49705, V57445, miscellaneous bones. Sec. 15, T. 4 S, R. 2 E, on SE side of Jackass Butte, Owyhee County, Idaho. Glenns Ferry Formation, Grand View local fauna, early Pleistocene.

USNM 23206, pectoral spine. From White Bulffs, 3-4 mi S of Hanford, Washington. Ringold Formation, early Pleistocene (Taylor, 1966). (Tentative identification.)

Description and Remarks.— The remains of catfishes from the Glenns Ferry Formation have been known since Cope's early work on Lake Idaho, but it is only recently that the fossils have been formally described (Miller and Smith, 1967). *Ictalurus vespertinus*, like *I. peregrinus*, is of considerable zoogeographic interest since there are no living representatives of the Ictaluridae W of the Continental Divide in the United States. At the time of original description *I. vespertinus* was known only from the Plio-Pleistocene Glenns Ferry Formation. Remains have recently been collected in the middle Pliocene Chalk Hills Formation of Idaho, and in the middle Pliocene Chalk Butte Formation of Oregon. The material from the Pleistocene Ringold Formation, in SE Washington is based on a small, badly worn pectoral spine and its identification must be considered tentative.

The following points on the anatomy of *I. vespertinus* are based on the Chalk Hills and Glenns Ferry material. The snout and supraethmoid are very broad. The cornua are robust and they bear mesial processes. The anterior fontanelle is unconstricted but the posterior one is nearly closed by the appression of the longitudinal supraoccipital crests. The supraoccipital process appears to be slightly shorter than in most other bullheads, and it is slender and tapered. The surface of the process, and usually a relatively large area on the longitudinal crests, is ornamented with strongly developed ridges, deep grooves and pits. The transverse crests on the supraoccipital are vertically oriented and they are not greatly expanded onto the base of the supraoccipital process. The pterotic wing is angular, and its surface is not deeply pitted. The posttemporal bone is divided into separate laminar and laterosensory components. The sphenotic process appears to be unreduced. The frontal crests extend anterior to the epiphyseal bar. The lateral ethmoid wing is short and horizontal and its posterodorsal edge is slightly truncated. The dorsal surfaces of the supraethmoid and lateral ethmoid have a spongy texture that has not been found elsewhere in the family. The foramen for the superficial ophthalmic nerves is not enlarged.

On the ventral side of the neurocranium the parasphenoid stem is tapered below the orbit and its ascending wings are not twisted. There are broad shelves developed on the orbitosphenoid and the optic foramen is small as in other bullheads. There appear to be a few sutures developed between the prootic and exoccipital but none between the prootic and basioccipital. The basioccipital in the larger individuals has a groove behind the median pit similar to the condition in *I. peregrinus*.

The lower jaw appears to be relatively large and there are 6 mandibular sensory pores, of which the first is re-

mote from the symphysis. The anteroventral crest of the dentary is moderately strong and the posterior edge of the coronoid process is steeply inclined. No strong symphyseal or articular processes are present. The tooth band on the dentary is relatively broad. Premaxillary teeth are uniformly developed and the premaxilla is moderately broad and rather long. The sublateral process is not enlarged and the posteromesial process is small. The palatine is short.

The structure of the hyomandibular is like that in most Recent bullheads, with well-developed levator arcus palatini and A_3 crests. A levator operculi crest is present and the adductor hyomandibularis process is short and rounded. The pterygoid elements are unknown.

The superficial ossification on the Weberian complex is well developed and the fifth centrum is strongly sutured to the complex. The anterior limb of the fourth transverse process is moderately expanded and the basal recess for the anterior limb of the tripus is broad. The vertical lamina of Weberian complex is not enlarged. The fourth neural spine is robust. The dorsal fin basals are well developed and the dorsal spine facets on the second basal are flat. The dorsal spine is well ossified and stout, but it is apparently somewhat shorter than in other bullheads. Ornamentation on the dorsal spine is weak and variable.

The posterior process of the cleithrum is moderately long and slender. Strong, irregularly developed tubercles are consistently present on the basal and ventral parts of the process. Seven or 8 coracoid sutures are present. The ventral coracoid keel is short, and the secondary keel is weak. The extensor fossa of the coracoid is short and narrow.

The pectoral spine is robust and sharp. Anterior distal serrae are absent or few and weakly developed. Anterior dentations of moderate strength are generally present, but these are irregularly spaced. The posterior dentations are very large, uniformly spaced and retrorse, and rarely multifid.

The evidence for a relationship between *I. vespertinus* and *I. peregrinus* was presented above. In a number of features *I. vespertinus* resembles the *catus* group of *Amiurus* (cf. Miller and Smith, 1967). The extremely broad supraethmoid bone of the fossil is most like that of *I. catus*. The strong, evenly spaced, and uniformly retrorse posterior dentations of the pectoral spine are similar to the condition in *I. serracanthus*. Neither *I. vespertinus* nor *I. peregrinus*, however, is known to possess the combination of derived features peculiar to the *catus* group, e.g., broadened premaxilla, extensive and uniform development of tubercles on the posterior process of the cleithrum, and increased number of coracoid sutures associated with a broad extensor fossa. On the other hand, *vespertinus* and *peregrinus* have a short lateral ethmoid wing, short palatine, deep pits on the supraoccipital process, and vertical transverse crests on the supraoccipital. These are believed to be advanced features of the *natalis* group and are taken as evidence for relationship. There does not appear to be any evidence to suggest a close relationship between these two fossil forms and a single living species or species pair of the *natalis* group. Rather, *vespertinus* and *peregrinus* may have a sister group relationship to the *natalis* group as outlined thus far, except perhaps for the middle Miocene *I. macgrewi*.

Ictalurus (Amiurus), Indeterminate Species

The following records are based on poorly preserved and/or very small individuals that cannot be identified to species.

Material, Localities, and Horizons.— Sec. 30, T. 27 N, R. 51 W, Marsland Quadrangle, Nebraska. Runningwater Formation, middle Miocene. UW 3296, pectoral and dorsal spines of small individuals. The pectoral spines are weakly ornamented and may represent *I. macgrewi* or *I. leidyi*.

Sparks, Cherry County, Nebraska, on Niobrara River. Middle Pliocene (data from specimen tag only). AMNH 2293, partial skeleton badly crushed. A small bullhead, no diagnostic characters visible.

Wolf Creek fauna. SDSM locality V521, SW¼, SE¼, Sec. 16, T. 35 N, R. 43 W, Shannon County, South Dakota. Ogallala Group, Wolf Creek fauna, lower Pliocene (Green, 1956). SDSM 5262, partial pectoral spine. The single spine bears moderately strong, erect and irregularly spaced posterior dentations. Occasional individuals of *I. leidyi* have similarly developed dentations but generally the spines of that species are less strongly ornamented.

