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## Jurassic Fishes from the Western United States, With Comments on Jurassic Fish Distribution

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### ABSTRACT

Seven genera of fishes from the Jurassic (upper Bathonian-Callovian) Sundance and Wanakah formations of western United States are described and their relationships discussed together with a review of their stratigraphic occurrence. The assemblage includes isolated teeth of the chondrichthyans *Hybodus* sp. and *Ischyodus* sp., in part from unrecorded Sundance localities near Hulett, Wyoming. Most common is the generalized neopterygian *Hulettia americana* (Eastman), new genus of unknown relationship, which occurs in the Sundance of Montana and Wyoming, and in the Wanakah of Colorado (including the Pony Express Limestone) and New Mexico (Todilto Limestone). *Lepidotes* sp. and *Caturus dartoni* (Eastman), which belong to a monophyletic species group within the genus *Caturus*, are both present in the Sundance and the Wanakah. *Occithrissops willsoni*, new genus, new species from the Sundance, is an ich-

thyodectiform teleost, but not assignable to suborder. *Todiltia schoewei* (Dunkle), new genus from the Wanakah, is a teleost compared with *Ascalabos* and *Leptolepis*, but its affinities remain unknown.

The problem of *incertae sedis* genera and species (e.g., the monotypic *Hulettia*) is discussed in regard to identification and relationships of Jurassic fishes from other parts of the world. Included tables and paleogeographic maps show temporal and spatial distribution of these fishes, but variable preservation, inadequate description, and superficial systematic analysis usually preclude detailed comparisons of Jurassic taxa from the literature. It is probable, however, that most Jurassic fish assemblages, like those of the Sundance-Wanakah, are mixtures of form genera and monotypic genera whose relationships are imprecisely known.

### INTRODUCTION

Our knowledge of diversity among various groups of fishes that existed during the Jurassic is mostly derived from a few major collecting areas in England, France, and Germany. Specimens obtained from these localities have been studied longer and more intensively than those from rocks of similar age in other parts of the world. But in order to obtain a broader understanding of both the elasmobranch and osteichthyan fishes during this significant interval in their history, it is obviously desirable to search for localities outside of Europe. The European taxa will, of course, continue to play a major role in working out the subtleties of relationship and diversification, but well-preserved specimens from elsewhere should provide additional insights into phylogeny and paleobiogeography.

For the Western Hemisphere, only the Late Oxfordian Jagus Formation in western Cuba

has yielded a fish assemblage that approaches the diversity of the European ones (Gregory, 1923; D. H. Dunkle, personal commun.). Unfortunately, this fauna is mostly unstudied. More recently Arratia (1982), and others have reported on Oxfordian fishes from northern Chile. In regard to North America, fishes have long been known from the Sundance Formation in South Dakota (Eastman, 1899b) and from the Todilto Limestone in New Mexico (Koerner, 1930). The primary purpose of the present paper is to describe and consider the relationships of the fishes from the Sundance Formation in northeastern Wyoming and from the Wanakah Formation (including the Todilto), and equivalent units, in northern New Mexico and Colorado. With assistance from members of the United States Geological Survey, an effort has also been made to clarify the age and somewhat enigmatic stratigraphic relation-

ships of the rock units containing these fishes. A second objective is to summarize the available information on marine and non-marine Jurassic fish assemblages from various parts of the world in relation to their distribution, composition and to current problems of identification and relationship.

## METHODS AND MATERIALS

We have not been successful in making total acid preparations of specimens from the American Jurassic localities mentioned in this report. However, many morphological details have been enhanced by local application of formic or acetic acid, by Smooth-On® peels obtained from natural or prepared negative specimens and by the use of alizarin to distinguish bone from matrix. Also, the good to excellent preservation of various neopterygian specimens has permitted interpretation of the dermal skull, some deeper skull structures, and certain aspects of the postcranial skeleton. The catalogued specimens listed for each taxon have been selected for their information content, and are the ones on which the descriptions are based.

## ACKNOWLEDGMENTS

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The fieldwork involved in obtaining the fish specimens from the Sundance Formation around Hulett, Wyoming was made possible through the kindness and cooperation of the late Mr. Earl Willson and his daughter, on whose property most of the collecting was carried out, and of Mr. Arthur Meike, who permitted us to excavate at a nearby ranch road locality. The late Mr. John Callquist provided many courtesies and facilities during numerous stays in Hulett.

Mr. J. C. Merrill granted permission to collect fishes in the Todilto Limestone on his ranch in Quay County, New Mexico. Dr. John P. Bradbury assisted in collecting fishes at several Todilto localities north of Santa Fe.

Mr. R. J. Greffenius of the U.S. Forest Service provided information about the fish locality in the Pony Express Limestone in Piedra River Canyon, Colorado, and Dr. G. D. Johnson for the locality near Hot Springs, South Dakota.

The regional geology and stratigraphic relationships of the Sundance Formation and the Todilto Limestone and Pony Express Limestone members of the Wanakah Formation have been clarified through the generous assistance of Drs. George Pippingos (retired) and Robert B. O'Sullivan of the U.S. Geological Survey. Additional information has been supplied by Drs. Jennie L. Ridgley and J. Platt Bradbury, also of the Survey, and by Dr. W. F. Tanner. Drs. Ralph Imlay, Anthony Hallam, John H. Callomon, Hans-Peter Schultze, and John Utgaard provided opinions on problems of correlation and dating. Drs. David H. Dunkle and Joseph T. Gregory supplied data regarding the Todilto Limestone at the Bull Canyon Todilto fish locality in northeastern New Mexico. The writers are greatly indebted to all of these colleagues for their assistance and cooperation.

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Mr. Walter Sorensen accompanied Schaeffer during the first few collecting trips in Wyoming and New Mexico, and he has prepared most of the specimens. Mr. Gilbert F. Stucker served in this capacity during the remainder of the field program. Additional field assistance was provided at various times by Ms. Marlyn Mangus, Dr. Gareth J. Nelson, Dr. Richard Lund and Mr. Richard W. Schaeffer.

The drawings were made by Mr. Juan C. Barberis of the Graphic Arts Department at the American Museum and by Dr. Colin Patterson. The photographs were taken by Messrs. Emile Javorsky and Richard Sheridan at the American Museum and by the late Dr. Eugene S. Richardson.

Various individuals and institutions have kindly lent specimens from both the Sundance and the Todilto. These include Dr. Nicholas Hotton and Mr. Robert Purdy, National Museum of Natural History, Smithsonian Institution; Dr. Keith S. Thomson,

Peabody Museum, Yale University; Dr. Peter Robinson, The Museum, University of Colorado; Dr. Philip R. Bjork, Museum of Geology, South Dakota School of Mines; Dr. Barry S. Kues, Department of Geology, University of New Mexico, Albuquerque; Mr. Peter L. Larson, Black Hills Institute of Geological Research, Hill City, South Dakota; and Dr. Hans-Peter Schultze, Museum of Natural History, The University of Kansas. The Black Hills Institute has generously presented several specimens from the Bull Canyon locality of the Todilto Limestone to the American Museum of Natural History. Dr. T. T. Zwick presented several specimens from the Sundance in Clarks Fork Canyon, Wyoming. An additional collection from Bull Canyon, which has not been examined for this study, is in the Museum of Paleontology, University of California, Berkeley (J. T. Gregory, personal commun.).

## ABBREVIATIONS

### INSTITUTIONAL

AMNH, American Museum of Natural History  
BHI, Black Hills Institute of Geological Research  
BM(NH), British Museum (Natural History)  
KUMVP, University of Kansas, Museum of Natural History  
MCZ, Museum of Comparative Zoology, Harvard University  
NMNH (USNM), National Museum of Natural History, Smithsonian Institution  
SDSM, South Dakota School of Mines and Technology, Museum of Geology  
YPM, Peabody Museum, Yale University

### ANATOMICAL

ang, angular  
ao, antorbital  
aol, housing of aortic ligament  
apa, autopalatine  
ar, anal fin radial  
asc, ascending process of parasphenoid  
bexo, basi-exoccipital  
bhc, buccohypophysial canal  
bht, basihyal toothplate  
bpt, basiptyergoid process of parasphenoid  
br, brachioistegal ray  
bsp, basisphenoid  
cl, cleithrum  
cor, coracoid  
csc, caudal scute  
dch, distal ceratohyal

den, dentary  
dhc, dorsal hemichordacentrum  
dpcl, dorsal postcleithrum  
dpl, dermopalatine  
dpt, dermopterotic  
dptl, descending lamina of dermopterotic  
dr, dorsal fin radial  
dsp, dermosphenotic  
ecp, ectopterygoid  
enp, endopterygoid  
ep, epural  
epi, epioccipital  
epn, epineural process  
esc, extrascapular  
ff, fringing fulcrum  
fica, foramen of internal carotid artery  
fm, foramen magnum  
fmcv, foramen of middle cerebral vein  
foa, foramen of occipital artery  
fotb, ventral otic fissure  
fpsa, foramen of efferent pseudobranchial artery  
fr, frontal  
frd, foramen for sensory canal branch of trigeminal nerve  
frf, descending lamina of frontal  
frl, foramen of sensory canal nerves in frontal  
fst IX, foramen of supratemporal branch of glossopharyngeal nerve  
fst X, foramen of supratemporal branch of vagus  
gpn, groove for palatine nerve  
grao, groove for dorsal aorta  
hh, hypohyal  
hmf, hyomandibular facet  
hpu, preural haemal spine  
hym, hyomandibula  
hyp, hypural  
ic, intercalary  
id, interdorsal (dorsal intercalary)  
io, infraorbital  
iop, interopercular  
iv, interventral (ventral intercalary)  
jg, jugular groove  
lc, lateral commissure  
le, lateral ethmoid  
ll, lateral line canal in scales  
md, mandible  
mes, mesethmoid  
mpt, metapterygoid  
mx, maxilla  
na, nasal  
nc, notochordal calcification  
neu, neural arch  
not, notochordal pit  
npu, preural neural spine  
occ, occipital arch  
op, opercular  
opo, opisthotic  
ors, orbitosphenoid



pa, parietal  
 pas, parasphenoid  
 pch, proximal ceratohyal  
 ph, parhypural (haemal spine of pu 1)  
 pmx, premaxilla  
 pop, preopercular  
 pro, prootic  
 prp, parapophysis  
 pto, pterotic  
 pts, pterosphenoid  
 ptt, posttemporal (suprascapular)  
 pu, preural centrum  
 pv, pelvis  
 qj, quadratojugal  
 qu, quadrate  
 ro, rostral  
 rode, rostrodermethmoid  
 san, supraangular  
 sbo, suborbital  
 scl, supracleithrum  
 sl, standard length  
 smx, supramaxilla  
 sn, supraneural  
 soc, supraoccipital  
 sop, subopercular  
 spg, spiracular groove  
 spic, spiracular canal  
 spo, autosphenotic  
 sr, sclerotic bone  
 sue, supraethmoid  
 suo, supraorbital  
 sym, symplectic  
 u, ural centrum  
 ud, urodermal  
 un, uroneural  
 una, ural neural arch  
 vhc, ventral hemichordacentrum  
 vo, vomer  
 vpcl, ventral postcleithrum  
 IV, trochlear foramen  
 VII, facial foramen  
 X, vagus foramen

### GEOLOGIC OCCURRENCE

This section includes a resume of the stratigraphy and sedimentology of the Sundance and Wanakah formations with particular reference to units (members) from which fossil fishes have been obtained (figs. 1, 2). Where pertinent, comments on the history of discovery are also included. Two objectives of this discussion are (1) to attempt some conclusion regarding the environments in which the fishes lived and (2) to provide an opinion on the age of the fish-bearing rock units. As is frequently the case with epicontinental sed-

iments lacking diagnostic invertebrates, the salinity of the water occupied by the fishes remains equivocal. But the possibilities are set forth, and the correlations of the fish-bearing units are discussed, mostly on the basis of recently published regional reports and field studies plus consideration of the scanty ammonite and other invertebrate evidence.

### SUNDANCE FORMATION

The paleogeography and sedimentology of the lower Sundance Formation in the Black Hills region has been discussed recently by Peterson (1972), Wright (1973), Rautman (1975, 1978) and Imlay (1980). The basal Canyon Springs Sandstone Member and the lower part of the partly contemporaneous Stockade Beaver Shale Member (both of which contain fishes) were deposited during a marine transgression over the Wyoming shelf, an east-west trending tectonic feature in east-central Wyoming that was uplifted during the Bajocian. The cross-bedded sandstones of the Canyon Springs Sandstone suggest deposition under tidal influence, as in the present shallow North Sea. The Stockade Beaver Shale is a shallow, near-shore marine deposit formed in quiet water, as indicated by the fine grain-size and by regional facies changes (see paleogeographic map in Rautman, 1978, fig. 13).

According to Imlay (1980, p. iii) the calcareous sands forming the Canyon Springs Sandstone were deposited in the southeastern part of the late Bathonian Sea in a shallow-water environment that was partly intertidal or supratidal, while the limy mud that became the Stockade Beaver Shale was laid down farther to the west and north, also in shallow water. The discovery of the ammonite *Warrenoceras* in the Canyon Springs Sandstone in the Hartville uplift in southeastern Wyoming indicates a "not younger than middle" Bathonian age for this part of the member (Imlay, 1980, p. 85; J. H. Calomon, personal commun.). However, the Canyon Springs Sandstone becomes progressively younger from Wyoming into Colorado where it interfingers with the base of the Pine Butte Member of the Sundance, which may be about middle Callovian (Imlay, 1980; Pirringos and O'Sullivan, 1976, sect. 12).

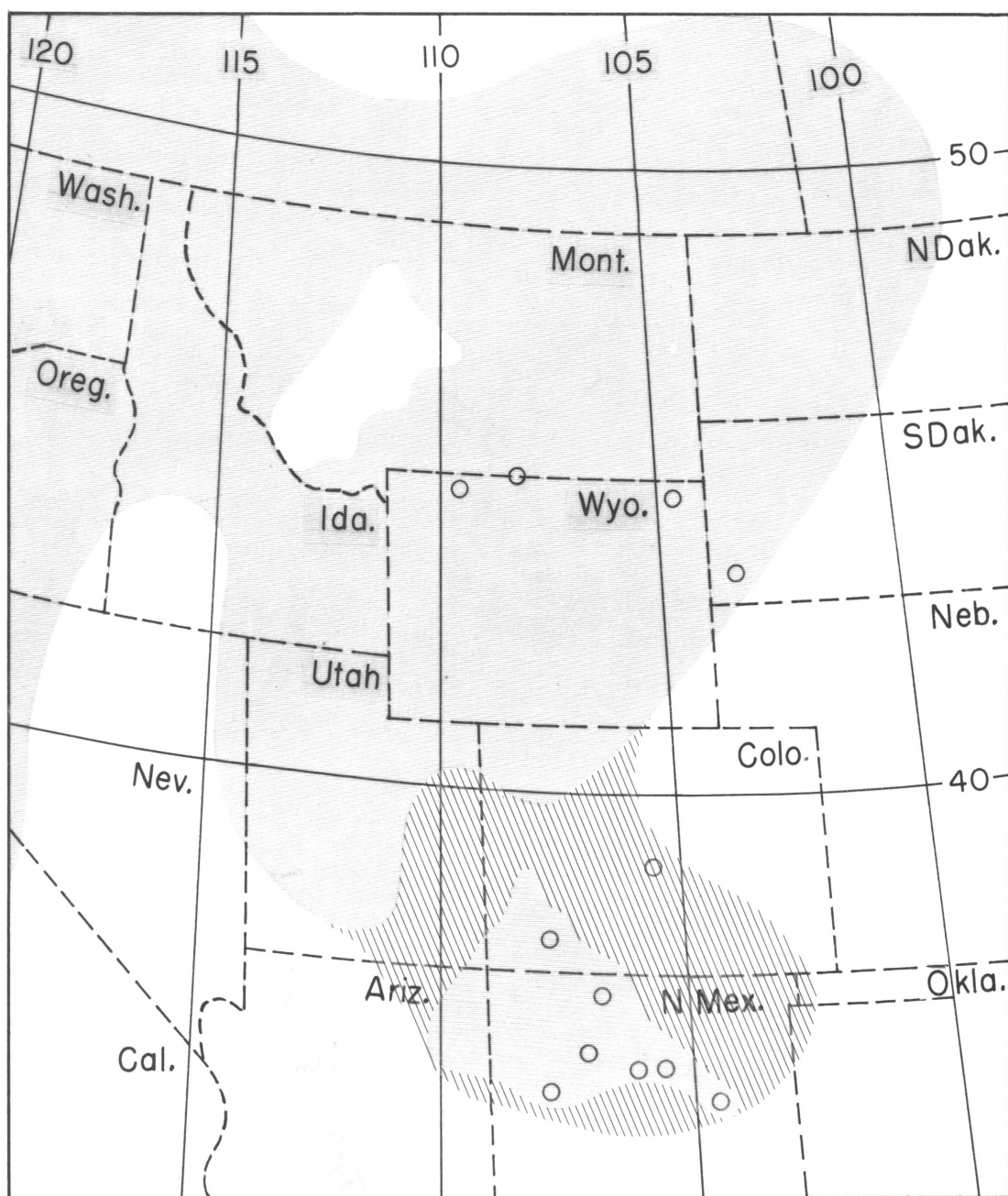


FIG. 1. Map of western North America showing the approximate extent of the transgressive inland sea during the Middle Jurassic. Diagonal ruled area represents the Wanakah depositional area including depositional basin of the Todilto and Pony Express limestones (shaded region in Arizona, New Mexico, and Colorado). Modified from Anderson and Kirkland (1960) and Imlay (1980). The circles indicate the areas from which fishes have been collected in the Sundance and Wanakah formations. Details in text.

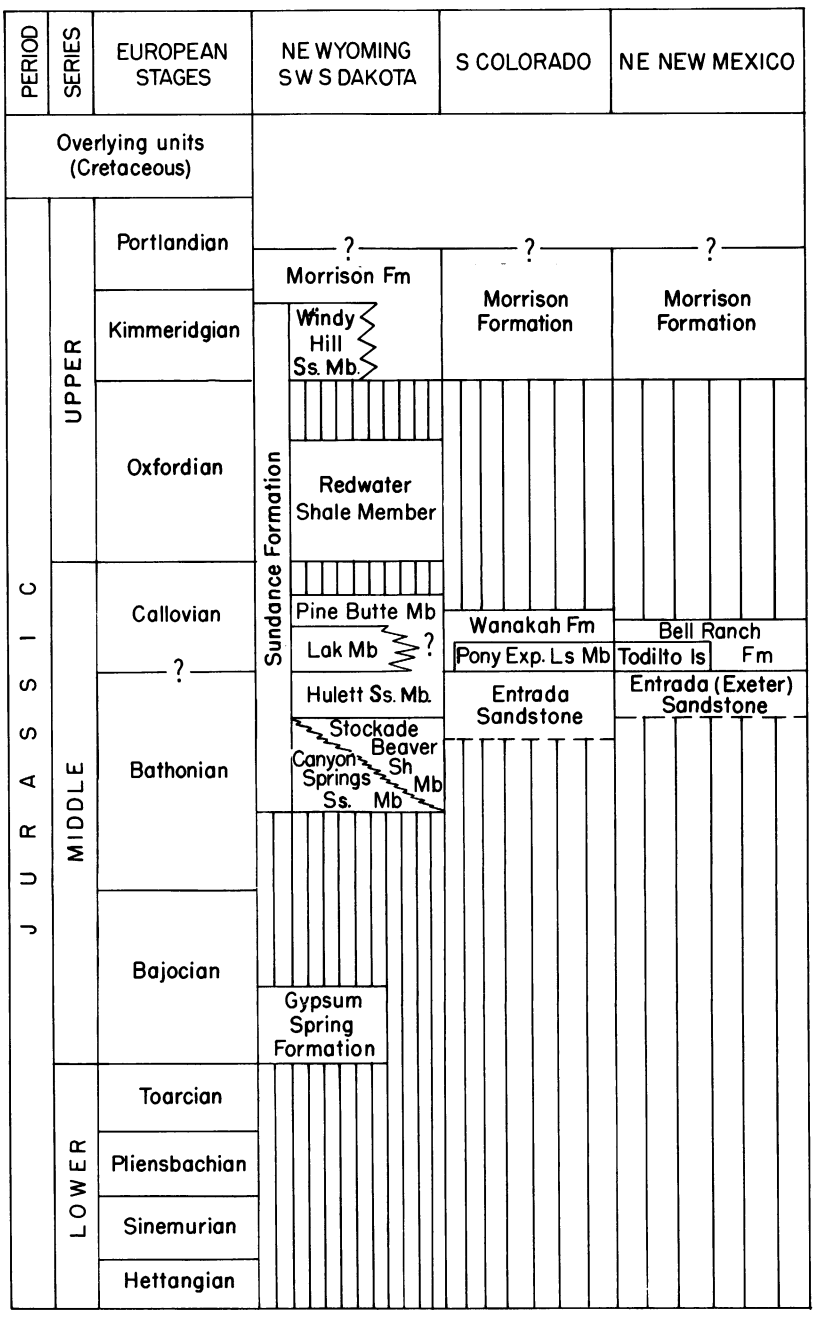


FIG. 2. Stratigraphic correlation chart for fish localities around Hot Springs, South Dakota; Hulett, Wyoming; Piedra Canyon, Colorado; Guadalupe and Quay counties, New Mexico. (Based mostly on Pippingos and O'Sullivan, 1976, 1978, and Imlay, 1980.)

Wright (1974, p. 38) notes that part of the Wyoming shelf was raised during the early Callovian (or late Bathonian according to Imlay, 1980) to form a northeast-southwest

trending submarine barrier (the Sheridan Arch) roughly between Lander and Buffalo, Wyoming. This barrier greatly influenced the sedimentation around it, and Wright believes that brackish conditions developed east of the barrier, particularly during Stockade Beaver deposition. These sediments lack foraminifera but in places have a rich ostracod fauna along with a *Meleagrinella* bivalve assemblage. The Sundance fishes apparently lived near shore but the bottom environment had become unfavorable for benthic invertebrates.

The fish localities in the Sundance Formation are as follows:

1. Hot Springs area, South Dakota: The initial discovery of fishes in the Sundance Formation was made by N. H. Darton in 1898 at a locality described by him as "about 1 mile ESE from the railroad station or one-half mile south of the Catholicon Springs Hotel" (foundation still visible in 1966) in Hot Springs, Fall River County, South Dakota. It is further described as "in a small draw which heads in the sandstone ridge lying east of the Red Bed valley" (Darton, 1899, pp. 388–389). On the basis of these landmarks, it appears that the locality is near the base of the high ridge (Seven Sisters Range) that extends in a nearly north-south direction immediately to the east of Hot Springs (G. D. Johnson, personal commun.). Both the Canyon Springs Sandstone and the Stockade Beaver Shale members occur along the eastern margin of the valley in which Hot Springs is situated (see detailed geologic map of the Hot Springs quadrangle in Wolcott, 1967). The locality is therefore in the NW  $\frac{1}{4}$ , Sec. 25, R5E, T7S, Fall River County, South Dakota.

Comparison of the stratigraphic section measured by Darton (1899, p. 389) in the vicinity of the Catholicon Springs Hotel with those by Wolcott (1967) and by Rautman (1975) near the town of Minnekahta (12 mi or 19 km west of Hot Springs) suggests that the fish collected by Darton were derived from the upper part of the Canyon Springs Sandstone. Darton noted that the specimens occur in a soft, fine-grained, thin-bedded (laminated) sandstone which is above the orange-tored, cross-bedded sandstone that constitutes most of this unit. This conclusion regarding

stratigraphic occurrence is supported by the facies maps of Rautman (1975, fig. 3; 1977, fig. 4) and of Pipiringos (personal commun.). It should be noted, however, that the Canyon Springs is replaced in part or entirely by the shaly Stockade Beaver Member northwest of Hot Springs. In regard to the depositional environment of the fish layer at Hot Springs, Anderson and Kirkland (1960, p. 43) remark that "Darton's fish were not directly associated with a marine fauna, but were the only fossils found in a sandstone below the marine sequence and about 3 feet above an eroded surface of redbeds (Darton, 1899, p. 399)." But it must be emphasized that, except for occasional specimens, marine fossil fishes are rarely found in association with benthic invertebrates.

From Darton's (1899, p. 389) description of the fish occurrence, it was apparently restricted both horizontally and vertically. An effort to relocate the spot in 1966 was unsuccessful. Outcrops of the Canyon Springs and the Stockade Beaver are rare except where gullies have eroded through the grass cover. On the basis of Darton's small collection, now in the National Museum of Natural History, Smithsonian Institution, and the Museum of Comparative Zoology, Harvard University, specimen preservation is generally good enough to warrant a further search for the productive horizon.

2. Hulett area, Wyoming: In terms of specimen number and diversity the most important fish locality in the Sundance Formation is on the former Earl Willson Ranch in Burnt Hollow, which is about 6.5 mi (10.5 km) north of Hulett, Crook County, Wyoming in SE  $\frac{1}{4}$ , Sec. 19, T55N, R64W. The first specimens were found in 1910–1912 by a Hulett resident. More were discovered in later years and numerous well-preserved examples were uncovered in the 1950s when a bulldozer was employed by Earl Willson to build a stock dam across the intermittent stream in Burnt Hollow. Some of these specimens were examined in 1957 by the late James D. Bump, then director of the Natural History Museum at the South Dakota School of Mines in Rapid City, who informed Schaeffer about the locality. The first collection for the American Museum was made in 1958, and additional specimens were obtained at intervals through

1975. The laminated, unbioturbated, calcareous siltstone containing the fishes may yield fairly complete specimens following weathering in place or in isolated blocks. A primary reason for returning to this locality during successive field seasons was to increase the diversity of the fish assemblage. Unfortunately, this was not particularly successful. Of the nearly 800 remains of individual fishes collected at the Burnt Hollow locality, only five taxa are represented. Of these about 90 percent can be referred to the single new monotypic genus *Hulettia*.

The fish zone is in the lower part of a calcareous siltstone unit about 20 feet (6.5 m) thick that is well exposed immediately to the east of the Willson stock dam in Burnt Hollow. The exposure is limited to the north side of the intermittent stream that flows through the Hollow and joins the Belle Fourche River in Sec. 20, R65W, T55N. It extends eastward for about 300 feet (100 m) from the dam, where it is covered by grass-covered alluvium. There is no evidence of this calcareous siltstone unit elsewhere in Burnt Hollow, nor is it present in an excellent exposure of the lower Sundance along the Belle Fourche River opposite the mouth of Burnt Hollow, also in Section 20.

During the 1966 field season, the siltstone unit was excavated from its contact with the overlying soft, greenish shale to the bottom of the fish zone. *Lingula* sp. and the bivalve *Meleagrinnella orbiculata* Whitfield occur in the poorly bedded upper part of the unit along with rare remains of *Lepidotes* and some isolated bone fragments and scales. About 4 feet (1.3 m) below the top of the massive siltstone and through a thickness of approximately 3 feet (1 m), there are several concentrations of decapod crustaceans. According to Herrick and Schram (1978), these include *Antrimpos* sp., *Bombus* sp., *Mecochirus* sp., an aglypheid and some unidentified anomuran remains.

The fish zone, about 3 feet (1 m) thick, is readily distinguished from the massive siltstone above it by being finely laminated. Locally there is some fine cross-bedding. Invertebrates are absent, but concentrations of bedded, fine-grained black pyrite with a distinctive dendritic or stellate pattern are common and restricted to this zone. The pyrite may occur on the same bedding plane as a

fish specimen, but the skeleton is never pyritized.

The laminated calcareous siltstone unit rests unconformably on a layer of ledge-forming limestone containing irregular masses of chert, and below this there is a bed of reddish, fissile shale. In 1966, a reconnaissance of the area between the Burnt Hollow fish locality and the Belle Fourche River with G. W. Imlay and G. N. Pipiringos reinforced the opinion that the laminated calcareous siltstone in Burnt Hollow has a local distribution, and that it overlies the Gypsum Spring Formation (see Pipiringos and O'Sullivan, 1978, pp. A20–A21, in regard to the J-2 unconformity at the top of the Gypsum Spring Formation). According to the earlier stratigraphic studies of Imlay (1947), Mapel and Bergendahl (1956) and of Robinson, Mapel, and Bergendahl (1964), the fish zone would be placed in the lower part of the Canyon Springs Sandstone Member of the Sundance Formation. As shown in the stratigraphic sections compiled by Robinson, Mapel, and Bergendahl (1964, pl. 2), siltstone occurs above the limestone in the Hulett area in a unit they designate as the Canyon Springs. However, field studies of the facies changes in the Sundance for northeastern Wyoming and the adjacent part of South Dakota (Imlay, 1947, pp. 251–252; Pipiringos, 1968, p. D19 and fig. 19; Rautman, 1978) indicate that the Stockade Beaver Member unconformably overlies the Gypsum Spring Formation, and the Canyon Springs Sandstone Member interfingers with the Stockade Beaver well south of Hulett, and in South Dakota, within a short distance north of Hot Springs. On the basis of this evidence, therefore, the fish zone in Burnt Hollow is placed by us in the lower part of the Stockade Beaver Shale Member. This interpretation is supported by the absence of cross-bedded sandstones in Burnt Hollow, which are characteristic of the Canyon Springs Member. In any case, the fish layers near Hot Springs, South Dakota and the fish zone in Burnt Hollow are roughly contemporaneous (Imlay, 1947, fig. 3; Rautman, 1978, fig. 5; this paper, fig. 1).

In Bush Canyon, which is the next parallel drainage to the south of Burnt Hollow, the limestone layer at the top of the Gypsum

Spring Formation is overlain by a soft shale and shaly limestone unit containing *Meleagrinea* and *Lingula* (see stratigraphic sections in Imlay, 1947; Robinson, Mapel, and Bergendahl, 1964) as does the siltstone unit in Burnt Hollow above the fish zone. These two units are probably correlated, but the detailed sedimentary sequence is different, and no fish have yet been found in Bush Canyon.

Another limited exposure of the laminated calcareous siltstone containing fishes is located about 2.5 air mi (4 km) SSE of the Burnt Hollow locality. This layer forms the surface of a little-used road on the Meike (Everson) Ranch near a wide loop in the Belle Fourche River in NE  $\frac{1}{4}$ , Sec. 5, T54N, R64W. As preserved, it is about 1 foot (0.3 m) thick, and lies directly on limestone containing chert. Extensive soil and grass cover make it difficult to determine the total thickness of this siltstone unit away from the road. There is, however, a bed of soft, greenish fissile shale on the west side of the road that forms a gentle slope below the base of the Hulett Sandstone. In Burnt Hollow this same greenish fissile shale, which is characteristic of the upper part of the Stockade Beaver Shale Member (Robinson, Mapel, and Bergendahl, 1964, p. 15), is about 137 feet (42 m) thick to the base of the Hulett Sandstone. It is easily recognized by its erosional pattern compared with the underlying, nearly vertical face of the siltstone unit near the Burnt Hollow stock dam and with the overlying cliff-forming Hulett Sandstone.

A third and also limited exposure of the fish-bearing siltstone is present along the road leading to the original Willson Ranch buildings. This is in Sec. 4, T54N, R64W and is about a half-mile (0.8 km) north of State Highway 24.

3. Two additional Sundance fish collecting areas have been brought to our attention. One is at the mouth of Clarks Fork Canyon, Park County, Wyoming in the NW  $\frac{1}{4}$ , NW  $\frac{1}{4}$ , Sec. 5, T56N, R103W, Deep Lake 15' Quadrangle (T. T. Zwick, personal commun.). The specimens have been found in a platy calcareous siltstone, and those recovered to date may be referred to *Lepidotes* sp. According to the investigations of Pippingos and O'Sullivan (1978, pl. 1, section E'-E, locality W1), the specimens occur in the lower part of the Rier-

don Formation, which is the lateral equivalent of the Canyon Springs and Stockade Beaver members farther south in Wyoming. The other area includes four localities in the vicinity of Gypsum Creek, Carbon County, Montana; Sec. 28, 33, T9S, R27E and in Big Horn County, Wyoming; Sec. 21, T58N, R96W. According to J. Utgaard and M. L. Dejarnett (personal commun.), who have investigated the stratigraphy, sedimentology and invertebrates of the Sundance Formation in this region, the fishes occur in laminated carbonates in the Hulett Sandstone Member. All the individuals found to date may be referred to *Hulettia americana* according to information and specimens kindly provided by Dr. H. P. Schultze.

In regard to the depositional environment of the fish zone around Hulett, it must have been mostly azoic. However, this refers to the preservation environment for the fishes, and not to the waters above the bottom where the fishes must have lived. We have found no direct criteria to indicate whether this habitat was marine, brackish or fresh water, even though the massive siltstone above the fish zone contains marine pelecypods and *Lingula*. The presence of *Lepidotes* bones and scales in association with benthic invertebrates in the massive siltstone probably reflects the relative durability of these skeletal elements prior to burial. It is reasonable to assume, however, that the fish occupied a marine environment as the basal Stockade Beaver contains marine invertebrates to the north, south and west.

#### WANAKAH FORMATION

In this report the correlation of the fish-bearing Jurassic rock units in northeastern Wyoming and southwestern South Dakota with those in Colorado and New Mexico is based on Imlay (1980) and other papers mentioned below. Of particular importance in this regard is the correlation of some 23 stratigraphic sections between Douglas, Wyoming and the Ralston Reservoir, Colorado (Pippingos and O'Sullivan, 1976, and their related paper of 1978). Conclusions pertinent to this study are summarized below, hopefully in enough detail to provide a useful stratigraphic background.

The Morrison Formation is mostly or entirely Kimmeridgian in age (Pipiringos and O'Sullivan, 1978, p. A26). According to these authors, the Ralston Creek Formation (Frederickson, 1956; Johnson, 1962) at the type locality at Ralston Reservoir, Colorado, consists of a lower unit, the Canyon Springs Sandstone, and an upper unit which is actually the lower part of the Morrison Formation. Fossils from the upper part of the Ralston Creek Formation near the town of Morrison, Colorado are of Kimmeridgian age and are mostly identical with those from the Morrison Formation elsewhere (Imlay, 1952, p. 961; Scott, 1963, p. 92; see also Schultze and Encisco, 1983).

There are no rocks of Oxfordian age in New Mexico and most of Colorado. The Redwater Shale Member of the Sundance Formation, which is widespread in northern Wyoming, is middle Oxfordian in age (Imlay, 1980, p. 87), but unfortunately is not known to contain fishes.

The Wanakah Formation, of middle and possibly lower Callovian age, is present in central Colorado and extends southward into New Mexico. The fish horizon in the Piedra River Canyon, Colorado is in the basal part of the Wanakah (in the Pony Express Limestone Member), as probably are the fish localities in New Mexico east of Santa Rosa. The Todilto Limestone, which is regarded as the basal member of the Wanakah by Pipiringos and O'Sullivan (1976, pl. 1, section C-C'), immediately overlies the Entrada Sandstone. In the Fort Wingate area, New Mexico, the Cow Springs Sandstone overlies the Todilto Limestone (Kehler, 1975). There is now evidence (Peterson, 1974) that the Cow Springs is a bleached zone in the upper part of the Entrada Sandstone. If further field study confirms this possibility, then the Todilto beneath the Cow Springs could be lower Callovian.

A fish-bearing unit north of Canon City, Colorado (Schoewe, 1930; Dunkle, 1942) has been identified as part of the Ralston Formation, although it is stratigraphically below the Morrison (Frederickson, DeLay, and Saylor, 1956, p. 2138). In view of the evidence cited above, plus the recent work on the extent and relationships of the Wanakah Formation, these beds may now be assigned with

some confidence to the Wanakah, following Imlay (1952, p. 961). The Wanakah Formation (in part) may be equivalent to the Lak Member of the Sundance Formation in Wyoming (Pipiringos and O'Sullivan, 1978, pl. I and p. 24).