Sentinel Butte, Golden Valley County, North Dakota. Sentinel Butte Shales, age uncertain, reported to be Paleocene (Keroher et al., 1966). AMNH 2801, articulated cleithrum, pectoral spine and midportion of crushed skull; 4013, partial skull and anterior vertebrae; 4014, partial skull and anterior vertebrae; 4015, supracleithrum, basipterygium and miscellaneous crushed elements; 4016, Weberian complex. The available material of this form is badly crushed and fragmentary but it is certain that it represents a species of bullhead. In overall structure the Sentinel Butte catfish most closely resembles *I. nebulosus*. The pectoral spine is large and robust (Fig. 6 A, B). Its anterior edge is worn but a few irregularly spaced anterior dentations are visible. The posterior dentations are short, blunt, erect and proximally they attach the dorsal half of the spine shaft. The posterior process of the cleithrum bears strong tubercles at least ventrally. The skull roof is broad and the longitudinal crests of the supraoccipital are rounded and nearly appressed over the posterior cranial fontanelle. The supraoccipital process is moderately long and its dorsal surface is deeply pitted. The transverse crest along the rear edge of the skull roof is nearly vertical and

FIGURE 6

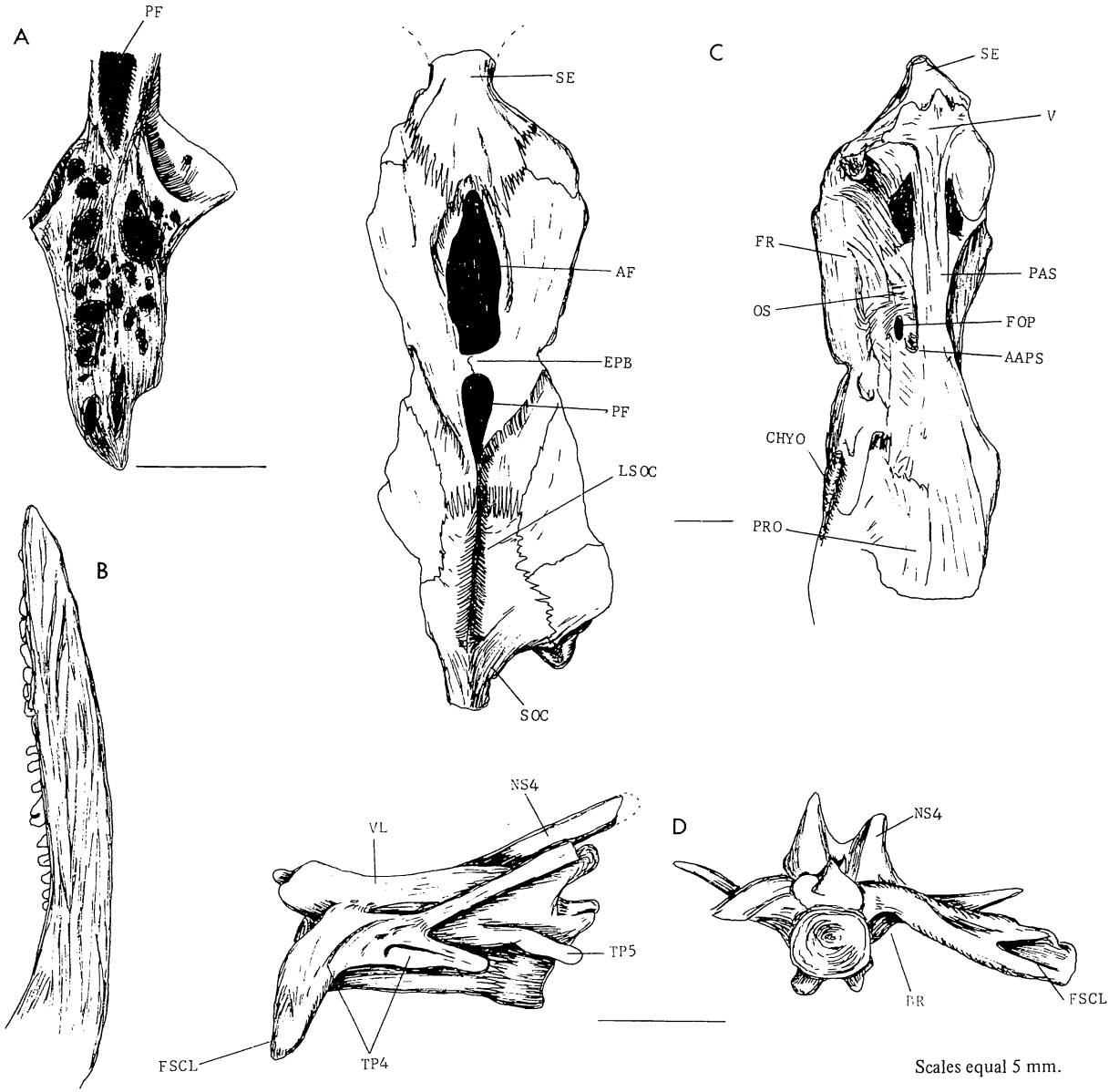


Fig. 6. (A) Indeterminate species of fossil bullhead from Sentinel Butte, North Dakota, AMNH 4014, supraoccipital. (B) Indeterminate species of fossil bullhead from Sentinel Butte, North Dakota, AMNH 2801, pectoral spine. (C) Indeterminate species of fossil *Ictalurus* from Oligocene of South Dakota, UMMP V14591, dorsal and ventrolateral views of skull. (D) Fossil *Noturus?* from Pleistocene of Idaho, UMMP V58001, lateral and frontal view.

not expanded onto the supraoccipital process. The upper limb of the supracleithrum appears to be sharply truncated posteriorly. The pelvic girdle has a lateral process but no lateral lamina. The age of the Sentinel Butte Shale is uncertain (Skinner and Cavender, pers. comm.). Most workers have considered this deposit to be early Tertiary, but based on the presence of what appears to be an advanced bullhead I would suggest at least a middle Tertiary age.

Ictalurus, Indeterminate Subgenus and Species

Material, Localities, and Horizons.— White Butte local

fauna. East central part of White Buttes, NE¼, Sec. 25, T. 134 N, R. 101 W, Slope County, North Dakota. White Butte local fauna, ?early Miocene. F:AM 10656, pectoral spine; 10658, pectoral spine.

Leo Fitterer Ranch, SW¼, Sec. 7, T. 137 N, R. 97 W, Stark County, North Dakota. Late Oligocene. F:AM 10660, pectoral spine and Weberian centrum fragment.