The Wanakah Formation in the San Juan Basin area includes variable amounts of limestone, mudstone, siltstone, sandstone, and gypsum. The Todilto Limestone Member thickens eastward in McKinley and Sandoval counties and is continuous at least as far as Las Vegas in San Miguel County (Harshbarger, Repenning, and Irwin, 1957). It is nowhere more than 10 feet (3 m) thick. The gypsum beds, which attain a thickness of over 100 feet (30 m) in the San Juan Basin, overlie the limestone but may grade into it, and into sandstones around the periphery of the evaporite basin.

Benthic invertebrates are generally absent in the Todilto Limestone Member. However, near-shore sediments contain fresh or brackish water ostracods (Swain, 1946, p. 553), algal nodes (Perry, 1963), tracheids of vascular plants (Anderson and Kirkland, 1960), and two families of aquatic hemipterid insects (Bradbury and Kirkland, 1966). Fishes have been found at several places near the edge as well as toward the middle of the Todilto depositional area (Tanner, 1970 and personal commun.; Bradbury and Kirkland, 1966 and personal commun.). These localities include Lamy, Santa Fe County; La Liendre, a ghost town south of Las Vegas in San Miguel County; Hot Springs and Echo Amphitheater on U.S. Highway 84 between Abiquiu and Cebolla in Rio Arriba County. As noted above, the fish locality in the Piedra River Canyon, about 5 mi (8 km) north of the town of Piedra in Achuleta County, Colorado, is in the Pony Express Limestone Member of the Wanakah (Read et al., 1949), which is equivalent to the Todilto Limestone Member (R. B. O'Sullivan, personal commun.).

The Todilto Limestone has been mapped eastward to Las Vegas, New Mexico by Baltz (1972) and Johnson (1974). The fish-bearing limestone in Guadalupe and Quay counties in northeastern New Mexico has the same stratigraphic position within the Wanakah as the Todilto farther west, and is lithologically

very similar. In agreement with Imlay (1952) and Anderson and Kirkland (1960), this unit is regarded here as Todilto. In northeastern New Mexico, Peterson (1972) and Dinwiddie and Clebsch (1973) refer to the Wanakah equivalent as the Bell Ranch Formation.

The Todilto Limestone Member in Guadalupe and Quay counties, New Mexico contains a fish assemblage identical with that in the Todilto in the San Juan Basin and related areas. Many specimens have been collected in this limestone unit in Bull Canyon, Guadalupe County (Sec. 28, 32, and 33, T9N, R26E) following their discovery in 1929 (Koerner, 1930), and by Schaeffer et al., in 1964, on the nearby Merrill Ranch in Quay County (sec. 5 and 6, T8N, R27E).

Interpretation of the Todilto depositional environment has been confused and contradictory. Tanner (1970, 1972, 1974 and personal commun.) has proposed that the Todilto Limestone in the San Juan Basin was deposited in one or more large lakes that extended eastward to the Las Vegas area. The evidence in favor of Todilto deposition in a nearly closed gulf or embayment of the Late Jurassic epeiric sea during Summerville-Curtis time remains equivocal (Anderson and Kirkland, 1960, p. 45). However, "preliminary carbon, oxygen and sulfur isotope studies of bulk rock samples of the Todilto and Pony Express Limestone suggest a marine origin for these formations. Carbon and sulfur isotopes cluster within normal marine range. Oxygen isotopes are light; the variations are a result of diagenesis" (J. L. Ridgley, U.S.G.S., personal commun.). Anderson and Kirkland have calculated that the area of Todilto Limestone deposition was about 34,600 sq mi (89,600 km<sup>2</sup>). Assuming a sea connection, they favor a mixed paralic basin environment with the evaporites derived mostly from the surrounding drainage area.

A paralic condition for at least part of the Wanakah depositional area is also implied in Imlay's (1980, figs. 32, 33) paleogeographic maps for the western interior during the early Callovian. The Wanakah "embayment" was presumably widely open to the interior sea during this interval (fig. 1), and marine or tidal flat conditions could have alternated with an essentially freshwater, continental envi-

ronment. It is thus possible that the Todilto and Pony Express limestones were deposited under variable conditions. The lighter color of the unweathered Todilto Limestone in the southwest part of the San Juan Basin together with the concentrations of algal material indicate shallow, well-oxygenated water. In the central and eastern parts of northern New Mexico and in Colorado, the Todilto and Pony Express limestones are dark brown and rich in organic matter suggesting a lower oxygen bottom environment. The invertebrate remains (particularly the hemipterid aquatic insects), also from the southwestern margin of the Todilto depositional area, further indicate the presence of at least local freshwater and brackish environments. Specimens of the teleost *Todiltia*, new genus, have been found on the same bedding plane as the ostracods (J. P. Bradbury, personal commun.).

The Sundance fish assemblage by comparison with various European Jurassic assemblages may be regarded as marine (see table 3). Although only two Sundance fish taxa are also present in the Todilto (*Hulettia*, new genus, and *Caturus*), there is reason for suggesting that these fishes entered the Todilto Basin from the western interior ("Sundance") sea. *Todiltia schoewei*, which is common in the Todilto and Pony Express limestones, but is apparently absent in the Sundance, may have been a freshwater form, but obviously this cannot be ascertained directly from the specimens.

In summary, the fishes discussed in this report range in age from the last half of the Bathonian to about the middle of the Callovian. There is no present evidence that this time span will be narrowed, but at least the regional correlation of the involved rock units appears to be much clearer than it was a decade ago. Contrary to Schultze and Encisco (1983), the lowest two members of the Sundance Formation (Canyon Springs Sandstone and Stockade Beaver Shale) have recently been pushed back into the Late Bathonian on the basis of ammonite evidence (Imlay, 1980; J. H. Callomon, personal commun., 1982), and that the Hulett Sandstone Member, which is in the zone of *Kepplerites maclearni*, may also be Bathonian (J. H. Callomon, personal commun., 1982).



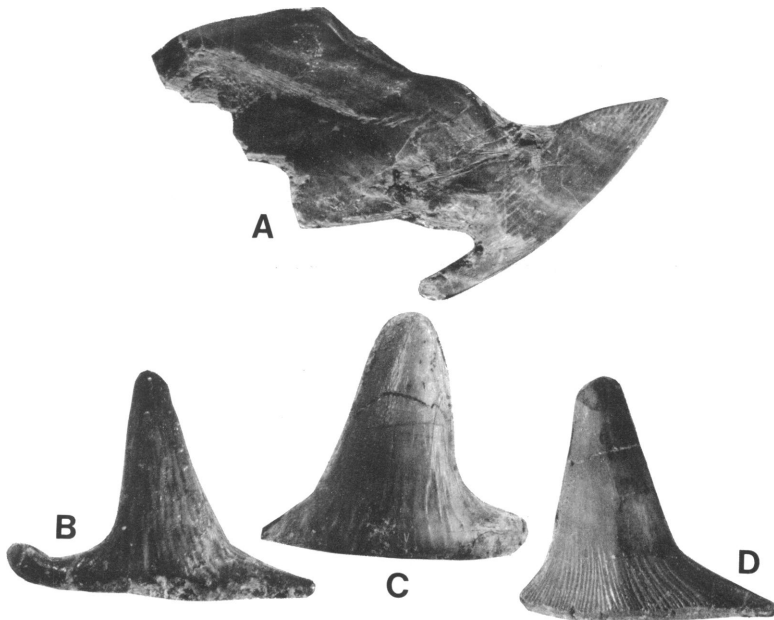


FIG. 3. A. *Ischyodus* sp. AMNH 8727. Incomplete right mandibular toothplate. B. *Hybodus* sp. AMNH 10995. Isolated tooth crown. C. *Hybodus* sp. AMNH 8726. Isolated tooth crown. D. *Hybodus* sp. AMNH 8725. Isolated tooth crown. From Hulett area.  $\times 2.75$ .

## SYSTEMATICS

### CHONDRICHTHYES

#### ELASMOBRANCHII

#### HYBODONTIDAE OWEN, 1846

#### GENUS *HYBODUS* AGASSIZ, 1837

DIAGNOSIS: See Woodward, 1916, p. 3; Maisey, 1982, fig. 17.

TYPE SPECIES: *Hybodus reticulatus* Agassiz (designated by Woodward, 1916, p. 4).

DISTRIBUTION: See Blot, 1969, p. 729, and tables 3, 4.

#### *Hybodus* sp.

Figure 3B–D

HORIZON AND LOCALITY: Stockade Beaver Member, Sundance Formation, Burnt Hollow near Hulett, Crook County, Wyoming. For details see section on geologic occurrence.

REFERRED SPECIMENS: AMNH 10995 (fig. 3B), isolated tooth from Burnt Hollow locality at top of massive siltstone unit. Three additional teeth, also referred to *Hybodus*,

collected by E. O. Hovey in 1891 in "Jurassic beds" 2 mi (3.2 km) east of the Devils Tower (AMNH 8726, fig. 3C; AMNH 8728) and 4 mi (6.4 km) southwest of Hulett (AMNH 8725, fig. 3D). According to the map of this area in Robinson, Mapel, and Bergendahl (1964), they were found in the Sundance, and probably in the Stockade Beaver Member.

DISCUSSION: As in *Hybodus grossiconus* Agassiz, from the Bathonian and (according to Priem, 1911) Oxfordian of Europe, the principal cusp is high, broad at the base, well separated from the lateral denticles, and bears close-packed striae extending about halfway up the labial face. With so little material and the problems of species determination within *Hybodus*, we prefer to leave our specimens as *Hybodus* sp. There are two pairs of lateral denticles on AMNH 8728, and one pair on AMNH 10995 and AMNH 8726.

The only previous record of *Hybodus* in the American Jurassic is a tooth from the "Atlantosaurus beds" near Piedmont, South Dakota, referred by Marsh (1899) to *H. poly-*

*prion* Agassiz. Our specimens do not resemble that species.

## HOLOCEPHALI

CHIMAERIDAE BONAPARTE, 1831

GENUS *ISCHYODUS* EGERTON, 1843

DIAGNOSIS: See Woodward, 1932, p. 96; Heimberg, 1949, p. 76.

TYPE SPECIES: *Chimaera townsendii* Buckland, 1835 (designated by Woodward, 1891, p. 64).

DISTRIBUTION: Middle Jurassic-Paleocene, Europe; Middle Jurassic, western interior sea of North America; Cretaceous, New Zealand.

*Ischyodus* sp.

Figure 3A

HORIZON AND LOCALITY: Unknown, but probably from the Sundance Formation "5–6 miles (8–10 km) sw of Sundance, Wyo."

REFERRED SPECIMEN: AMNH 8727 (fig. 3A). Collected by E. O. Hovey in 1891. Incomplete right mandibular toothplate.

DISCUSSION: The toothplate is similar to those of the Bathonian *Ischyodus emarginatus* Egerton and the Callovian-Kimmeridgian *I. egertoni* (Buckland). According to Woodward (1891, p. 60) those two species are "only provisionally retained distinct." Reliable species determination seems impossible in *Ischyodus* on mandibular toothplates alone (Woodward, 1891; Heimberg, 1949), and we leave the specimen under open nomenclature. This Sundance specimen is apparently the first record of *Ischyodus* in the western hemisphere.

OSTEICHTHYES

ACTINOPTERYGII

NEOPTERYGII

HALECOSTOMI INCERTAE SEDIS

*HULETTIA*, NEW GENUS

TYPE SPECIES: *Pholidophorus americanus* Eastman.

DISTRIBUTION: Upper Bathonian, Wyoming; Lower Callovian, New Mexico and Colorado.

ETYMOLOGY: After Hulett, Crook County, Wyoming.

DIAGNOSIS: A generalized halecostome neopterygian with the following combination

of primitive and derived characters: braincase with persistent otico-occipital fissure; no supraoccipital; intercalar without membranous outgrowths; parasphenoid broad, toothed, with foramina for efferent pseudo-branchial and internal carotid arteries; vomer median; nasals separated by rostral. Nasal processes of premaxillae simple, meeting in midline and occasionally fusing; maxilla free and mobile, extending beneath posterior part of orbit, no supramaxilla. Quadratojugal independent and splintlike. Interopercular present. Post-temporal (suprascapular) with internal process. Large, median basihyal toothplate; no gular. Vertebral column with separate neural arches and dorsal intercalaries throughout; separate ventral intercalaries present only in anterior part of caudal region; unpaired neural spines in posterior half of column. Dorsal and ventral chordal hemicentra meeting as annular chordacentra in mature individuals. No ossified ural/neural arches. At least seven epurals. Hypocaudal skeleton with five elongated preural haemal spines and at least eight unmodified hypurals. No clavicle. Scales rhomboidal, composed of enameloid and bony base; dentine absent. Basal and fringing fulcra on all fins.

*Hulettia americana* (Eastman)

Figures 4–18

*Pholidophorus americanus* Eastman, 1899a, p. 642.

*Pholidophorus americanus* Eastman; Eastman, 1899b, p. 398, pls. 45–57.

*Pholidophorus americanus* Eastman; Knight, 1900, p. 386 (name only).

*Pholidophorus americanus* Eastman; Gilmore, 1905, p. 89 (name only).

*Pholidophorus americanus* Eastman; Merrill, 1907, p. 15.

*Pholidophorus americanus* Eastman; Koerner, 1930, p. 463 (name only).

*Pholidophorus americanus* Eastman; Dunkle, 1942, p. 61 (name only).

*Pholidophorus americanus* Eastman; Schultze and Enciso, 1983, p. 1056.

HOLOTYPE: NMNH 4788a (Eastman, 1899b, pl. 45, fig. 1; fig. 4A here) and counterpart NMNH 4788b (Eastman, 1899b, pl. 46, fig. 1). From Canyon Springs Sandstone Member, Sundance Formation, near Hot Springs, South Dakota.

DIAGNOSIS: As genus, only species.

REFERRED SPECIMENS: Partial and nearly

complete specimens of *Hulettia americana* showing specific morphological features are mentioned by catalogue number at pertinent places in the description. The numbers listed below by formation and locality represent catalogued specimens examined for this study. From the Sundance Formation, Canyon Springs Sandstone Member, near Hot Springs, South Dakota: NMNH 4784, 4787, 4789, 4790; MCZ 6623, 9696. From the Sundance Formation, Stockade Beaver Shale Member, near Hulett, Wyoming: AMNH 10824, 10831, 10837, 10838, 10839, 10841, 10857, 10858, 10860, 10862, 10872, 10875, 10876, 10877, 10880, 10881, 10884, 10885, 10887, 10888, 10897, 10903, 10917, 10918, 10919, 10921, 10922, 10923, 10926, 10928, 10931, 10932, 10940, 10941, 10943, 10944, 10948, 10954, 10956, 10957, 10986, 11071, 11072, 11073, 11075, 11077, 11437; SDSM 5780, 5781, 5782, 54361, 59144, 59145. From Wanakah Formation, Pony Express Limestone Member, Piedra River Canyon, Colorado: AMNH 11454. From Wanakah Formation, Todilto Limestone Member, Bull Canyon area, New Mexico: AMNH 6339, 10927, 10968; BHP 5, P 1.25, 950F, P 1.10, YPM 8199, 8200. From Wanakah Formation, Todilto Limestone Member, Merrill Ranch, New Mexico: AMNH 11021, 11025, 11028, 11443.

## DESCRIPTION

**MEASUREMENTS AND PROPORTIONS:** The smallest measurable specimen (AMNH 11075b) is about 50 mm SL, and the largest (AMNH 10954) is 155 mm. The proportional changes with increase in size are indicated in the graph (fig. 7). Although maximum body depth is difficult to approximate because of compression, it is evident that the body form remained relatively constant with increase in size—at least above about 50 mm. It is also apparent that within this size range the skull is about one-quarter of the standard length. According to this analysis, *Hulettia* is monotypic, which is verified by the scale and fin ray counts. The measured sample includes specimens from the Sundance (Burnt Hollow locality, Wyoming), the Pony Express Limestone (Piedra Canyon, Colorado), and the Todilto Limestone (Bull Canyon, New Mexico).

**SNOUT:** The pattern of the dermal snout has been mostly worked out on the basis of specimens from the Hulett localities. The ethmoid region is covered by a keystone-shaped, median rostral bone that overlies the nasal processes of the premaxillae and houses the prominent ethmoid commissure, which extends transversely through the bone close to its anteroventral margin. The nasals, which are separated by the rostral, presumably fitted into the concave lateral margins of this element. The L-shaped antorbitals, readily identified by the triradiate pattern of their sensory canals, are in contact with the rostral, the premaxillae and the infraorbital elements as shown in figure 11. There must have been space between the antorbital and the nasal for the anterior and posterior nasal openings.

The snout pattern is similar in most respects to that of *Acentrophorus*, *Dapedium*, and a parasemionotid as interpreted by Patterson (1975, figs. 134, 136, 137). The supraorbital sensory canal passes through the nasal bone and terminates above the rostral commissure. The sensory canal extension in the rostral process of the antorbital ends blindly. The extent of the rostral-premaxilla overlap in figure 11 has been determined by the ornamentation on the premaxillae, which must have been exposed below the margin of the rostral.

**ROOF:** The relatively short, broad frontal bones, which are not quite twice the length of the parietals, give the skull roof a blunt, widened aspect much as in *Acentrophorus* (Gill, 1923) and in many of the paleopterygians with a nearly vertical suspensorium (Schaeffer, 1973). The frontals are slightly narrowed anteriorly and their anterior borders are rounded and ruffled for the attachment of the connective tissue that also connected the snout elements. The well-spaced pores of the supraorbital sensory canals have elevated borders. On the ventral surface of the frontal there is a prominent, rounded ridge beneath the sensory canal that has ventral digitations in front of and behind the ossification center of the bone (fig. 12A), forming a poorly defined descending lamina.

The rectangular parietals are indistinguishably fused in several specimens (fig. 12A) but in most they are clearly separate. The anterior

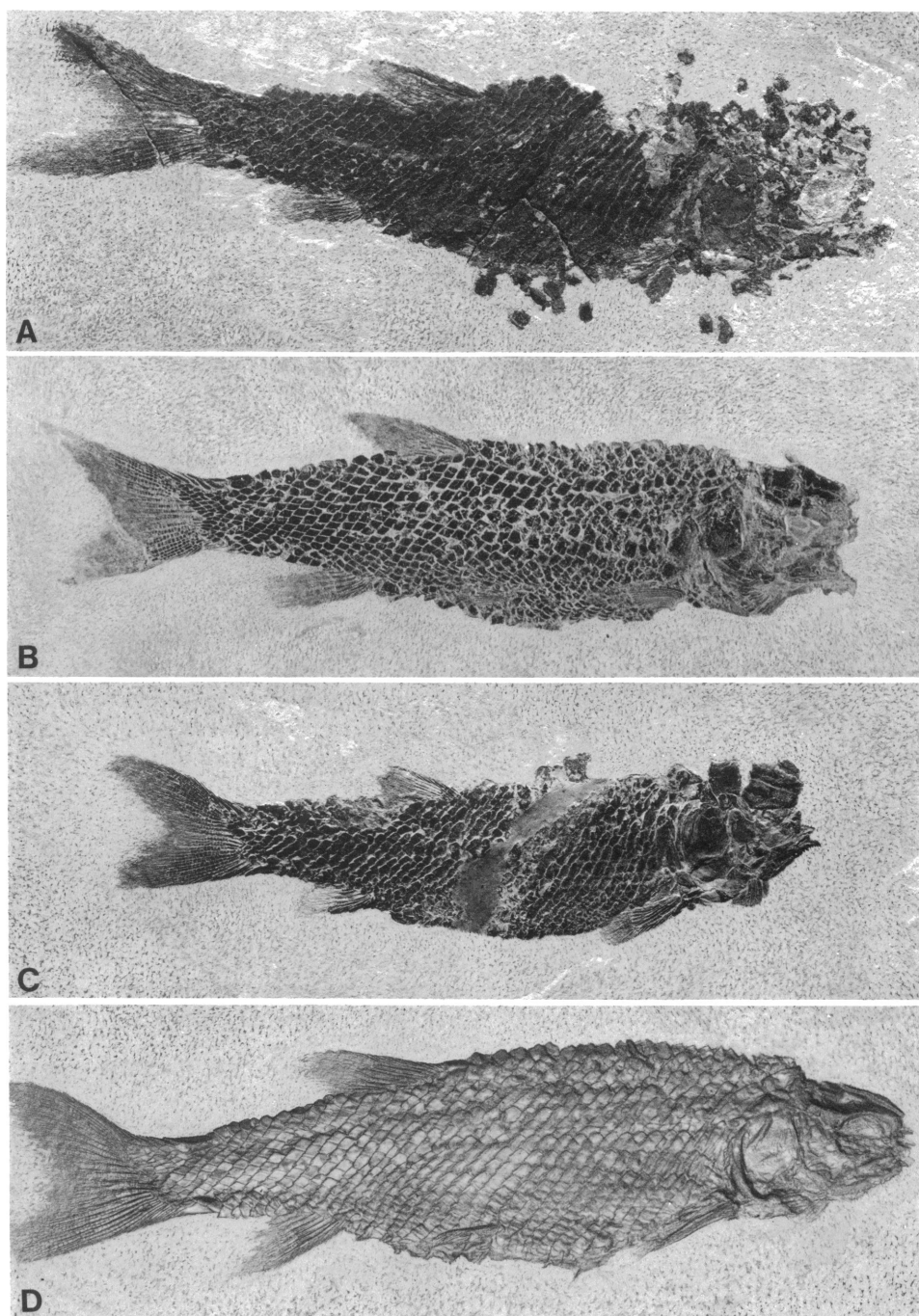


FIG. 4. *Hulettia americana*. A. NMNH 4788a. Holotype.  $\times .90$ . B. SDSM 59144.  $\times .68$ . C. AMNH 10921.  $\times .70$ . D. AMNH 10903.  $\times 1.1$ . From Hot Springs, S.D. and Hulett, Wyoming.

pit lines are extensions of the supraorbital canals on the parietals. The rarely observed

middle pit lines are evident in AMNH 10872. The dermopterotics require no particular

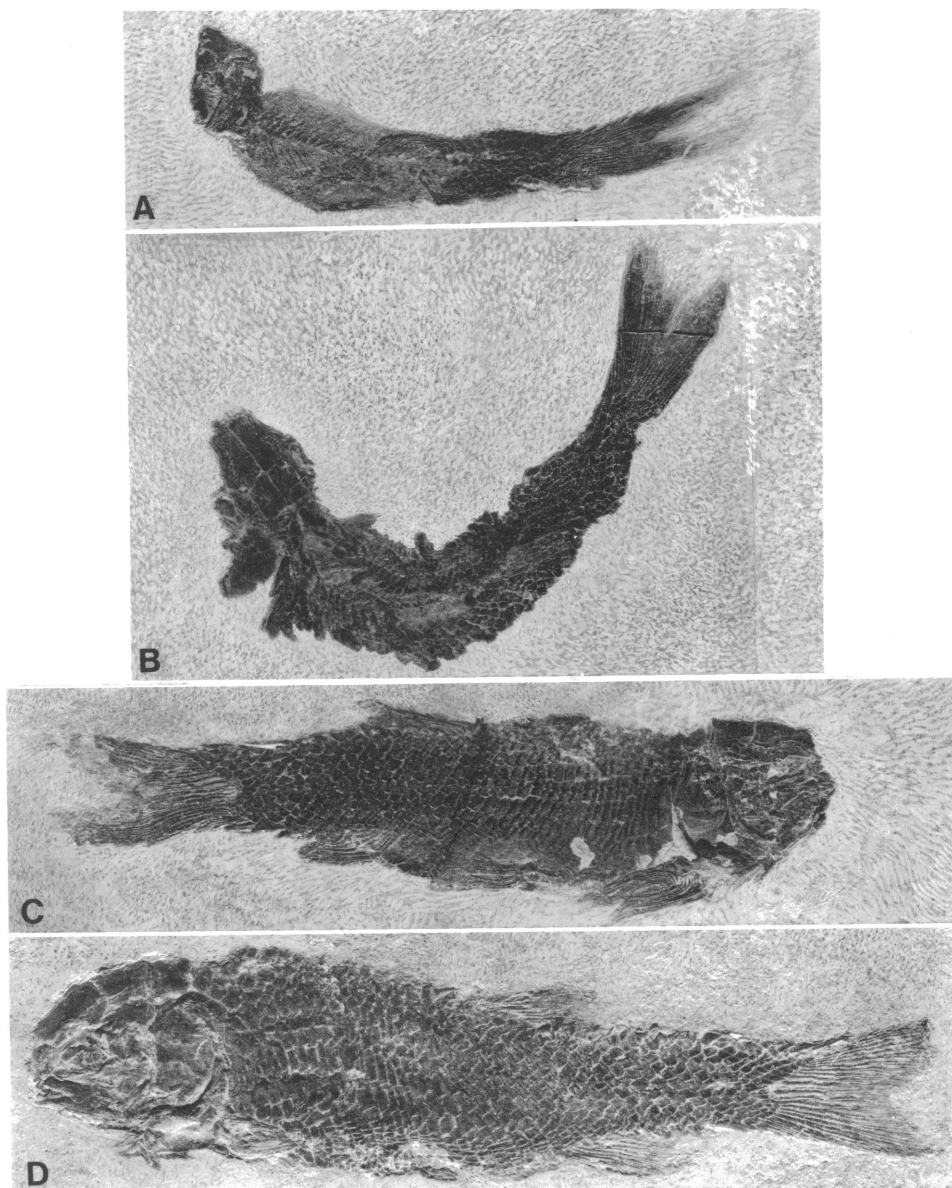


FIG. 5. *Hulettia americana* growth series. A. AMNH 10860.  $\times 1.32$ . B. AMNH 10837.  $\times 1.50$ . C. AMNH 10838.  $\times 1.30$ . D. AMNH 10881.  $\times 1.16$ . From Hulett, Wyoming.

comment except to note that the bone surrounding the temporal sensory canal is thickened and forms a descending lamina posteroventrally (figs. 8A, 12A). Also there is no pronounced posterior extension of the dermopterotic around the canal, although this process is presumably present to some degree in most primitive actinopterygians (Patterson, 1975, p. 552).

**OPERCULAR SERIES AND CHEEK:** The opercular series, including the well-developed interopercular, has a characteristic, primitive neopterygian pattern. The narrow, nearly vertical preopercular is covered dorsally by a large suborbital. There are about 13 branchiostegals. The gular plate is absent.

The suborbital series includes one large element (sbo<sub>1</sub>, fig. 11B), and a variable number

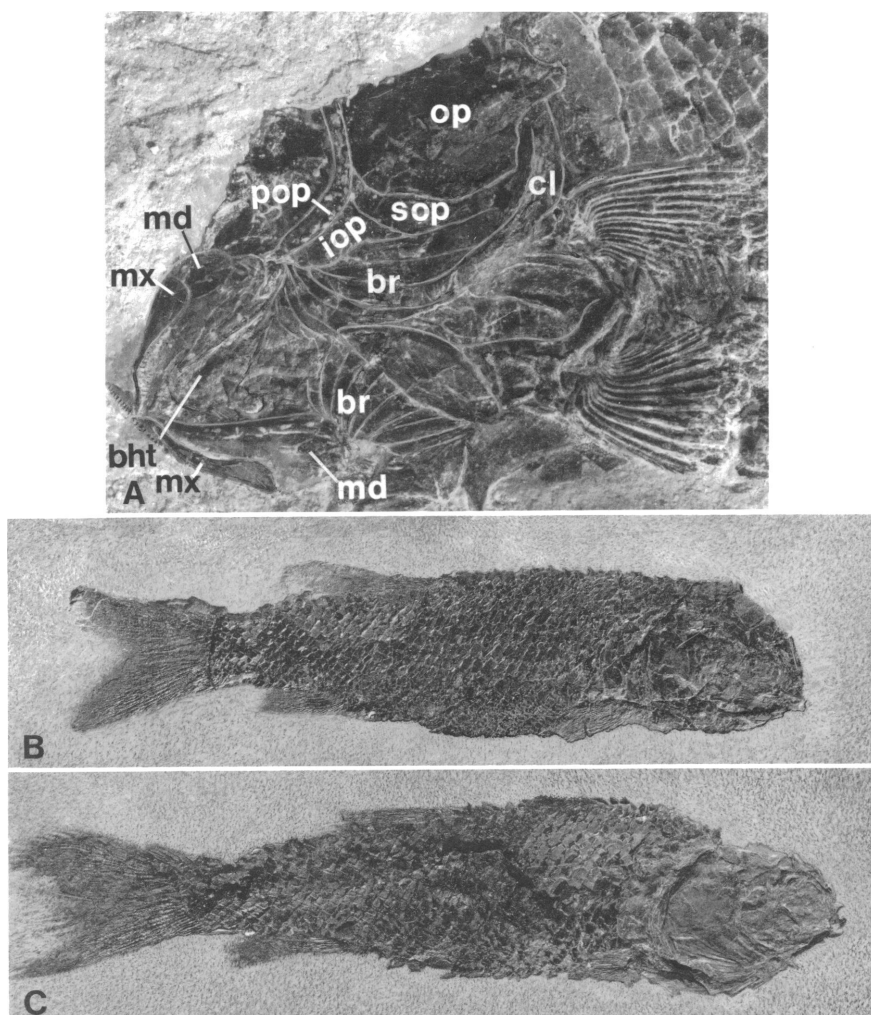


FIG. 6. *Hulettia americana*. A. AMNH 11443. Throat region of specimen from Merrill Ranch, New Mexico.  $\times 2.5$ . B. BHI P110. From Bull Canyon, New Mexico.  $\times .80$ . C. AMNH 11454, from Piedra River Canyon, Colorado.  $\times .88$ .

of smaller ones. There seems usually to be at least one small suborbital anterodorsal to the large bone ( $sbo_2$ , fig. 11B). In AMNH 10831a there are three small bones in this position on the right side and two on the left. Several specimens show a suborbital ( $sbo_3$ , fig. 11B) ventral to the large one, but in other specimens this is evidently absent.

The circumorbital series (fig. 11B) is interrupted only in the region of the posterior nasal opening, between the dorsal process of the antorbital and the foremost supraorbital. *Hulettia* usually has three, sometimes only two

supraorbitals in front of the dermosphenotic. The last is sutured to the frontal and the dermopterotic as in *Perleidus*, semionotids and primitive teleosts, and does not form part of the skull roof as in *Ophiopsis* (Bartram, 1975), amiids and caturids (Patterson, 1973, pp. 244, 279). There are six infraorbitals, the third (counting back from the antorbital) enlarged as in parasemionotids, *Ophiopsis* and many of the primitive teleosts. The two narrow anterior infraorbitals form little more than a tube around the infraorbital sensory canal.

In mature individuals all the cranial der-

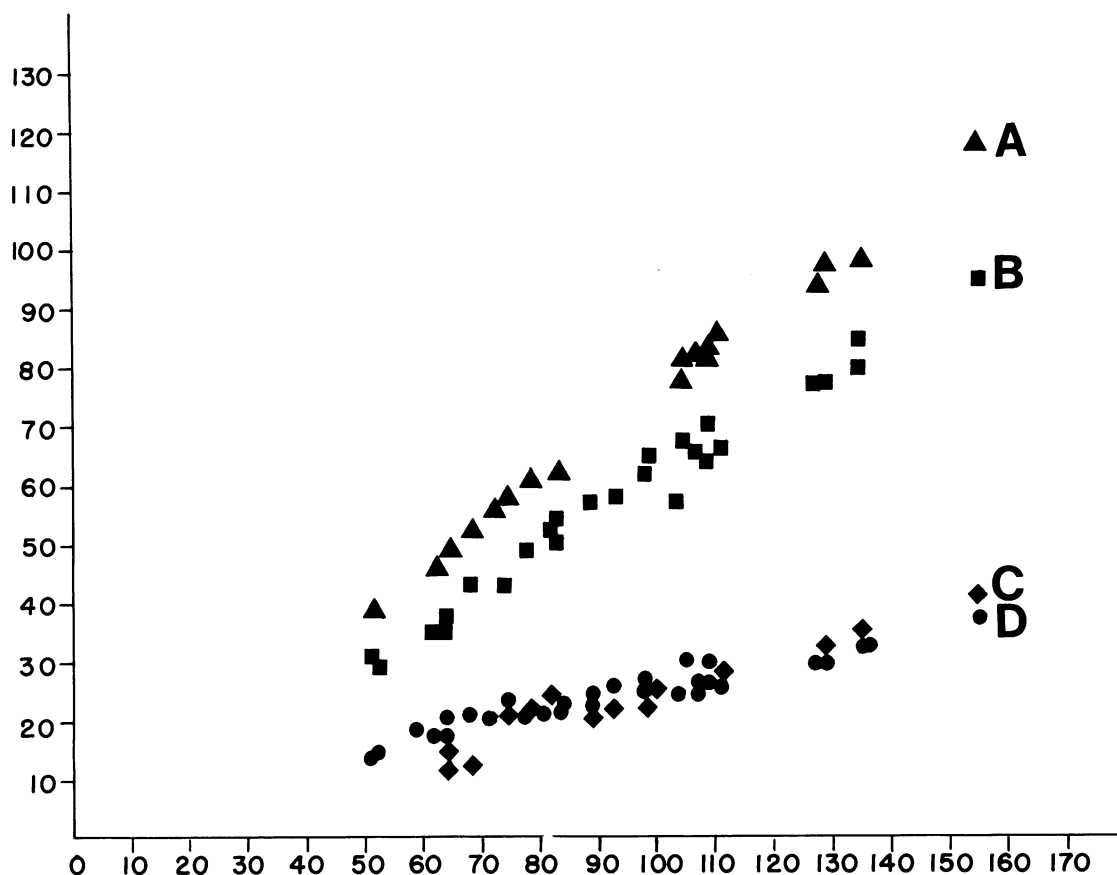


FIG. 7. *Hulettia americana*. Regressions in mm of SL (measured from the tip of snout, to posterior end of lateral fin) on horizontal axis and: A, distance from snout to origin of anal fin; B, snout to origin of dorsal fin; C, estimated body depth; D, snout to posterior border of opercular bone. Sample includes specimens from South Dakota, Wyoming, Colorado, and New Mexico.

mal bones are covered to some extent with ganoin ridges and tubercles. On some bones such as the dentary, the density of these elevations gives a rugose appearance. On the opercular, interrupted ridges radiate from an area near the anterior border.

**SENSORY CANALS:** As in most non-teleostean actinopterygians, the supraorbital and infraorbital canals of *Hulettia* are not joined. The supraorbital canal extends into the parietal where it is replaced by the anterior pit line (fig. 11). The middle pit line extends from the parietal into the dermopterotic. In the snout region, the right and left infraorbital canals are joined by the rostral commissure. The dorsal spur of the infraorbital canal in the antorbital bone is characteristic of

neopterygians generally and is known in some paleopterygians. Sensory canal pores with somewhat elevated rims are present on the frontals of mature individuals. Pores are also evident along the mandibular sensory canal but are otherwise difficult to locate.