The spine bases are lacking from all of the above specimens from North Dakota so that it is impossible to determine the position of attachment of the proximal posterior dentations. Distally, however, these dentations are strongly developed, uniformly retrorse and spaced, and moderately strong. This is a rather primitive pattern of spine ornamentation and is comparable to that of the Recent *Ictalurus (Ictalurus) punctatus* and *Ictalurus (Amiurus) serracanthus*. Without information on the proximal dentations I am unable to identify the fossils to subgenus.

Oreodon Beds. Breaks of Pass Creek, S of Kadoka, Washabaugh County, South Dakota. White River series, Oreodon Beds, middle Oligocene. UMMP V14591, partial skull (Fig. 6 C; Pl. VIII C). This is the oldest fossil ictalurid that is known with certainty to have extensive jaw muscle origin on the skull roof. Unfortunately, the remainder of the anatomy of this form is so poorly known that evaluation of its systematic position is difficult. Another better-preserved individual, which almost certainly represents this species, has recently been discovered but this has not been available for detailed study.

A number of features of this fossil are shared with the subgenus *Ictalurus*. These include the relatively slender supraethmoid, arched skull roof, probably lack of forward extension on the frontal of the levator arcus palatini muscle, weakly developed sphenotic process, and narrow orbitosphenoid. Of these, the narrow orbitosphenoid is a derived feature shared with the *punctatus* group. The fossil lacks, however, an enlarged optic foramen which is a specialization found in all Recent and fossil species of *Ictalurus* (s.s.).

The fossil shares no derived features with *Amiurus* as a group, but the supraoccipital is peculiar in having a somewhat shortened and tapered process, strongly developed longitudinal crests that are appressed over the posterior fontanelle, and transverse crests that are expanded onto the base of the supraoccipital process. These are advanced features that are most similar to *I. lavetti* and *I. natalis*, rather specialized bullheads. Except in their possession of a broader supraoccipital process a few individuals of *I. lupus* and *I. dugesi* also approach these conditions. It is somewhat surprising to find such advanced conditions of jaw muscle origin in what appears to be (taking the fossil record at face value) an early representative of the modern Ictaluridae.

The other features of the neurocranium that can be determined are generalized. These include an open anterior fontanelle, smooth pterotic surface, narrow parasphenoid stem, straight, ascending parasphenoid wings, dorsally directed posterior edge of the adductor arcus palatini scar, and large descending frontal wings.

Little Corral Draw, 1 mi S of Z-Bell Table, Pennington County, South Dakota. Sec. 6, T. 4 S, R. 12 E. Lower part of Ahearn Member, Chadron Formation, lower Oligocene. PU 16301, fragment of pectoral spine base. This specimen is unidentifiable to genus, but has been reported as *Ictalurus* sp. by Clark et al. (1967).

McGuires Canyon, about 2.5 mi S of Norden Post Office on the N side of Niobrara River, Keya Paha County, Nebraska. Valentine Formation, Burge Member, early Pliocene. F:AM 10616, dorsal spine.

Genus *Noturus* Rafinesque

Material, Localities, and Horizons.— Ree Heights locality, in Sec. 22, T. 111 N, R. 70 W, Hand County, South Dakota. Pleistocene. Two specimens of a species of *Noturus* were referred to as *Noturus* cf. *N. hildebrandi* by Ossian (1973, p. 111, pl. 2). I have examined one of the specimens. This is the only certain fossil occurrence of the genus *Noturus*.

In addition, a nearly complete Weberian complex (UMMP V58002) from the early Pleistocene Grand View local fauna, Jackass Butte, Idaho, is strikingly similar to *Noturus*. The fourth neural spine is short and broad, and the angle between it and the vertebral axis is small. The anterior limb of the fourth transverse process is only slightly expanded distally, and the basal recess is hardly developed. Also, the superficial ossification is weakly developed (Fig. 6 D).

If this specimen represents a species of *Noturus* it constitutes a significant range extension for the group. Associated with the single specimen are numerous elements of *Ictalurus (Amiurus) vespertinus*. Although the Weberian complex of *I. vespertinus* is known only from fragments, it is certain that this was not a greatly depressed catfish, and the Weberian structure should be like that in other bullheads, e.g., with an elongated and slender fourth neural spine, an expanded anterior limb of fourth transverse process, and broad, deep basal recess.

Genus *Pylodictis*

Pylodictis olivaris (Rafinesque)

(Pl. VIII H, Pl. X B, C)

Middle Miocene Records: Material and Localities.— Miscellaneous localities in Sioux County, Nebraska. Sheep Creek beds. AMNH 2913, cleithrum; 2908, cleithrum and partial suspensorium; 2905 (part), partial lower jaw; 2907, pectoral spines; 2917, basioccipital, premaxilla; 2919 (part), vertebra; 2914, opercle and partial Weberian complex.

Runningwater Quarry, N½, SW¼, Sec. 5, T. 28 N, R. 52 W, Box Butte County, Nebraska. Type locality of the Runningwater Formation. F:AM 10540, cleithrum.

Pole Creek, channel deposit S side of Niobrara River, 2 mi W of Pole Creek, Cherry County, Nebraska. Beds equivalent to Runningwater Formation. F:AM 10609, partial Weberian complex.

Late Miocene Records: Material and Localities.– Echo Quarry, Antelope Draw, Sioux County, Nebraska. Lower Snake Creek. F:AM 10574, pectoral spine; 10575, Weberian centrum; 10576, partial neurocranium; 10577, 10579, articulars; 10580, partial neurocranium; 10581, 10582, lower jaws.

Mill Quarry, Antelope Draw, Sioux County, Nebraska. Lower Snake Creek. F:AM 10596, complete neurocranium.

New Surface Quarry. East Sinclair Draw, Sioux County, Nebraska. Lower Snake Creek. F:AM 10584, 10586, lower jaws; 10585, partial neurocranium.

East Sand Quarry, West Sinclair Draw, Sioux County, Nebraska. Lower Snake Creek. F:AM 10600, pectoral spine.

Humbug Quarry, Ranchhouse Draw, Sioux County, Nebraska. Lower Snake Creek. F:AM 10591, lower jaw, partial cleithrum and coracoid.

Miscellaneous localities in Sioux County, Nebraska. Snake Creek beds. AMNH 2921 (part), nearly complete neurocranium; 2262, partial skull; 2922, vertebrae.

Trinity River Pit No. 1, 7 mi NE of Cold Spirng, San Jacinto County, Texas. Upper part of Fleming Formation, age equivalent of lower Snake Creek fauna. F:AM 10652, basioccipital; 10653, 10654, 10655, pectoral spines.

Lapara Creek locality, SE of Normana, Bee County, Texas. Upper Miocene or lower Pliocene (Quinn, 1955). TMM 31081-135, partial Weberian complex and centra; 31081-850, 31081-624 (part), first centrum; 31081-872, dentaries; 31081-366, 31081-99, pectoral spines.

Pliocene Records: Material and Localities.– Egelhoff Ranch local fauna, Keya Paha County, Nebraska. Valentine Formation, Crookston Bridge Member, lower Pliocene. UMMP V56528 (part), pectoral spines; V57361 (part), pectoral spine, hyomandibular, dentary.

Burge Quarry, SE¼, NW¼, Sec. 10, T. 31 N, R. 21 W, Brown County, Nebraska. Lower Pliocene. UMMP V56-405 (part), first centrum.

Whiteface Quarry, on Snake River, NW¼, Sec. 27, T. 32 N, R. 30 W, Cherry County, Nebraska. Valentine Formation, Burge Member, early Pliocene. F:AM 10623, posterior skull elements.

Lucht Quarry, on Bone Creek, center of N side of Sec. 10, T. 21 N, R. 31 W, Brown County, Nebraska. Valentine Formation, Burge Member, early Pliocene. F:AM 10624, 10627, partial skulls; 10628, partial suspensorium; 10629, supraethmoid and dentary.

June Quarry, on Plum Creek, 4.5 mi N of Johnstown, Brown County, Nebraska. Valentine Formation, Burge Member, early Pliocene. F:AM 10637, Weberian complex centrum.

Verdigre Quarry, E bank of an unnamed tributary to Verdigre Creek, NW¼, SE¼, Sec. 16, T. 29 N, R. 7 W, about 7.5 mi S and 5.5 mi W of the town of Verdigre, Knox County, Nebraska. Valentine Formation, lower Pliocene (Voorhies, 1969). UW 3294, pectoral spine.

Bone Creek (Alligator Slide), S of Lucht Quarry, Brown County, Nebraska. Basal Ash Hollow Formation, early Pliocene. F:AM 10605, supracleithrum and basicranial elements; 10604, partial skull.

Pratt Quarry, on Plum Creek N of Johnstown, Brown County, Nebraska. Beds equivalent to Ash Hollow or X-mas Quarry, late early Pliocene. F:AM 10635, pectoral spine; 10636, frontals and lateral ethmoid.

Pleistocene Records: Material and Localities.– Red Light local fauna. Bramblett Ranch, SE part of Hudspeth County, Texas. Nebraskan, Pleistocene (Akersten, 1970). TMM 40664-275, basioccipital; 40664-230, partial Weberian complex; 40664-228, centrum; 40664-233, partial supraethmoid; 40664-232, pectoral spine.

Moore Pit local fauna. T-2 Terrace, Trinity River, Dallas County, Texas. Late Pleistocene. Material as listed and described by Uyeno and Miller (1962).

Centipede Cave local fauna. Rock shelter above Rio Grande near Langtry, Val Verde County, Texas. Late Pleistocene. Lundelius (1963) reported remains of *Pylodictis* from this locality.

CONCLUSIONS

This review of the fossil record is part of a larger study of the evolutionary relationships of and within the family Ictaluridae. A quantitative phyletic analysis of the relationships among living species of this family will be presented elsewhere. The major conclusions from that part of the study along with those drawn from the paleontological review will be summarized here.

Twenty-two modern species of the Ictaluridae representing all living genera and subgenera were included in the quantitative analysis. The cladistic relationships among these species and numerous fossil species are summarized in Figure 7.

At the generic level the results support previous suggestions that (1) *Satan* is most closely related to *Pylodictis* (Hubbs and Bailey, 1947; Suttkus, 1961), (2) *Prietella* is most closely related to *Noturus*, and (3) these four genera form a monophyletic group (Taylor, 1969). The results also suggest that the genus *Ictalurus* as currently conceived may be paraphyletic in that the subgenus *Amiurus* might share a more recent common ancestry with the *Noturus*-