**BRAINCASE:** The available material of the braincase of *Hulettia* consists of five specimens: three isolated, dorsoventrally crushed braincases, AMNH 10880 (fig. 8A), 11071, 11073, the last two lacking the occipital ossification; SDSM 54361, a specimen in which the braincase and parasphenoid (fig. 8B) have drifted free from the adjacent skeleton and roofing bones; and AMNH 10926 (fig. 9), an isolated occipital ossification. Except for the latter specimen, the braincases are severely

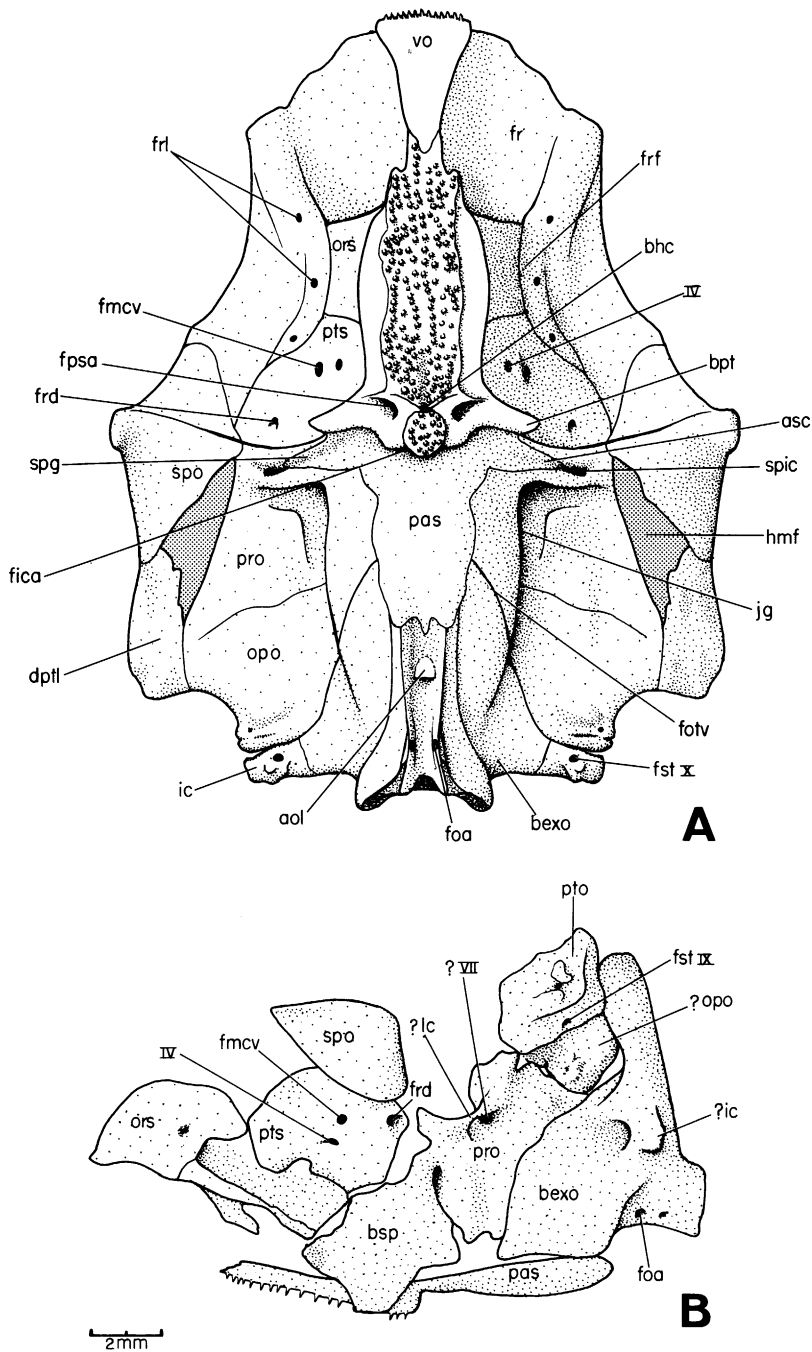


FIG. 8. *Hulettia americana*. Braincase. A. Restoration in ventral view, based mainly on AMNH 10880. Ethmoid ossifications omitted and vomer shown in outline only, since details are unknown. B. Interpretative sketch of braincase in left lateral view as preserved in SDSM 54361.

crushed, so that only external structures are known in any detail.

The occurrence of isolated occipital ossifications and of braincases lacking that por-



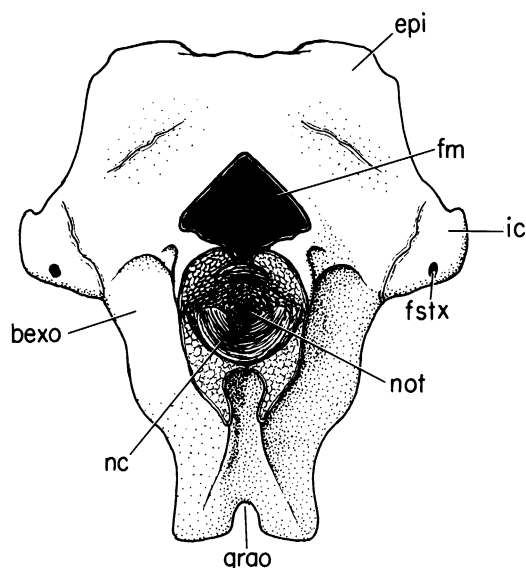


FIG. 9. *Hulettia americana*. Occipital ossifications of braincase in posterior aspect. Based on AMNH 10926.  $\times 7.6$ .

tion shows that the braincase of *Hulettia* was divided into occipital and pre-occipital sections by a persistent cranial fissure. We are unable to say with certainty what parts of the otico-occipital fissure were perichondrally lined, but AMNH 10926 and SDSM 54361 show that the dorsolateral part of the fissure (epioccipital opposed by the pterotic) and the region above the vagus foramen (intercalar) were so lined. A perichondrally lined otico-occipital fissure occurs in palaeoniscoids, *Australosomus*, and certain pholidophorids. Parts of the fissure retain perichondral lining in *Perleidus*, some parasemionotids, pachycormids, aspidorhynchids, and some pholidophorids and leptolepids (Patterson, 1975). We surmise that in *Hulettia* the extent of perichondral lining was about as it was in *Perleidus* or *Pholidophorus germanicus* (Patterson, 1975, pp. 461, 417), from the vagus canal up to the lateral part of the roof of the braincase.

The ossification pattern of the braincase in *Hulettia* is suggested by residual sutures separating paired epioccipitals and intercalars from a basi-exoccipital in AMNH 10926 (fig. 9), and by SDSM 54361 (fig. 8B), which shows an orbitosphenoid and pterosphenoid in the

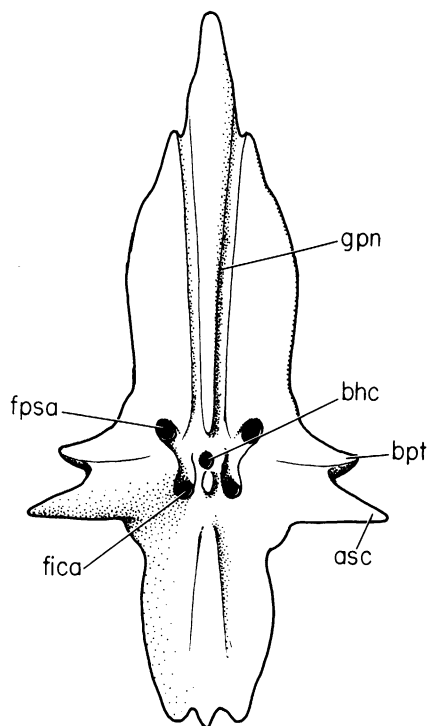


FIG. 10. *Hulettia americana*. Parasphenoid in dorsal aspect. Mainly based on AMNH 10957.  $\times 6.7$ .

orbit, an autosphenotic forming the postorbital process, and a dorsolateral pterotic, resembling that bone in, for example, *Perleidus* and parasemionotids (Patterson, 1975, figs. 97, 98, 115, 116). AMNH 10926 shows that no supraoccipital was present and the only uncertainties concern the lower parts of the otic and sphenoid regions, where in the generalized actinopt pattern (Patterson, 1975, p. 472) there is a basisphenoid, and paired prootics and opisthotics. SDSM 54361 (fig. 8B) is not sufficiently well preserved to demonstrate those bones, but we infer their presence, an inference supported by an apparent suture between the opisthotic and prootic in AMNH 10880 (fig. 8A). In the ethmoid region, there is a single ossification, recalling that in *Acentrophorus* (Patterson, 1975, fig. 136), which probably ossified from paired lateral ethmoid centers. Thus *Hulettia* presents all the endocranial ossification centers expected in generalized actinopterygians, and

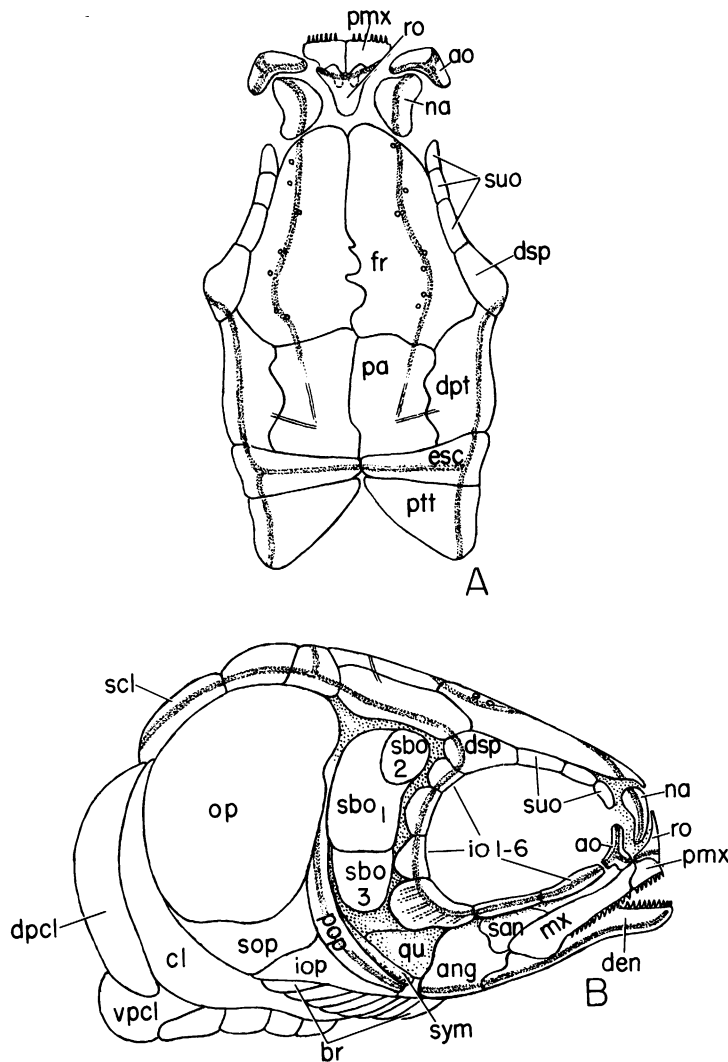


FIG. 11. *Hulettia americana*. Restoration of dermal skull in (A) dorsal and (B) lateral aspects. Snout bones in A spread in one plane.

lacks a supraoccipital, a bone so far known only in pholidophorids and higher teleosts. In the full-grown braincase of *Hulettia* the bones fused with one another within the otic region and the occipital region, as in other primitive actinopt. In juvenile specimens 35–45 mm SL, the braincase appears to be unossified or very lightly so. By about 50 mm SL, at least the sphenotic and pterotic are ossified (AMNH 11076).

In form and proportions of the braincase,

so far as they can be estimated, *Hulettia* is generally similar to palaeoniscoids and pholidophorids (Patterson, 1975, p. 287) in having a short occipital region, about 10 percent of the total length of the braincase, and the postorbital and orbital length about equal, roughly 40 percent of the total length. But the braincase of *Hulettia* appears to be broader, with the breadth across the postorbital processes almost 80 percent of the total length, against about 50 percent in pholidophorids.

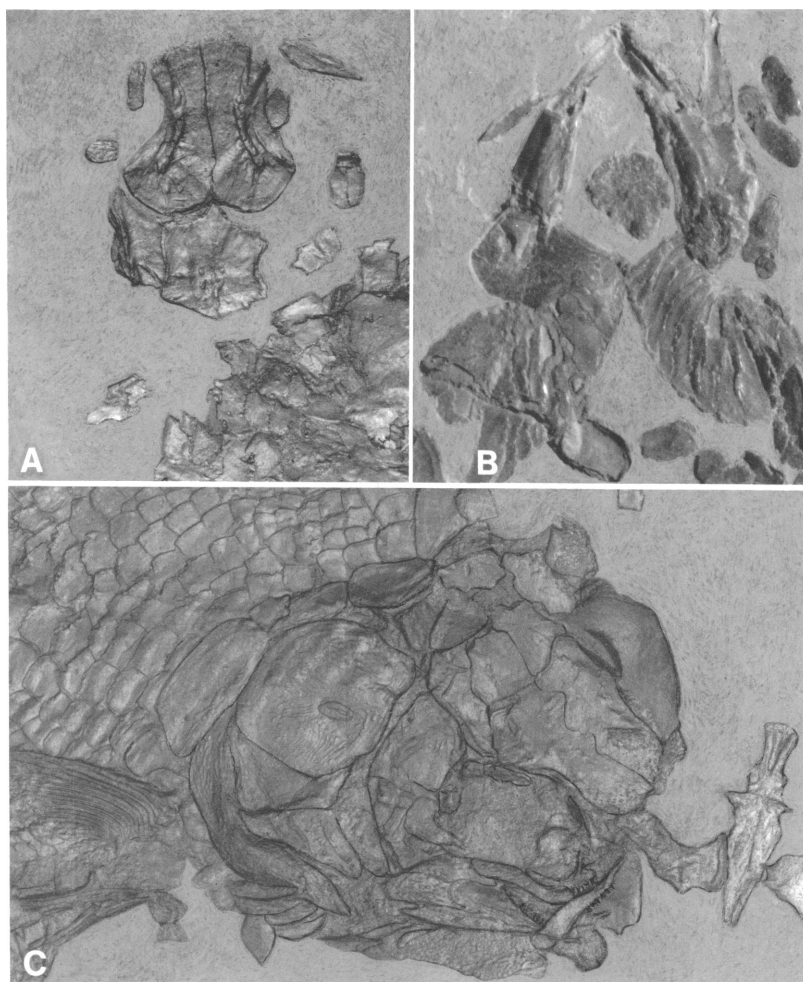


FIG. 12. *Hulettia americana*. A. AMNH 10824. Partial skull roof in ventral aspect with median parietal.  $\times 1.8$ . B. AMNH 10862. Branchiostegals, mandibles and basihyal toothplate in ventral aspect.  $\times 3.3$ . C. AMNH 10940. Dermal skull. From Hulett, Wyoming.  $\times 1.8$ .

The ethmoid ossifications are nowhere well preserved, and no details can be described. The orbitosphenoid (fig. 8) is confined to the dorsal part of the orbit, and there was no ossified interorbital septum. The pterosphe-noid contains three foramina. There are two near the center of the bone, the larger one dorsal to the smaller, presumably respectively for the middle cerebral vein and trochlear nerve (Patterson, 1975, p. 409). The third foramen is posteriorly directed and lies close to the posterodorsal margin of the bone; it probably carried a lateral line nerve to the skull roof.

The basisphenoid region is nowhere well preserved, but it appears to have been rather extensive, and to contain paired vertical canals for the internal carotids (AMNH 11073). The autosphenotic forms the postorbital process, as usual, and is limited posteroventrally by the hyomandibular facet, a space which was cartilage-filled in life. No foramina have been found in the autosphenotic, and the spiracular canal (fig. 8A) enters the prootic, a condition otherwise known only in *Lepidotes* (Patterson, 1975, p. 399).

In the prootic, the lateral commissure is short—little more than a strut of cartilage

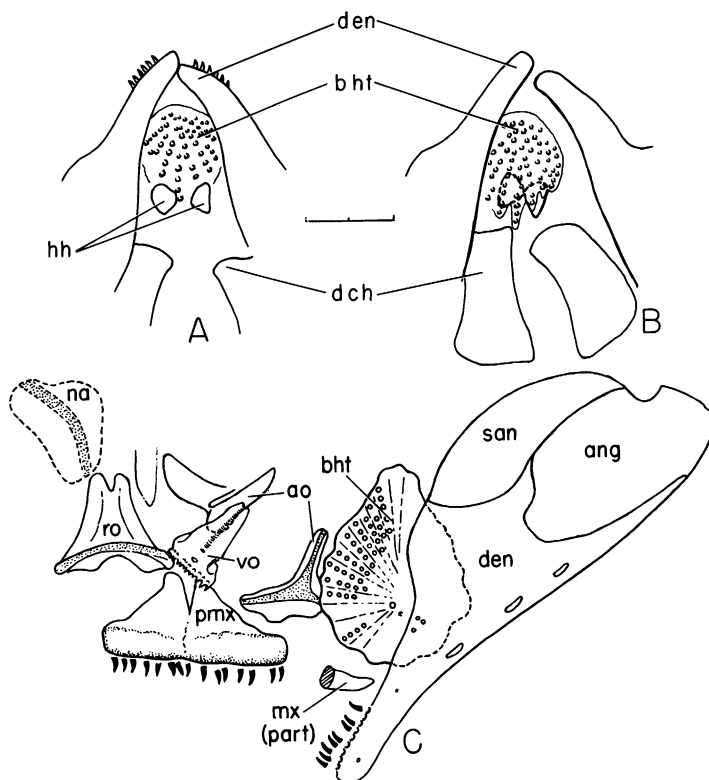


FIG. 13. *Hulettia americana*. A. AMNH 11076. Basihyal toothplate, hypohyals and distal ceratohyals. B. AMNH 10885. Same. C. SDSM 5781. Dissociated snout bones, basihyal toothplate, and mandible.  $\times 4.7$ .

bone overlaid by the ascending process of the parasphenoid carrying the spiracular groove to the opening of the spiracular canal. A shallow jugular groove leads back from the jugular canal beneath the lateral commissure, and another groove leads dorsally, toward the anterior part of the hyomandibular facet, immediately behind the lateral commissure. The latter groove may mark the course of the hyomandibular nerve. There is no marked subtemporal fossa. The myodome remains unknown. The opisthotic is assumed to ossify from a center over the external semicircular canal, at the posterior margin of the otic region. Here the otic capsule meets the intercalar in a rather well-ossified shelf, with grooves and a small foramen probably marking the passage of nerves or vessels from the vagus canal, which lies medial to this point. In front of these grooves there is a ridge or

eminence on the ventral surface of the opisthotic, probably marking the ampulla of the posterior semicircular canal, or the posterior part of the external canal. The glossopharyngeal foramen has not been identified. The pterotic is visible in only one specimen (fig. 8B). It forms the posterodorsal shoulder of the otic capsule, and its upper surface has thickened areas which contacted the parietal, separated by grooves for nerves and vessels. On the lateral face of the pterotic, which presumably formed the medial wall of a posttemporal fossa, there is a small, ventrally directed foramen transmitting the supratemporal branch of the glossopharyngeal to the skull roof. The posterior face of the pterotic appears to be perichondrally lined, and is opposite the epioccipital in the dorsolateral part of the cranial fissure.