FIGURE 7

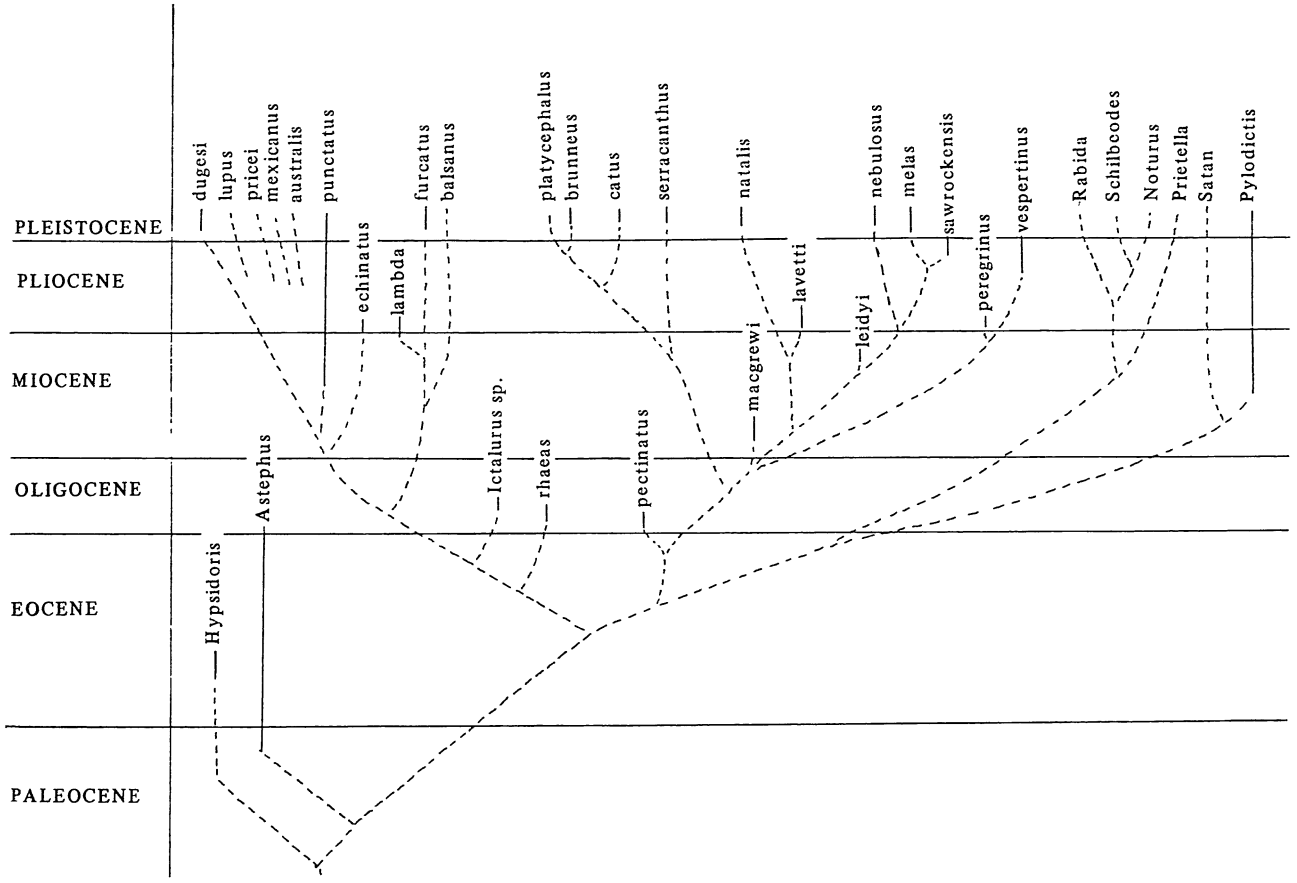


Fig. 7. Summary of cladistic and chronistic relationships of fossil and living Ictaluridae. The cladistic relationships were estimated using Wagner methods (Lundberg, 1970). *Ictalurus* sp., located near the base of the line leading to the *punctatus* and *furcatus* groups, refers to the undescribed Oligocene skull (UMMP V14591); see page 45. The living ictalurid *Troglanis pattersoni*, because of its uncertain relationships, is not included in the figure.

Pylodictis group than with the subgenus *Ictalurus*. However, trees on which *Ictalurus* and *Amiurus* share a most recent common ancestry with each other and with *Noturus* are not greatly different from that described above in terms of parsimonious fit of the data set. The phylogenetic position of *Trogloglanis* remains uncertain.

Within the subgenus *Ictalurus* there are two distinct subgroups – the *furcatus* group and the *punctatus* group. The *furcatus* group includes two living species, *I. furcatus* and *I. balsanus*, and an extinct Mio-Pliocene form, *I. lambda*, that is morphologically very close to *I. furcatus*. The *punctatus* group includes *I. punctatus* and a number of poorly known representatives in Mexico. An abundance of fossil remains of *I. punctatus* indicates that this species has remained morphologically stable since the middle Miocene. In addition there is a lower Pliocene species, *I. echinatus*, with highly ornate pectoral spines, that is probably related to the *punctatus* group. A middle Oligocene form from South Dakota (UMMP V14591) may be an early member of the subgenus *Ictalurus*, but it lacks the enlarged optic foramen that is peculiar to this group. No known fossil catfishes bridge the structural gap between the subgenus *Ictalurus* and other living groups of the Ictaluridae.

The middle Oligocene fossil, *Ictalurus pectinatus*, appears to be the earliest known member of the bullheads, subgenus *Amiurus*. This form lacks the characteristic dorsal position of the basal posterior dentations of the pectoral spine that is found in all other bullheads. Nevertheless, *I. pectinatus* is not structurally intermediate between modern *Amiurus* and any other group of catfishes. The remainder of *Amiurus* is divided into two subgroups – the *catus* group and the *natalis* group. Of Recent species the former includes the highly advanced flathead bullheads, *I. platycephalus* and *I. brunneus* and two relatively primitive species, *I. catus* and *I. serracanthus*. *Ictalurus catus* has often been considered an intermediate species between the two subgenera of *Ictalurus*, but this species

apparently has a relatively advanced position in the family and this suggests that its "intermediate" features may be secondary. Overall, *I. serracanthus* has retained more primitive features than any other living bullhead. There are no fossil species of this group.

The *natalis* group of *Amiurus* comprises three living species of which *I. melas* and *I. nebulosus* are each other's closest relative. This group has an extensive fossil record that begins with the apparently primitive *I. macgrewi* in the middle Miocene. The lower Pliocene *I. lavetti* represents the *I. natalis* line, and *I. leidyi* and *I. sawrockensis* represent the *nebulosus-melas* line. *Ictalurus sawrockensis* is probably most closely related to *I. melas*. In addition, a pair of extinct Pliocene-Pleistocene species, *I. peregrinus* and *I. vespertinus*, extend the known former geographical range of the *natalis* group, and the family as a whole, westward into southern Idaho and eastern Oregon and Washington. No modern bullhead species can be traced back in the fossil record farther than middle Pleistocene. This is quite unlike the situation with *Ictalurus punctatus* and *Pylodictis olivaris* which are known from the middle Miocene.

Within *Noturus* much evidence supports Taylor's hypothesis of a close relationship between the subgenera *Noturus* and *Schilbeodes*. These together form the sister group of *Rabida*. As expected the fossil record of *Noturus* is poor, but there is a fragmentary Weberian complex from the Pleistocene of Idaho that is strikingly similar to the complex of *Noturus*. If this identification is correct, it indicates a marked westward extension of the former range of *Noturus*, as in the *natalis* group of *Amiurus*.

Pylodictis olivaris is a highly advanced member of the Ictaluridae yet well-preserved remains of middle Miocene age indicate long morphological stability for this species. Given the probable sister group relations of *Pylodictis*, both *Satan* and the *Noturus-Prietella* group must have evolved by the middle Miocene also.

Turning to more ancient fossil catfishes, similarities in the structure of the suspensorium, pelvic fin and girdle are taken as evidence for relationship between the early Cenozoic genera *Astephus* and *Hypsidoris* and modern ictalurids. Of these, *Astephus* is known from the upper Paleocene to lower Oligocene and may be more closely related to the modern ictalurids than is *Hypsidoris* on the basis of an increased number of pelvic fin rays.

Hypsidoris is known from middle Eocene deposits only. If the evidence for the relationship of this genus to modern ictalurids is interpreted correctly, the presence of maxillary teeth in *Hypsidoris* almost certainly indicates multiple loss of this dentition in the Siluriformes.

Overall the Eocene fossils are more primitive than living ictalurids in lacking the jaw muscle invasion of the skull roof, in possessing a well-developed rib on the fifth vertebra, and in having teeth on the vomer. Each extinct genus is, however, specialized in its own direction, e.g., the upturned supraethmoid cornua of *Astephus*, and the elongated spines of *Hypsidoris*, thus excluding the fossils as possible direct ancestors of the modern forms.

Evidence bearing on the relationship of the Ictaluridae to other catfish groups is limited, but there are apparently derived features shared only with Old World groups. These include the presence of nasal barbels, muscle crests on the hyomandibular, longitudinally arranged dermal ridges on the supraoccipital, 6 or more infraorbitals, and reduction of the sphenotic spine. In these features the conditions of the Ictaluridae are most closely approached by the bagrid subfamilies Bagrinae and Bagroidinae, and the Ictaluridae appear to have a greater phenetic similarity to these groups than to other living siluriforms. When the North American Eocene catfishes are considered this similarity is even more striking. It would be premature, however, to strongly suggest a relationship between ictalurids and any bagrid subgroup, or any other subgroup of Asiatic catfishes, until those groups are better understood anatomically.

This review concludes with a classification of fossil and living Ictaluridae according to Lundberg (1970 and this paper) and Taylor (1969). Only taxa that have been formally described at generic and species level are included. Extinct taxa are marked with an asterisk.

FAMILY ICTALURIDAE

Genus **Hypsidoris** Lundberg and Case*
- *H. farsonensis* Lundberg and Case*

Genus **Astephus** Cope*
- *A. antiquus* (Leidy)*
- *A. calvus* (Cope)*
- *A. resimus* new species*

Genus **Ictalurus** Rafinesque

Subgenus **Ictalurus** Rafinesque

furcatus group
- *I. balsanus* (Jordan and Snyder)
- *I. furcatus* (Lesueur)
- *I. lambda* Hubbs and Hibbard*
- *I. rhaeas* (Cope)*

punctatus group
- *I. australis* (Meek)
- *I. dugesi* (Bean)
- *I. echinatus* new species*
- *I. lupus* (Girard)
- *I. mexicanus* (Meek)
- *I. pricei* (Rutter)
- *I. punctatus* Rafinesque

Subgenus **Amiurus** Gill
I. pectinatus (Cope)*
catus group
I. brunneus (Jordan)
I. catus (Linnaeus)
I. platycephalus (Girard)
I. serracanthus Yerger and Relyea
natalis group
I. lavetti new species*
I. leidyi new species*
I. macgrewi new species*
I. melas (Rafinesque)
I. natalis (Lesueur)
I. nebulosus (Lesueur)
I. peregrinus new species*
I. sawrockensis Smith*
I. vespertinus Miller and Smith*

Genus **Noturus** Rafinesque

Subgenus **Schilbeodes** Bleeker
N. exilis Nelson
N. gyrinus (Mitchill)
N. insignis (Richardson)
N. lachneri Taylor
N. leptacanthus Jordan
N. nocturnus Jordan and Gilbert
funebris group
N. funebris Gilbert and Swain
N. phaeus Taylor
N. gilberti Jordan and Evermann

Subgenus **Noturus** Rafinesque
N. flavus Rafinesque

Subgenus **Rabida** Jordan and Evermann
hildebrandi group
N. albater Taylor
N. baileyi Taylor
N. hildebrandi (Bailey and Taylor)
elegans group
N. elegans Taylor
N. eleutherus Jordan
N. trautmani Taylor
furiosus group
N. furiosus Jordan and Meek
N. munitus Suttkas and Taylor
N. placidus Taylor
N. stigmosus Taylor
miurus group
N. flavater Taylor
N. flavipinnis Taylor
N. miurus Jordan

Genus **Prietella** Carranza
P. phreatophila Carranza

Genus **Pylodictis** Rafinesque
P. olivaris (Rafinesque)

Genus **Satan** Hubbs and Bailey
S. eurystomus Hubbs and Bailey

Genus **Trogloglanis** Eigenmann
T. pattersoni Eigenmann

ACKNOWLEDGMENTS

I am sincerely grateful to the following individuals and institutions for loan of material or for use of the collections listed: Dr. Donn E. Rosen, Department of Ichthyology, Dr. Bobb Schaeffer, Department of Vertebrate Paleontology, Dr. Malcolm McKenna and Mr. Morris Skinner, Frick Laboratory, at the American Museum of Natural History; Dr. J. Alan Holman and Mr. Clair Ossian, Michigan State University; Dr. Dale Russell, National Museum of Canada; Dr. Robert Denison, Field Museum of Natural History; Dr. Donald Baird, Princeton University; Drs. Robert Wilson and Morton Green, South Dakota School of Mines and Technology; Dr. Walter Dalquest, Midwestern University; Mr. Bob Slaughter, Southern Methodist University; Drs. Jack Wilson and Ernest Lundelius, Texas Memorial Museum; Drs. J. T. Gregory and Howard Hutchinson, University of California, Berkeley; Dr. S. David Webb, University of Florida; Drs. W. R. Taylor and Clayton Ray, United States National Museum; Dr. J. Arnold Shotwell, University of Oregon; Dr. Richard L. Wilson, Southern Oregon College; Dr. Paul O. McGrew, University of Wyoming; Dr. Keith Thomson, Yale University; and Dr. Brian Patterson, Harvard University. Also, Drs. Reeve M. Bailey, Robert R. Miller, and Claude W. Hibbard allowed me to make full use of specimens in their care at The University of Michigan Museum of Zoology and Museum of Paleontology.

I am especially grateful to the members of my doctoral committee, Drs. Reeve Bailey, Robert Miller, Arnold Kluge, and Claude Hibbard, for their advice and criticism during the course of this study. I have benefited greatly from discussions with Drs. Gerald R. Smith and Ted M. Cavender, Mr. Jonathan Baskin and Mr. Morris Skinner. For their assistance in the field I thank Drs. Ted Cavender, Robert Miller, Teruya Uyeno, Gordon Edmund, and Mr. Fred Cichocki, and for technical assistance Mr. John Mosely. Dr. Masao Watenabe and Mr. Raymond Rigsbee generously assisted in the preparation of plates.

The present study was supported in part by a grant to Dr. N. G. Hairston of The University of Michigan from the National Science Foundation, GB6230, for research in Systematic and Evolutionary Biology and, in part, by grant GB4854 from the National Science Foundation to Dr. Robert R. Miller.

LITERATURE CITED

Akersten, W.A. 1970. Interpretation of sediments and vertebrate fossils in fill of Red Light Bolson, southeastern Hudspeth County, Texas. *In* Geology of southern Quitman Mountains area, Trans-Pecos, Texas. Soc. Econ. Paleont. Mineral., Permian Basin Sec., 1970 Biennial Field Trip Guidebook, Publ. 70(12): 82-87.

Alvarez, J. 1966. Contribucion al conocimiento de los bagres fosiles de Chapala y Zacoalca, Jalisco, Mexico. Paleoecologia (Mexico) 1:1-25.

Bjork, P.R. 1967. Latest Eocene vertebrates from northwestern South Dakota. J. Paleont., 41(1):227-236.

Brown, B. 1907. The Hell Creek beds of the upper Cretaceous of Montana. Bull. Amer. Mus. Nat. Hist., 23:823-845.

Casier, E. 1960. Note sur la collectiondes poissons Paleocenes et Ecocenes de l'Enclave de Babinda (Congo). Ann. Mus. v. Congo Belge, AIII, 1(2):1-48.