In the occipital section of the braincase,

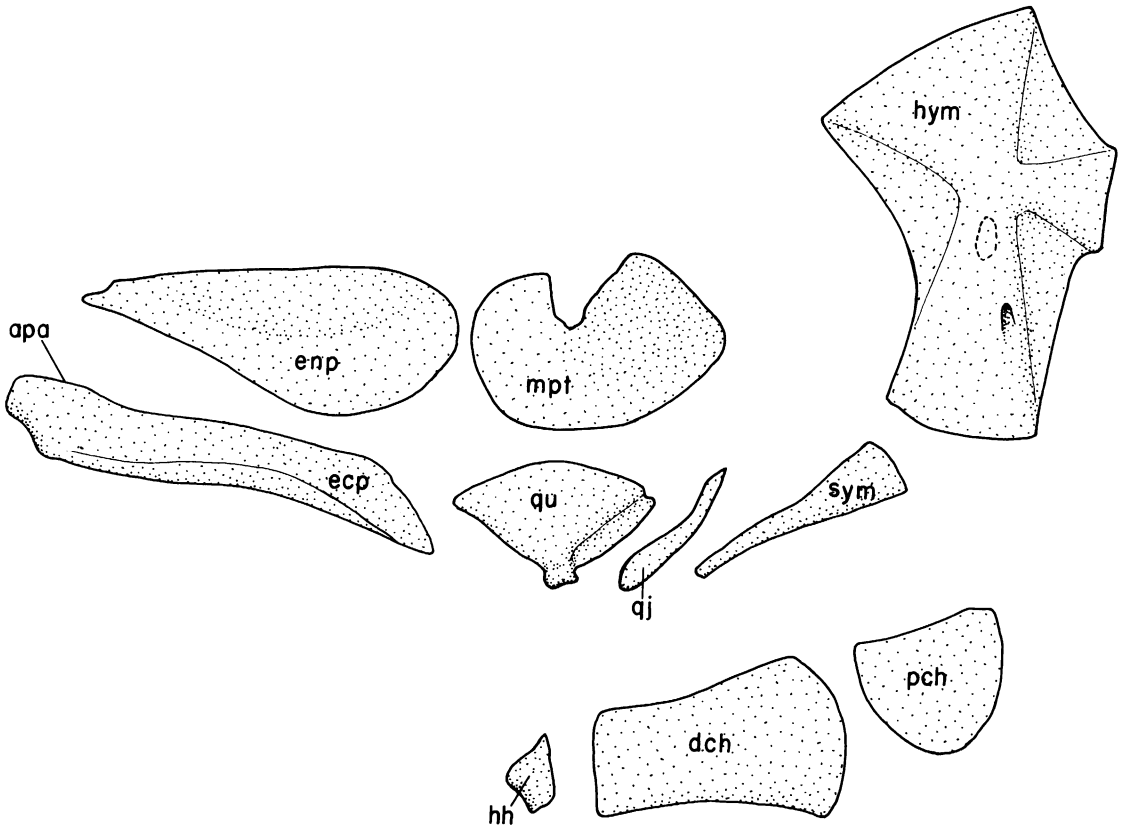


FIG. 14. *Hulettia americana*. Bones of left palate and hyoid arch in lateral view. The hyomandibula and symplectic and bones of the hyoid bar are shown in their natural relationship, other bones shown as if disarticulated. Foramen for the hyomandibular nerve on the medial face of the bone is indicated by a broken line. Based on AMNH 10831, 10948, 11077, and SDSM 54361.

the basi-exoccipital (figs. 8A, 9) shows no sign of separate basi- and exoccipital components, though we assume these existed in early ontogeny. The notochordal pit is deep, and partially lined by notochordal calcification. On the ventral surface, there is a deep aortic groove. The walls of this groove are perichondrally lined except at the extreme posterior end, where a very short aortic canal might have ossified later in life (Patterson, 1975, p. 319). In the roof of the aortic groove there is a cuplike housing for the aortic ligament, as in other "holostean"-level fishes (Patterson, 1975, p. 321). There is no more than one pair of foramina for occipital nerves in the wall of the foramen magnum, again a primitive condition (Patterson, 1975, p. 318).

The intercalar consists almost entirely of

cartilage bone, with only rudimentary thickenings of membrane bone rather than the extensive outgrowths that develop in most Jurassic actinopterygians. The intercalar has a posterior facet for tendinous attachment to the descending limb of the post-temporal, and is perforated by a canal for the supratemporal branch of the vagus. The epioccipital is a thin vertical plate of cartilage bone, perichondrally lined on both the anterior and posterior face. On the dorsal surface of the epioccipital there is a thickening which met the overlying post-temporal.

The sclerotic ring is ossified in two sections (SDSM 54361), not four as in pholidophorids and other primitive actinopterygians.

In general, the braincase of *Hulettia* is that of a primitive "holostean"-grade fish (cf. Pat-

terson, 1975, p. 563). Features of more primitive grade, as in palaeoniscoids, include the open, perichondrally-lined cranial fissure, the pattern of the cartilage bones, especially the large opisthotic and endochondral intercalar and their ontogenetic fusion, the canal for the middle cerebral vein, the position of the housing for the aortic ligament in front of the foramina for the occipital artery and the single occipital nerve. "Holostean"-level features include the slender lateral commissure and the presence of notochordal calcification in the notochord pit in the basioccipital. Derived features are the spiracular canal in the prootic (otherwise known only in *Lepidotes*) and the bipartite sclerotic, as in teleosts and various fossil "holosteans" (Edinger, 1929).

**PARASPHENOID AND VOMER:** The parasphenoid is exposed in dorsal view (fig. 10) in several specimens, but only one isolated braincase (AMNH 10880) shows it in ventral aspect (fig. 8A). Anteriorly, where it overlies the vomer, the parasphenoid tapers irregularly. Beneath the orbit, the bone is exceptionally broad, and carries an elongate, raised patch of rather large teeth which opposed the basihyal toothplate. In juveniles, the teeth are arranged in rows radiating from the opening of the buccohypophysial canal at the rear of the toothed area. In the adult, the posterior part of the tooth patch, behind the opening of the buccohypophysial canal, is raised on a roughly circular boss. Behind this boss there is a deep transverse crevice or pocket, as in *Perleidus* and parasemionotids (Patterson, 1975, p. 536), interpreted as the site of insertion of the subcephalic muscles. The dorsal surface of the parasphenoid (fig. 10) shows longitudinal grooves for the palatine nerves and arteries, and paired foramina for the efferent pseudobranchial and internal carotid arteries, with bilateral, curved grooves for commissures linking the two arteries, as in *Amia*, *Pholidophorus*, and *Leptolepis* (Patterson, 1975, figs. 142, 143). On the ventral surface of the parasphenoid there is no sign of these vascular foramina. The efferent pseudobranchial and internal carotid arteries evidently passed through the bone almost horizontally, so that their foramina are hidden in ventral view. The efferent pseudobranchial artery entered laterally, through a crevice at the base of the basipterygoid process, and the

internal carotid entered posteriorly, in the transverse crevice behind the raised, toothed boss.

The basipterygoid process of the parasphenoid is moderately long, pointed and formed of very thin bone. Presumably, the metapterygoid articulated with a cartilaginous extension from the basisphenoid lying in the groove on the dorsal surface of this dermal process. The ascending process of the parasphenoid is slender and passes up the lateral commissure to the opening of the spiracular canal in the prootic. Posteriorly, the parasphenoid extends beyond the ventral otic fissure (the prootic/basioccipital suture), but does not cover much of the ventral surface of the basioccipital. The posterior portion of the parasphenoid, behind the toothed area, forms roughly one-third of the total length of the bone, about as in *Perleidus* and primitive pholidophorids. This part of the bone is relatively shorter in palaeoniscoids, and longer in other actinopt (Patterson, 1975, p. 527).

The vomer (figs. 8, 13C) is poorly known, but is exposed in dorsal view in SDSM 5781 and 54361. The bone is median and unpaired, and is an elongate triangle with the tapering posterior part underlying the tip of the parasphenoid. Teeth are borne on the anterior part of the oral surface, but the extent of the toothed area is unknown. A median longitudinal canal for the terminal branches of the palatine nerves passes through the anterodorsal part of the bone.

The parasphenoid and vomer of *Hulettia* show certain derived features. The vomer is median, as in teleosts (including pholidophorids and *Ichthyokentema*), *Lepidotes*, *Dapedium*, pycnodonts and *Bobasatrania* (Patterson, 1977, p. 513). In the last four of these, the vomer bears crushing teeth, whereas in *Hulettia* and generalized teleosts the vomerine dentition is unmodified. The parasphenoid of *Hulettia* contains foramina for the internal carotid and efferent pseudobranchial arteries. An internal carotid foramen is known only in teleosts (including pholidophorids and *Ichthyokentema*), *Pachycormus*, *Dapedium*, *Boreosomus*, and possibly in *Saurichthys*. An efferent pseudobranchial foramen occurs only in teleosts (including pholidophorids and some individuals of *Ichthyokentema*) and in *Dapedium* (Patterson, 1975). The basipter-

yoid process of the parasphenoid is rather large in *Hulettia*. The distance across the two processes is about 40 percent of the total length of the bone, compared with about 33 percent in pholidophorids and 20 percent in leptolepids and *Ichthyokentema*. But this very high ratio in *Hulettia* is largely due to the breadth of the parasphenoid. The projecting portion of the basiptyergoid process is equal to about 10 percent of the total length of the bone in *Hulettia*, compared with about 15 percent in *Pholidophorus germanicus*, 8–9 percent in leptolepids and 5–6 percent in *Ichthyokentema*. The large dermal basiptyergoid process of *Hulettia* and these primitive teleosts is a derived condition, but an equally large dermal basiptyergoid process also occurs in *Lepidotes* (Patterson, 1975, fig. 109).

In other respects, the parasphenoid of *Hulettia* is relatively primitive. It is broad and heavily toothed; has a broad, transverse crevice for the subcephalic muscles, as in *Perleidus* and parasemionotids; has a short posterior portion, like *Perleidus* and primitive pholidophorids; has an open buccohypophyseal canal, and a slender ascending process, confined to the spiracular groove.

**PALATE, HYOID, AND GILL ARCH SKELETON:** Most of the bones of the palate are known by isolated examples in disarticulated skulls (fig. 14). The hyomandibular is broad, curved, inclined somewhat backward, and of generalized neopterygian type. It is perforated by a canal for the hyomandibular nerve in the usual way. The hyomandibular and symplectic were evidently ossifications within the same cartilage, as in all neopterygians, since they remain in their natural relationship (fig. 14) in disarticulated skulls (e.g., AMNH 10897a, SDSM 5780). The symplectic is long and tapers distally, where it lies close behind the quadrate. The symplectic shows no sign of a condyle for articulation with the lower jaw, such as occurs in halecomorphs (Patterson, 1973).

The metapterygoid has a broad dorsal notch between the medially inclined basal process and the vertical posterior part of the bone. There is no sign of a specialized articular surface for the basiptyergoid process, or of a dermometapterygoid. The triangular quadrate is not fused with the quadratojugal as the bones are separate in some disarticulated

skulls (e.g., AMNH 10831). The quadratojugal lies in a groove on the posterolateral face of the quadrate, and is broadest ventrally, where it ends in a swollen head buttressing the articular condyle of the quadrate.

The elongate endopterygoid bears small, pointed teeth over most of its oral surface. The ectopterygoid and autopalatine are not clearly distinguishable from one another in the few specimens showing them, except by the contrast between cartilage bone (autopalatine) anteriorly and dermal bone (ectopterygoid) posteroventrally. It appears that the autopalatine was rather extensive, extending posteriorly as an ossified area in the palatoquadrate cartilage, which, in turn, lay in the groove formed by the ridge along the lower margin of the lateral face of the ectopterygoid, as in *Amia*. No ectopterygoid teeth are visible. The autopalatine ends in a broad anterodorsal process which articulated with the ethmoid. No dermopalatine has been observed *in situ*, but teeth are visible in the dermopalatine position in some dorsoventrally crushed specimens. Small toothplates adjacent to the autopalatine in disarticulated specimens might be dermopalatines or coronoids.

No interhyal has been seen in the hyoid arch. The proximal ceratohyal (fig. 14) is semicircular; the distal ceratohyal is broad, short and slightly waisted. There is a single nodular hypohyal. Many specimens show a large, unpaired toothplate between the lower jaws (figs. 12B, 13). The toothplate is rounded anteriorly, digitate posteriorly, and in juveniles bears rows of teeth radiating from a growth center near the anterior margin (fig. 13A, B). The toothplate evidently opposed the parasphenoid dentition, and lies in front of the hypohyals (fig. 13A, B) whose junction with the median copula marks the front end of the first basibranchial (Nelson, 1969, p. 506). We therefore regard the toothplate as a basihyal rather than a basibranchial structure. There is no sign of an endoskeletal basihyal (known only in teleosts) beneath the toothplate. Among non-teleostean actinoptes, *Lepisosteus* has a series of paired basihyal toothplates, and the Triassic *Bobasatrania* (Nielsen, 1952) and *Errollichthys* (Nielsen, 1955) have a large median toothplate between the lower jaws. In *Bobasatrania* and

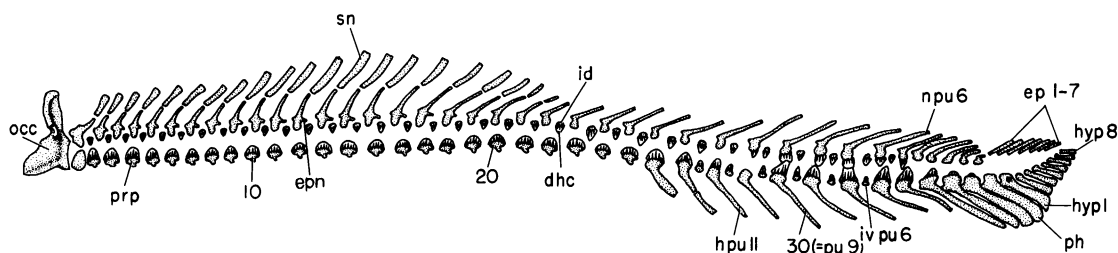


FIG. 15. *Hulettia americana*. Restoration of axial skeleton (ribs omitted) and occipital ossification of braincase, based mainly on AMNH 10917, SL ca. 95 mm. Elements missing in that specimen (supraneurals, neural arches 12–28, epurals, hypurals 3–8) restored on the basis of specimens shown in figures 16 and 17. Cartilage bone stippled, notochordal calcifications hatched.

*Errolichthys* this toothplate, which may be basibranchial or basihyal or both, opposes a large vomer and lies mainly behind the hypohyals over a single basibranchial ossification.

Ossified, paired gill-arch elements are preserved in several specimens, but we have learned nothing useful about their pattern. No ossified basibranchials have been observed, or any gill-arch dentition or gill-rakers.

**JAWS:** The premaxillae meet in the midline throughout most of the length of their nasal processes. In some large specimens they are fused together (fig. 13C). The apposition of the nasal processes suggests that the nasal septum, which appears to separate these processes in *Acentrophorus*, was less elevated in *Hulettia* (Patterson, 1975, figs. 136, 137). The thickened dentigerous portion supports about eight sharply pointed teeth.

The maxilla (fig. 11B) is entirely separated from the cheek. The internal process, which articulates with the vomer and ethmoid, is attenuated and recurved in typical neopterygian fashion. The maxilla expands posteriorly to a slight degree, and extends in that direction about as far as the apex of the mandibular coronoid process. There is no indication of a supramaxilla. About 13 maxillary teeth have the same shape as the premaxillary ones but decrease in size posteriorly.

The mandible has a well-developed coronoid process (fig. 13C). Laterally it exhibits the usual three primitive elements—dentary, angular, and supra-angular (Patterson, 1982, p. 248). A well-preserved medial surface has

not been found, but it was probably covered for the most part by the prearticular. The number of marginal teeth on the dentary exceeds 20.

The dermal skull of *Hulettia* can only be characterized as generally neopterygian. The snout design, including the premaxillae, is close to the pattern of a parasemionotid figured by Patterson (1975, fig. 137), as well as that of *Acentrophorus*, the semionotids, *Ophiopsis* Bartram (1975) and *Amia*. Unfortunately, the dermal snout pattern in the palaeonisciforms is not well understood, and a reasonable approximation of the *Hulettia* condition is not known.

*Hulettia*, *Acentrophorus* (Gill, 1923) and *Lepisosteus* are the only primitive neopterygians known to lack a supramaxilla. The absence of this superfluous-looking bone, which is doubled in pholidophorids and in generalized teleosts, is still another primitive character and is hence of little systematic significance. In summary, there are no apparent derived characters in the *Hulettia* dermal skull that indicate special affinity with any other known actinopterygian.

**AXIAL SKELETON:** The axial skeleton is partially visible in immature individuals, 35–50 mm SL, in which the squamation is incompletely developed (fig. 16), and in two mature specimens in which the squamation was stripped off postmortem, AMNH 10917, ca. 95 mm SL (fig. 15 is mainly based on this specimen), and AMNH 10875, ca. 105 mm SL (fig. 17), which is poorly preserved.