Cavender, T.M. 1968. Freshwater fish remains from the Clarno Formation, Ochoco Mountains of north-central Oregon. Ore Bin, 30(7):125-141.

Clark, J, J.R. Beerbower, and K.K. Kietzke. 1967. Oligocene sedimentation, stratigraphy, paleoecology and paleoclimatology in the Big Badlands of South Dakota. Fieldiana: Geol. Mem., 5:1-158.

Cope, E.D. 1872. Notices of new Vertebrata from the upper waters of Bitter Creek, Wyoming Territory. Proc. Amer. Philos. Soc., 7:483-486.

Cope, E.D. 1873. On the extinct Vertebrata of the Eocene of Wyoming observed by the expedition of 1872, with notes on the geology. Sixth Rept. U.S. Geogr. Surv. Terr., 545-649.

Cope, E.D. 1874. Supplementary notices of fishes from the freshwater Tertiaries of the Rocky Mountains. Bull. U.S. Geol. and Geogr. Surv. Terr., 1(2):49-51.

Cope, E.D. 1883. On the fishes of the Recent and Pliocene lakes of the western part of the Great Basin, and of the Idaho Pliocene lake. Proc. Acad. Nat. Sci. Phila., 1883:134-166.

Cope, E.D. 1884. The Vertebrata of the Tertiary formations of the West. Rept. U.S. Geol. Surv., 3:1-1009.

Cope, E.D. 1891. On Vertebrata from the Tertiary and Cretaceous rocks of the Northwest Territory. I. The species from the Oligocene or lower Miocene beds of the Cypress Hills. Geol. Surv. Canada, Contr. to Canadian Paleont., 3:1-25.

Dalquest, W.W. 1964. A new Pleistocene local fauna from Motley County, Texas. Trans. Kansas Acad. Sci., 67(3):499-505.

Eastman, C.R. 1917. Fossil fishes in the collection of the United States National Museum. Proc. U.S. Nat. Mus., 52:235-304.

Estes, R., and J. Tihen. 1964. Lower vertebrates from the Valentine Formation of Nebraska. Amer. Mid. Natur., 72(2):453-472.

Frizzell, D.L. 1965. Otoliths of a new fish (*Vorhisia vulpes*, n. gen., n. sp. Siluroidei?) from the upper Cretaceous of South Dakota. Copeia, 1965(2):178-181.

Frizzell, D.L., and J.H. Dante. 1965. Otoliths of some early Cenozoic fishes of the Gulf Coast. J. Paleont., 39(4):687-718.

Gardiner, B.G. 1966. Catalogue of Canadian fossil fishes. Life Sci. Contr. Roy. Ontario Mus., Univ. Toronto, 68:1-154.

Getz, L.L., and C.W. Hibbard. 1965. A molluscan faunule from the Seymour Formation of Baylor and Knox counties, Texas. Pap. Michigan Acad. Sci., Arts, Letters, 50:275-297.

Green, M. 1956. The lower Pliocene Ogallala-Wolf Creek vertebrate fauna, South Dakota. J. Paleont., 30(1):146-169.

Green, M. 1965. New late Miocene locality in South Dakota. J. Paleont., 39(1):103-107.

Hay, O.P. 1902. Bibliography and catalogue of the fossil Vertebrata of North America. Bull. U.S. Geol. Surv., 179:1-868.

Hay, O.P. 1924. Description of some fossil vertebrates from the upper Miocene of Texas. Proc. Biol. Soc. Washington, 37:1-19.

Hay, O.P. 1929. Second bibliography and catalogue of the fossil Vertebrata of North America. Publ. Carnegie Inst. Washington, 390:1-2003.

Hibbard, C.W. 1943. The Rezabek fauna, a new Pleistocene fauna from Lincoln County, Kansas. Kansas Univ. Sci. Bull., 29(2): 235-247.

Hibbard, C.W. 1951. An antilocaprid from the lower Pliocene of Beaver County, Oklahoma. Trans. Kansas Acad. Sci., 54:387-390.

Hibbard, C.W., and W.W. Dalquest. 1966. Fossils from the Seymour Formation of Knox and Baylor counties, Texas, and their bearing on the late Kansan climate of that region. Contr. Mus. Paleont., Univ. Michigan, 21(1):1-66.

Hibbard, C.W., D.E. Ray, D.E. Savage, D.W. Taylor, and J.E. Guilday. 1965. Quaternary mammals of North America. *In* H.E. Wright, Fr., and D.G Frey (eds.)
Wright, Jr., and D.G. Frey (eds.), The Quaternary of the United States. Princeton Univ. Press, Princeton, N.J., 509-525.

Hibbard, C.W., and D.W. Taylor. 1960. Two late Pleistocene faunas from southwestern Kansas. Contr. Mus. Paleont., Univ. Michigan, 16:1-223.

Hirschfeld, S.D., and S.D. Webb. 1968. Plio-Pleistocene magalonychid sloths of North America. Bull. Florida St. Mus., 12(5): 213-296.

Hubbs, C.L., and R.M. Bailey. 1947. Blind catfishes from artesian waters of Texas. Occ. Pap. Mus. Zool., Univ. Michigan, 499:1-17.

Hubbs, C.L., and C.W. Hibbard. 1951. *Ictalurus lambda*, a new catfish, based on a pectoral spine from the lower Pliocene of Kansas. Copeia, 1951(1):8-14.

Jordan, D.S. 1923. A classification of fishes including families and genera as far as known. Stanford Univ. Publ., Biol. Sci., 3: 79-243.

Keroher, G.C., et al. 1966. Lexicon of geological names of the United States. Bull. U.S.G.S., 1200, 1448 pp.

Leidy, J. 1873a. Notice of remains of fishes in the Bridger Tertiary Formation of Wyoming. Proc. Acad. Nat. Sci. Phila., 1873:97-99.

Leidy, J. 1873b. Contributions to the extinct vertebrate fauna of the Western Territories. Rept. U.S. Geol. and Geogr. Surv., Washington, 1873:14-358.

Leidy, J. 1889. Notice and description of fossils in caves and crevices of the limestone rocks of Pennsylvania. Ann. Rept. Geol. Surv. Pennsylvania, 1877:1-20.

Lundberg, J.G. 1967. Pleistocene fishes of the Good Creek Formation, Texas. Copeia, 1967(2):453-455.

Lundberg, J.G. 1970. The evolutionary history of North American catfishes, family Ictaluridae. Ph.D. Dissert., Univ. Michigan, 524 pp.

Lundberg. J.G., and J.N. Baskin. 1969. The caudal skeleton of the catfishes, order Siluriformes. Amer. Mus. Novitates, 2398: 1-49.

Lundberg, J.G., and G.R. Case. 1970. A new catfish from the Eocene Green River Formation, Wyoming. J. Paleont., 44(3): 451-457.

Lundelius, E.L. 1963. Non-human skeletal material. *In* J.F. Epstein, Centipede and damp caves: excavations in Val Verde County, Texas, 1958. Texas Arch. Soc. Bull., 33:127-129.

Lynn, W.G., and A.M. Melland. 1939. A fossil catfish (*Felichthys stauroforus*) from the Maryland Miocene. J. Washington Acad. Sci., 29(1):14-20.

Macdonald, J.R. 1960. An early Pliocene fauna from Mission, South Dakota. J. Paleont., 34(5):961-982.

Malde, H.E., and H.A. Powers. 1962. Upper Cenozoic stratigraphy of western Snake River Plain, Idaho. Geol. Soc. Amer. Bull., 73(10):1197-1220.

Matthew, W.D. 1918. Contributions to the Snake Creek fauna. Bull. Amer. Mus. Nat. Hist., 38:183-229.

McGrew, P.O. 1959. The geology and paleontology of the Elk Mountain and Tabernacle Butte Area, Wyoming. Bull. Amer. Mus. Nat. Hist., 117(3):117-176.

Miller, R.R. 1959. Origin and affinities of the freshwater fish fauna of western North America. Zoogeography, A.A.A.S., Publ. 51:187-222.

Miller, R.R. 1965. Quaternary freshwater fishes of North America. *In* H.E. Wright, Jr., and D.G. Frey (eds.), The Quaternary of the United States. Princeton Univ. Press, Princeton, N.J.: 569-581.

Miller, R.R., and G.R. Smith. 1967. New fossil fishes from Plio-Pleistocene Lake Idaho. Occ. Pap. Mus. Zool., Univ. Michigan, 654:1-24.

Ossian, C.R. 1973. Fishes of a Pleistocene lake in South Dakota. Publ. Mus., Michigan St. Univ., Paleont. Ser. 1(3):101-124.

Quinn, J.H. 1955. Miocene Equidae of the Texas Gulf Coastal Plain. Bur. Econ. Geol., Univ. Texas Publ. 5516:1-102.

Semken, H.A., Jr. 1966. Stratigraphy and paleontology of the McPherson *Equus* Beds (Sandahl local fauna), McPherson County, Kansas. Contr. Mus. Paleont., Univ. Michigan, 20(6): 121-178.

Shotwell, J.A., and D.E. Russell. 1963. Mammalian fauna of the upper Juntura Formation, the Black Butte local fauna. *In* Shotwell, J.A. (ed.), The Juntura Basin: studies in earth history and paleoecology. Trans. Amer. Philos. Soc., N.S., 53(1):1-77.

Skinner, M.F., S.M. Skinner, and R.J. Gooris. 1968. Cenozoic rocks and faunas of Turtle Butte, south-central South Dakota. Bull. Amer. Mus. Nat. Hist., 138(7):383-436.

Smith, C.L. 1954. Pleistocene fishes of the Berends fauna of Beaver County, Oklahoma. Copeia, 1954(4):282-289.

Smith, C.L. 1958. Additional Pleistocene fishes from Kansas and Oklahoma. Copeia, 1958(3):176-180.

Smith, C.L. 1961. An ictalurid catfish, *Ictalurus decorus* (Hay), from the Miocene of South Dakota. J. Paleont., 35(5):923-926.

Smith, C.L. 1962. Some Pliocene fishes from Kansas, Oklahoma, and Nebraska. Copeia, 1962(3):505-520.

Smith, G.R. 1963. A late Illinoian fish fauna from southwestern Kansas and its climatic significance. Copeia, 1963(2):278-285.

Smith, G.R., and J.G. Lundberg. 1972. The Sand Draw fish fauna. *In* M.F. Skinner, and C.W. Hibbard (eds.), Early Pleistocene preglacial and glacial rocks and faunas of north-central Nebraska. Bull. Amer. Mus. Nat. Hist., 148(1):40-54.

Smith-Vaniz, W.F. 1968. Freshwater fishes of Alabama. Agr. Expt. Sta. Auburn Univ., Auburn, Alabama, 211 pp.

Smith-Woodward, A. 1901. Catalogue of the fossil fishes in the British Museum. Part IV. London, 636 pp.

Suttkus, R.D. 1961. Additional information about blind catfishes from Texas. Southwest. Natur., 6(2):55-64.

Swift, C. 1968a. Fossil bony fishes from Florida. The Plaster Jacket, Florida St. Mus., Gainesville, 7:1-11.

Swift, C. 1968b. Pleistocene freshwater fishes from Ingleside Pit, San Patricio County, Texas. Copeia, 1968(1):63-69.

Taylor, D.W. 1965. The study of Pleistocene non-marine mollusks in North America. *In* H.E. Wright and D.E. Frey (eds.), The Quaternary of the United States. Princeton Univ. Press, Princeton, N.J.

Taylor, D.W. 1966. Summary of North American Blancan non-marine mollusks. Malacologia, 4(1):1-172.

Taylor, W.R. 1969. A revision of the catfish genus *Noturus* Rafinesque with an analysis of higher groups in the Ictaluridae. U.S. Nat. Mus. Bull., 282:1-315.

Uyeno, T. 1963. Late Pleistocene fishes of the Clear Creek and Ben Franklin local faunas of Texas. J. Grad. Res. Cen., Southern Methodist Univ., 31(3):168-173.

Uyeno, T., and R.R. Miller. 1962. Late Pleistocene fishes from a Trinity River Terrace, Texas. Copeia, 1962(2):338-345.

Uyeno, T., and R.R. Miller. 1963. Summary of late Cenozoic freshwater fish records for North America. Occ. Pap. Mus. Zool., Univ. Michigan:631-634.

Voorhies, M.R. 1969. Taphonomy and population dynamics of an early Pliocene vertebrate fauna, Knox County, Nebraska. Univ. Wyoming Contr. Geol., Spec. Pap. 1:1-69.

Weigel, R.D. 1963. Fossil vertebrates of Vero, Florida. Florida Geol. Surv. Spec. Publ. 10:1-59.

Wilson, R.L. 1968. Systematics and faunal analysis of a lower Pliocene vertebrate assemblage from Trego County, Kansas. Contr. Mus. Paleont., Univ. Michigan, 22(7):75-126.

Yerger, R.W., and K. Relyea. 1968. The flat-headed bullheads (Pisces: Ictaluridae) of the southeastern United States, and a new species of *Ictalurus* from the Gulf Coast. Copeia, 1968(2): 361-384.

PAPERS ON PALEONTOLOGY: No. 11

J.G. LUNDBERG: NORTH AMERICAN FOSSIL CATFISHES