The boundary between the ural and preural regions of the vertebral column is marked by



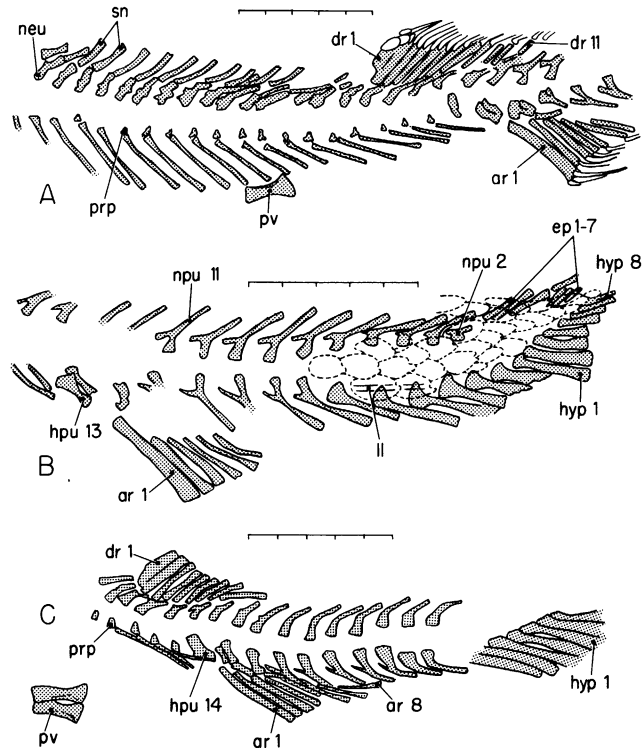


FIG. 16. *Hulettia americana*. Axial skeleton as preserved in three immature specimens: A, AMNH 10860, SL ca. 50 mm; B, AMNH 11075b, SL ca. 50 mm, scales drawn in transparency; C, AMNH 11072, SL ca. 41 mm. Bars equal 5 mm.

the bifurcation of the dorsal aorta (Nybelin, 1963). Behind this point, the aortic canal in the haemal arch is eliminated, and the (preural) haemal spines are replaced by the (ural) hypurals. In fossil non-teleost actinoptes, the location of the bifurcation is not always evident. In *Amia* (Nybelin, 1963, fig. 16) and in some individuals of *Lepisosteus* (Nybelin, 1977, fig. 2) it is marked by an anterior embayment in the proximal part of the first hypural with an anterior process below it. In some fossil forms an anterior process also occurs on several preceding preural haemal arches (e.g., Patterson, 1968, figs. 1-4; Nybelin, 1977, fig. 3). In *Hulettia*, mature individuals show similar anterior processes (figs. 15, 17), and we designate the last bone with a process as the first hypural. In AMNH 10917 (fig. 15) this bone contains a foramen at the level of the haemal canal. In *Pholidophorus bechei* a foramen may also occur in this po-

sition in the first hypural (Patterson, 1968, fig. 2B). In AMNH 10917, as in *P. bechei*, the first hypural is the fifth bone supporting lower caudal fin-rays. In other specimens of *Hulettia* we have recognized the preural/ural boundary by comparison with AMNH 10917. On this basis, there are 38 preural vertebrae in AMNH 10917, and 38 or 39 in AMNH 10875, the only two specimens in which the entire column is visible. There was thus one vertebra to each scale row, a relationship also shown by the translucent squamation of immature individuals (fig. 16B). In AMNH 10917, the 38 vertebrae comprise 25 abdominals and 13 caudals (with haemal arches and without ribs), but the number of caudals apparently ranged from 12 (fig. 17) to 14 (fig. 16C). The preural count of 38-39 is thus 25-27 abdominals plus 12-14 caudals.

There is a marked difference between the vertebrae of immature and mature individ-

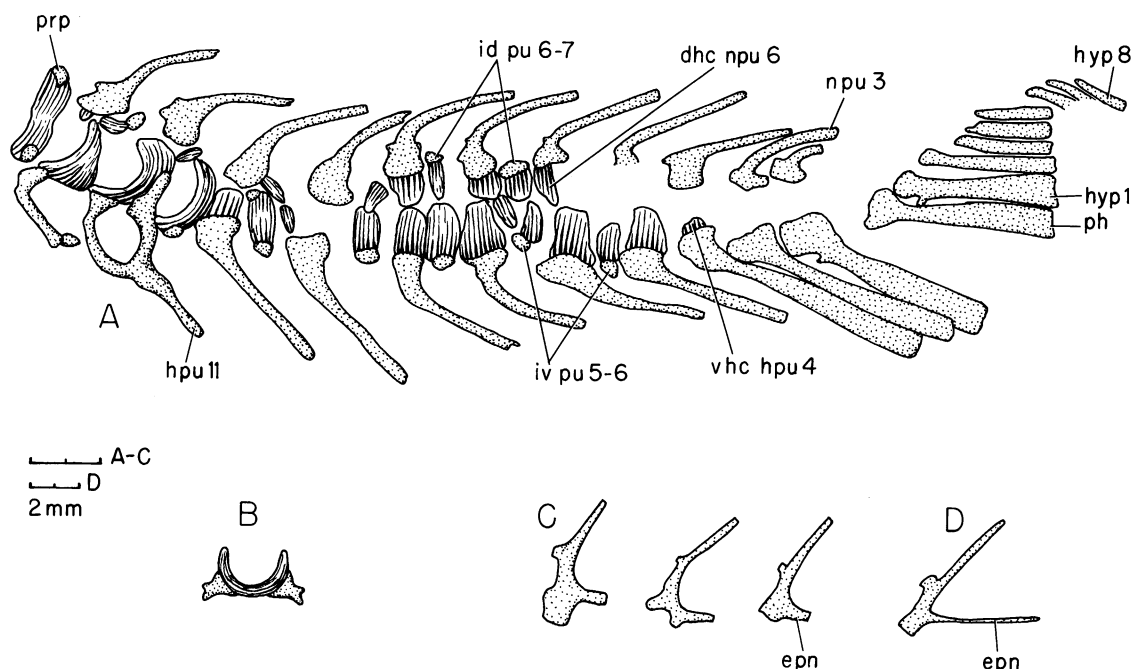


FIG. 17. A–C. *Hulettia americana*, axial skeleton of AMNH 10875, SL ca. 105 mm: A, interpretation of caudal vertebrae and hypurals as preserved; B, ventral hemichordacentrum and parapophyses of vertebra 22, from the posterior abdominal region, in anterior view; C, detached abdominal neural arches in lateral aspect, the first lying below vertebrae 8–9, the second above vertebrae 18–19, the third above vertebrae 15–16. D. *Pholidophorus bechei*, a neural arch from the posterior abdominal region of an acid-prepared BMNH specimen, Lower Lias, Lyme Regis, Dorset.

uals. Immature specimens (fig. 16) have no centra, no ossified interdorsals or interven-trals (intercalaries), and the vertebrae appear monospondylous. In mature individuals (figs. 15, 17) there are ossified interdorsals in front of each neural arch except the first and the last four or five. There are ossified interven-trals in the midcaudal region and crescentic dorsal and ventral hemichordacentra, which have a diplospondylous relationship. The adult vertebral column will be described first, and ontogenetic differences in young individ-uals will be noted afterwards.

Above the notochord, the paired neural arches are separate from each other back to the origin of the dorsal fin at vertebra 20–21, and are fused distally into a median neural spine beyond that point (fig. 16B). There are rodlike median supraneurals distal to the first 20–21 neural spines, the last supraneural lying just in front of the first dorsal radial (fig. 16A).

In the two adult specimens, the neural arches are missing in AMNH 10917 from vertebra 12 to 28 (from PU 11 forward), and are dis-articulated and scattered from PU13 forward in AMNH 10875 (fig. 17). The first few neural arches of AMNH 10917 show traces of short posterolateral processes. However, some of the disarticulated neural arches in AMNH 10875 (fig. 17C) have relatively longer pro-cesses, suggesting that these outgrowths of the neural arches were present throughout much of the abdominal region. We assume that the posterolateral processes are homologous with the short epineural processes on the anterior neural arches of various palaeoniscoids and other fossil actinopts (Patterson, 1973, p. 237; Rosen et al., 1981, p. 244), and with the much longer epineural processes of pholidophorids (fig. 17D) and other primitive teleosts. The last few neural spines decrease progressively in length, and the diminutive last neural arch

and spine is that of PU2 (figs. 16B, 17A); in AMNH 10917 (fig. 15) the last five neural arches are concentrated so that they oppose only three haemal arches. There are no ossified ural neural arches. Epurals are preserved only in one immature specimen (fig. 16B), where there are seven. The first epural appears to be aligned with the short neural spine of the last ossified neural arch.

The paired interdorsals, which are small blocks of cartilage bone, are present in front of each neural arch except the first and the last four (AMNH 10875) or five (AMNH 10917). Their relationship with the abdominal neural arches and parapophyses is not clear and it is not possible to determine whether the abdominal interdorsals lay close in front of the neural arch bases as in *Amia*, close behind them as in *Australosomus* (Nielsen, 1949), or whether the arrangement was varied along the column. In figure 15 the neural arch bases and interdorsals are shown as equally spaced. The abdominal interdorsals either opposed or alternated with the parapophyses beneath the notochord. As preserved in the two adult specimens, they appear to alternate, but this could be due to crushing following preservation. The arrangement shown in figure 15 is therefore conjectural. In the caudal region, the interdorsals lie midway between the neural and haemal arches.

There are paired parapophyses in the abdominal region beneath the notochord. Except for the first pair, they all bear lateral processes (fig. 17B) with an articular facet for the long, rather stout pleural ribs. At the transition from the abdominal to the caudal region (*ca.* PU14), vertebra 26 or 27 has a pair of enlarged, elongated and waisted parapophyses without ribs. These appear to meet distally and form a haemal canal in some specimens (fig. 16A, C), but to be separated in others (fig. 16B). We regard this vertebra as the first caudal one. The succeeding vertebra has a shorter haemal arch bearing a separate median haemal spine, which lies behind the proximal ends of the first two anal fin radials (fig. 16A, C). The remaining caudal haemal arches bear long haemal spines, the last four of which are expanded distally to support lower caudal fin-rays. If the ural/preural boundary is correctly identified (see

above), there are at least eight ossified hypurals (figs. 16B, 17A). No distal caudal radials have been observed.

Paired interventrals (ventral intercalaries) are present in front of the haemal arches of PU6–11 (AMNH 10917, fig. 15) or PU5–10 (AMNH 10875, fig. 17A). They are small blocks of cartilage bone resembling the interdorsals.

The centra of adult specimens consist of separate dorsal and ventral hemichordacentra. The ventral crescents are larger than the dorsal (figs. 15, 17A). A dorsal hemichordacentrum joins each pair of interdorsals across the midline. The only neural arches bearing hemichordacentra are those in the midcaudal region between PU5 and PU10 (fig. 15). In these five segments the dorsal hemichordacentra are diplospondylous.<sup>3</sup> The loss or disarticulation of the precaudal neural arches in the adult specimens indicates that they had no intimate connection with the notochordal sheath.

Large ventral hemichordacentra are associated with each pair of parapophyses and with the haemal arches from the occiput back to PU2 (AMNH 10917) or PU4 (AMNH 10875), except for the haemal arch of PU10 (AMNH 10917) or PU9 (AMNH 10875) (see below). Each of the five pairs of interventrals in the midcaudal region, PU5–10 or PU6–11, carries a hemichordacentrum. These five segments are thus diplospondylous, each with two dorsal and two ventral hemichordacentra.

In the middle of the diplospondylous region, the dorsal and ventral hemichordacentra are in contact or nearly so (figs. 15, 17), but are not actually fused to form a ring centrum. The hemichordacentra are larger and

<sup>3</sup> By diplospondyly we mean two centra or two pairs of hemicentra to each segment. In actinoptes, diplospondyly is confined to the midcaudal region, where one centrum or pair of hemicentra is associated with the intersegmental neural and haemal arch and one with the intrasegmental intercalaries. This type of diplospondyly does not occur in teleosts above the pholidophorid level. It is known in the Triassic pholidopleurid *Australosomus* (Nielsen, 1949), in *Caturus* (Rosen et al., 1981, fig. 59), in *Amia* and fossil amioids, in *Notagodus* (Saint-Seine, 1949, fig. 86), and in pholidophorids (Patterson, 1968).

thicker throughout the column in AMNH 10875 (*ca.* 105 mm SL, fig. 17A, B) than in the smaller AMNH 10917 (*ca.* 95 mm SL, fig. 15). In the larger specimen the ventral hemichordacentra in the first 10 to 12 vertebrae extend well above the horizontal midline of the notochord. It appears that calcification of the chordacentra began in the midcaudal region, where they are largest (AMNH 10917; fig. 15) and then progressed backward from the occiput. In AMNH 10917 the haemal arch of PU10 may lack a chordacentrum, and since the same may be true for PU9 in AMNH 10875, this absence is unlikely to be an artifact of preservation. This condition indicates that PU9 or 10 was the last centrum to calcify, marking the junction between a possible rostrocaudal gradient from the occiput with a caudorostral gradient from the midcaudal region.

The first vertebra is poorly preserved in both adult specimens, but it appears to have extensive bases to the neural arch and parapophysis that almost surround the notochord.

In young specimens (up to 50 mm SL, fig. 16), the vertebral column differs from the adult condition in lacking any trace of chordacentra or of interdorsals and midcaudal intervertebrals, so that the column appears monospondylous. Interdorsals and intervertebrals were presumably present in cartilage. Epineural processes on the abdominal neural arches are suggested in some immature specimens (fig. 16A, middle of the abdominal region), but are much less prominent than in the adult (fig. 17C). We assume that these too were cartilaginous in the young.

The most notable features of the axial skeleton of *Hulettia* are: (1) a complete series of dorsal intercalaries; (2) ventral intercalaries in the midcaudal region only; (3) dorsal and ventral hemichordacentra which are diplospondylous in the midcaudal region; (4) epineural processes on most of the abdominal neural arches; (5) the series of supraneurals ends in front of the dorsal fin, and the neural spines are median from there onward; (6) at least seven epurals; and (8) no ossified ural neural arches. It is notable that the first four of these are undeveloped in immature individuals. Comparisons with other fishes are difficult because the axial skeleton is known

in few fossil lower actinoptes, where it is covered by ganoid scales.

Among the eight features listed above, the interdorsals (1), intervertebrals (2), and midcaudal diplospondyly are surely primitive features, widely distributed in lower actinoptes and other fishes (Schaeffer, 1967b; Andrews, 1977; Rosen et al., 1981). Hemichordacentra (3) and epineural processes (4) recall the pholidophorids, but hemichordacentra are much more widely distributed (*Australosomus*—Nielsen, 1949; *Turseodus*—Schaeffer, 1967a; macrosemiids—Bartram, 1977; *Caturus*—Rosen et al., 1981, fig. 59; and probably *Haplolepis*—Baum and Lund, 1974). The epineural processes of *Hulettia* are much shorter than those of pholidophorids (fig. 17C, D), yet, at present, such outgrowths of the neural arches are known to occur throughout the abdominal region only in pholidophorids and more derived teleosts (Patterson, 1977, fig. 19). Epineurals are unknown in cladistically more primitive teleosts (*sensu lato*) such as ichthyokentemids, pleuropholids, aspidorhynchids and pachycormids. However, epineural processes occur in the lower actinopterygians *Mimia*, *Boreosomus*, *Australosomus*, and *Caturus*. In *Mimia* they are present on the first 14 neural arches (Gardiner, 1984, p. 363).

The unpaired neural spines of *Hulettia* are a halecostome feature (Patterson, 1973). The seven epurals, and the fact that the supraneurals do not extend beyond the dorsal fin origin, are derived characters relative to the numerous epurals and supraneurals of chondrosteans and palaeoniscoids, but are generalized within halecostomes (there are seven epurals in *Pachycormus*, *Dapedium* and *Ionoscopus*—Patterson, 1973). The absence of ossified ural neural arches means only that their form cannot be used to relate *Hulettia* to actinopterygian groups such as teleosts or caturids.

In actinopterygians, vertebral centra may be composed entirely of chordal tissue (e.g., *Hulettia*, *Caturus*, and *Pholidophorus*); of a combination of chordal and perichordal (e.g., *Aspidorhynchus*, some leptolepids and some larval teleosts); or only of perichordal (e.g., *Polypterus*, *Amia*, and some teleosts). Among fossil paleopterygians, *Pygopterus* (Aldinger, 1937); *Haplolepis* (Baum and Lund, 1974);

*Turseodus* (Schaeffer, 1967a); *Australosomus* (Nielsen, 1949); and *Macroaethes* (Wade, 1935) have entirely chordal centra (as deduced from the histology) along with *Tetragonolepis*, *Pachycormus* (Patterson, 1973, p. 274) and, according to Bartram (1977, p. 215), *Propterus*, *Catervariolus* and *Euthynotus*. In our view, the distinction between chordal and perichordal centra needs restudy in these and other Mesozoic actinopterygians. Among the teleosts (as defined by Patterson, 1973), pholidophorids, pachycormids, and some aspidorhynchids and leptolepids have only chordal centra. *Aspidorhynchus comptoni* centra have an inner chordal ring and an outer perichordal bony one (AMNH 6363).

It is increasingly evident that the hemi- or annular centra of paleopterygians, if they develop at all during ontogeny, are invariably chordal, apparently with no perichordal addition. Among the neopterygians, as noted above, this is also the case in *Hulettia* and in various other Mesozoic forms.

In *Hulettia*, as shown in the restoration of the axial skeleton (fig. 15), all the haemal components are composed of replacement bone and are in contact with the narrow hemichordacentra. The same is true for the dorsal and the relatively few ventral intercalaries. It is of some interest that in diplospondylous actinopterygians where the entire vertebral column is known, chordal hemicentra are absent beneath the neural arch bases except for those in the midcaudal diplospondylous region. Chordal hemicentra are present, however, below all the dorsal intercalaries. This indicates that, as in *Caturus* (Rosen et al., 1981, fig. 59) and in pholidophorids (*sensu lato*), the hemichordacentra in the abdominal region were derived entirely from the chordal tissue related to the intercalaries. In Recent teleosts, where intercalaries are absent, the chordacentra develop only from ventral hemichordacentra (François, 1966, 1967; Cavender, 1970). The absence of chordal calcifications related to most of the neural arches in *Hulettia* probably represents the primitive actinopterygian condition. The variations in intercalary and centrum development in the non-teleost actinopterygians present a fascinating problem in pattern formation, which we plan to treat elsewhere.

**PAIRED FINS:** The endoskeletal shoulder girdle of *Hulettia* remains unknown so important characters involving the mesocoracoid arch cannot be discussed (Jessen, 1972; Patterson, 1973). As shown in figure 11, the dermal elements—extrascapular, post-temporal (suprascapular), supracleithrum and cleithrum—require little comment. The extrascapulars meet in the midline. The post-temporals diverge at about 45 degrees, have a well-developed internal process, and barely touch just behind the extrascapulars. The cleithrum has a prominent internal lamina, which is a primitive actinopterygian character. There is no evidence of a clavicle or of a "serrated appendage" (Bartram, 1977). The dorsal and ventral postcleithra have about the same relative proportions as in, for instance, *Ichthyokentema* (Griffith and Patterson, 1963), except that the ventral one projects farther posteriorly and has a rounded free border.

The pectoral fin is bordered anteriorly by about five basal fulcra and by fringing fulcra that extend the entire length of the anterior-most ray. It contains about 13 principal rays, all jointed.

The pelvic plates lie beneath vertebrae 18–20, and are more or less hourglass-shaped (fig. 16). The pelvic fins have only a few basal fulcra, numerous fringing fulcra, and eight or nine segmented rays. The origin of the pelvic is almost exactly halfway between the origin of the pectoral and the base of the hypocaudal lobe.

**UNPAIRED FINS:** The dorsal fin originates at about the level of vertebra 23, behind the pelvics. The fin contains eight or nine segmented rays, the first of which may or may not be branched, preceded by four or five unsegmented basal fulcra. Fringing fulcra are interposed between the last two basal fulcra, and are continued up the leading edge of the first one or two segmented rays. The fin is preceded by an enlarged ridge scale, and a row of about six small, rounded scales extends back along each side of the base of the fin. The dorsal fin is supported by about 11 radials (fig. 16A). The first radial has a large, platelike anterodorsal expansion, supports the basal fulcra and the first ray, and ends proximally behind the neural spine of vertebra 20 or 21. Ossified middle segments are pre-

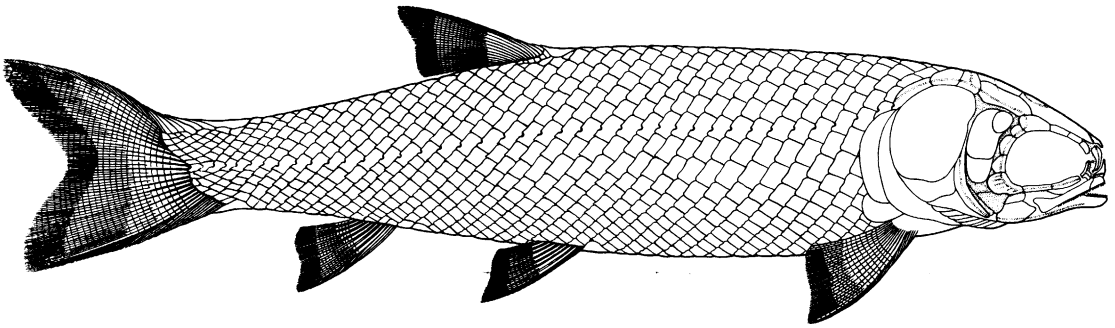


FIG. 18. *Hulettia americana*. Restoration of entire fish. Squamation based mainly on AMNH 10903.

served distal to the fifth and succeeding radials.

The anal fin originates at about the level of vertebra 29 (i.e., beneath PU10–11), midway between the pelvics and the base of the hypochordal lobe of the tail. The fin contains seven or eight branched and segmented rays, preceded by three or four unsegmented basal fulcra and three enlarged ridge scales. Fringing fulcra are interposed between the last two basal fulcra and continue up the leading edge of the first ray. The fin is supported by seven or eight radials (fig. 16B, C). The long first radial ends beneath the first haemal arch and supports the basal fulcra and the first ray. No ossified middle segments are preserved in the anal fin.

**CAUDAL FIN:** The hypochordal lobe of the caudal fin is supported by four elongated preural haemal spines and eight hypurals (see p. 29 for discussion of the problem of identifying the ural/preural boundary and the description of the caudal skeleton). The occurrence of only four preural haemal spines supporting caudal fin-rays in *Hulettia* appears to be a rare condition among non-teleost neopterygians, although the number may range from three to nine (fig. 15).

The caudal fin is nearly equilobate externally and includes 19 to 20 principal caudal rays, with 10 or 11 branched rays in the upper lobe and seven in the lower. As in other primitive neopterygians, the uppermost caudal rays decrease in size upward, and the last one is difficult to distinguish from the axial lobe squamation proximally. The uppermost ray is continuous proximally, with the longest

scale row in the axial lobe, and there are no epaxial fin-rays (cf. Bartram, 1977, p. 218). The caudal is bordered dorsally by an enlarged scute followed by seven or eight robust basal fulcra (unpaired, unsegmented) and by fringing fulcra. The ventral border of the fin also carries fringing fulcra and is preceded by a large scute and six or seven narrower basal fulcra, the last three segmented distally.

The relatively low number of principal caudal rays (19–20), with only eight in the lower lobe, distinguishes *Hulettia* from pholidophorids, which have 20–27 principal caudal rays, with 10 or more in the lower lobe (Patterson, 1968). In *Ichthyokentema* there are 19 principal caudal rays (Griffith and Patterson, 1963), as in *Hulettia*. There are fewer rays in pleuropholids (ca. 15) and aspidorhynchids (ca. 14), and many more in pachycormids (Wenz, 1968). In macrosemiids there are always eight lower principal rays, as in *Hulettia*, but the upper lobe contains only three to eight (Bartram, 1977). *Caturus* has about 25 principal caudal rays, *Dapedium* about 24 (Gill, 1923; Wenz, 1968), *Lepidotes* and *Semionotus* ca. 17–19, and *Acenotrophorus* 17.

The caudal skeleton and fin of *Hulettia* may be regarded as a primitive actinopterygian one in terms of the little modified haemal spines supporting the caudal rays, in the absence of epaxial fin-rays, and in the presence of well-developed basal and fringing fulcra. The absence of ural centra is probably also primitive. The absence of ossified ural neural arches, as noted above, is simply uninformative. The occurrence of seven epurals is

matched in a wide variety of neopterygians (e.g., *Dapedium*, *Pachycormus*, *Ionoscopus*). This number is derived relative to the much larger number in some chondrosteans (e.g., 15 in *Pteronisculus*, 30 in *Acipenser*), but primitive relative to the four or five in pholidophorids and the three in Recent teleosts.

**SQUAMATION:** The body scales (fig. 18) are rhomboidal, have well-developed peg-and-socket articulations, a smooth posterior border and lack a dentine layer. In the flank area the scales are about twice as deep as wide. Those covering the abdominal area are much smaller and narrower. All the fins are bordered by both basal and fringing fulcral scales (see fin descriptions for fulcral counts). Dorsal ridge scales are absent. In well-preserved specimens from both the Sundance and the Todilto the scale count along the lateral line is 37–38. The origin of the pelvic fin is behind the eleventh oblique scale row; that of the dorsal and anal behind the twenty-first or twenty-second oblique scale row. The apparent constancy in fin position in the Sundance and Todilto specimens is also indicated by the regressions of body length to fin position (fig. 7), and by immature specimens in which vertebral counts can be made (fig. 16B).

**ONTOGENETIC CHANGES:** Our material of *Hulettia americana* includes individuals ranging in standard length from about 35 mm to over 150 mm. We have noted no differences that can be interpreted as ontogenetic among specimens more than about 70 mm in standard length, but smaller specimens differ from the adult condition in squamation, fulcra, ornamentation of the dermal bones, and in the axial skeleton (the latter described under that heading).

In the smallest specimens (e.g., AMNH 11075a, ca. 35 mm SL), there are no scales apart from the large scutes above and below the caudal skeleton. Scales develop in larger specimens from the axial lobe of the tail forward. They extend to the posterior end of the anal fin insertion in specimens that range from 40 mm SL (AMNH 11072, 11437) to 50 mm SL (AMNH 11075b, fig. 16B). One individual (AMNH 10860, ca. 50 mm SL, fig. 5A) has scales as far forward as the origin of the anal fin. As in the Triassic redfieldiid *Brookvalia* (Wade, 1935), the early Cretaceous pholidophorid *Wadeichthys* (Waldman, 1971),

and Recent teleosts (van Oosten, 1957), the lateral line scales develop first: this is shown, for example, by AMNH 10919, ca. 45 mm SL, which has lateral line scales as far forward as the origin of the dorsal fin, but shows scales above and below the lateral line only from the middle of the anal fin backward. In *Brookvalia* Wade (1935) found that scales first appeared dorsal and ventral to the lateral line scales at both ends of the trunk, but in *Hulettia* we have seen no signs of anterior scales in incompletely scaled individuals, and the squamation appears to have developed from the tail forward, as is general in teleosts (van Oosten, 1957). In AMNH 10885, ca. 65 mm SL, the squamation is complete on the flank, but from the anal fin forward the scales do not reach the dorsal or ventral borders of the trunk. By about 70–80 mm SL, the squamation is complete.

When scales first appear, they lack ganoin, as in *Brookvalia* (Wade, 1935, p. 27). On individual scales, ganoin first appears as a spot at the posterior point or margin of the scale, and spreads forward from there (AMNH 11075a). It develops first on the dorsal and ventral caudal scutes, then on the caudal lateral line scales, and spreads forward dorsally and ventrally from there (AMNH 10885).

The cranial dermal bones and the fin-rays, like the scales, lack ganoin in small individuals. On the frontal, for example, AMNH 11075b (ca. 50 mm SL) shows a small patch of smooth ganoin close to the inferred growth center of the bone, but medial to the sensory canal. On other bones, such as the cleithrum and supracleithrum, ganoin first appears as dorsoventral strips or ridges, whereas on the opercular it appears in ridges concentric with the growth center at the articulation with the hyomandibular. The fin-rays develop ganoin at about the same time as the scales adjacent to them. Fringing fulcra seem to be absent on all the fins in the smallest specimens, and first appear at about 40–50 mm SL.

The fact that the scales, fin-rays and cranial dermal bones of *Hulettia* are well formed in bone before any ganoin is added to them matches Meinke's (1982) account of the dermal skeleton in *Polypterus*, where ganoin develops after bone, and is initially separate from it.

RELATIONSHIPS OF *HULETTIA*

Although *Hulettia* is now one of the better known Mesozoic actinopterygians, its relationships remain enigmatic. To recapitulate our comments in the descriptive sections, *Hulettia* retains many primitive features including: a large rostral separating the nasals; a fully open cranial fissure; an endochondral intercalar without extensive membrane bone outgrowths; no supraoccipital; a broad parasphenoid with an open bucco-hypophysial canal, a wide transverse crevice for subcephalic muscles and a short posterior part; no supramaxilla; a complete series of dorsal intercalaries; midcaudal diplospondyly; and a long series of unmodified hypurals. These features have varied distributions among actinopterygians, but are found together only in "chondrosteans" such as *Perleidus* or *Australosomus*.

However, *Hulettia* has a number of derived features, which show that it belongs in the Neopterygii. These neopterygian features include: premaxilla with nasal process; ant-orbital with long rostral process; one large suborbital plus one to three smaller ones; free maxilla with an internal head; narrow lateral commissure; two-part sclerotic; vertical suspensorium with a narrow, crescentic preopercular; an interopercular; symplectic developed in the same cartilage as the hyomandibular; a splintlike quadratojugal; articular with a coronoid process; unpaired neural spines from the origin of the dorsal fin onward; notochordal hemicentra; no clavicle; fin-rays equal in number to their supports in the dorsal and anal fin; axial lobe of tail reduced; and no dentine layer in the scales. Most of the neopterygian characters are widely distributed among "holosteans," but three of them, the free maxilla, the interopercular, and the median neural spines are defining characters of the Halecostomi (Patterson, 1973).

Finally, *Hulettia* shows a few derived characters of more restricted distribution. These include: (1) spiracular canal entering prootic, as in *Lepidotes*; (2) vomer median, as in *Lepidotes*, *Dapedium*, the pycnodonts, *Bobasatrania* and teleosts; (3) a foramen for the efferent pseudobranchial artery in the parasphenoid, as in *Dapedium*, perhaps *Macrosemius* (Bartram, 1977, p. 144; but we doubt

this interpretation of BMNH 37094) and teleosts; (4) a foramen for the internal carotid in the parasphenoid, as in *Pachycormus*, *Dapedium*, *Boreosomus*, and teleosts; (5) a long dermal basipterygoid process, as in *Lepidotes* and teleosts; (6) no gular, which is also absent in *Lepidotes*, macrosemiids, pycnodonts, aspidorhynchids, and many higher teleosts; (7) a large basihyal toothplate, as in *Lepisosteus*, many teleosts, and probably in *Bobasatrania* and *Errolichthys*. Among the fishes sharing derived characters with *Hulettia* are *Lepidotes* (spiracular canal, vomer, basipterygoid process, no gular), *Dapedium* (vomer, foramina in parasphenoid) and teleosts, including pholidophorids (vomer, foramina in parasphenoid, basipterygoid process).

In the currently accepted scheme of neopterygian relationships (Patterson, 1973, 1977; Wiley, 1976, 1979; Lauder, 1982), with *Amia* as the sister group of teleosts among Recent fishes, pholidophorid-level teleosts are widely separated from *Lepidotes* and *Dapedium*, so that the characters shared by *Hulettia* with pholidophorid-level teleosts and with *Lepidotes* or *Dapedium* would be treated as conflicting, and therefore uninformative. In an alternative scheme proposed by P. E. Olsen (personal commun.), the splintlike quadratojugal of *Lepidotes*, *Semionotus*, *Dapedium*, *Lepisosteus*, macrosemiids, *Hulettia* and teleosts (where it is fused to the quadrate) is regarded as a synapomorphy relating these fishes.

We cannot evaluate Olsen's scheme in detail here, but if it were accepted, the two foramina in the parasphenoid of *Dapedium*, *Hulettia*, and teleosts would also emerge as synapomorphous relative to the single foramen in *Pachycormus* and the lack of foramina in *Lepisosteus* and *Lepidotes*. We foresee problems with this pattern of relationships. One relates to the jaw joint. The paleoniscoid *Pteronisculus* is described (Nielsen, 1942, p. 175, figs. 35, 36) as having an articulation between the symplectic (interhyal of Patterson, 1982, fig. 1) and the posteromedial surface of the articular. This might be taken as homologous with the symplectic-articular joint in *Amia*, caturids, and parasemionotids (Patterson, 1973). However, the contact surfaces of the two bones in *Pteronisculus* are perichondrally lined, not cartilage-faced as in



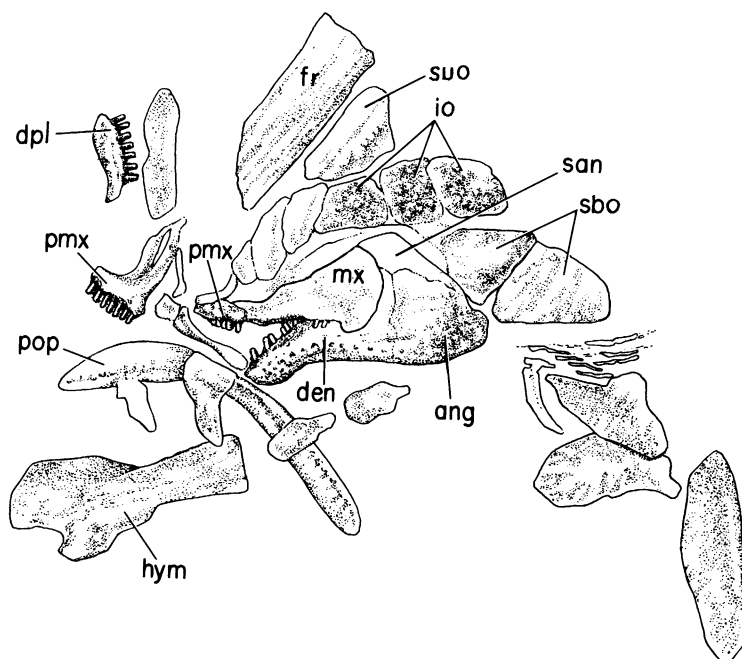


FIG. 19. *Lepidotes* sp. AMNH 11442. Partial, dissociated skull.  $\times 0.8$ . From Hulett, Wyoming.

true joint surfaces. In the Devonian paleoniscoids *Mimia* and *Moythomasia* (Gardiner, 1984, p. 346) the interhyal (=symplectic in Nielsen's usage) does not articulate with the lower jaw. Since Gardiner finds that *Mimia* and *Moythomasia* are successive sister taxa to the remaining actinopterygians, their lack of a hyoid arch-lower jaw contact appears to be the primitive actinopterygian condition. On this basis, we believe that the symplectic-articular joint in halecomorphs (amiids, caturids, parasemionotids) is synapomorphic for this group.

At present, we regard the characters that *Hulettia* shares with *Dapedium*, *Lepidotes*, and the pholidophorid-level teleosts as mutually incongruent. This means that *Hulettia*, although a halecostome, shows no unambiguous synapomorphy with any halecostome subgroup. Taxonomically, our options are to leave it as a genus *incertae sedis* in the Halecostomi, or to name a monotypic family or higher taxon for it, in order to emphasize its unique features. Given our present ignorance of the detailed structure of Mesozoic neopterygians, we can see no advantage in naming a higher taxon.

#### HALECOSTOMI

SEMIONOTIDAE WOODWARD, 1890

GENUS *LEPIDOTES* AGASSIZ, 1832

DIAGNOSIS: See Woodward, 1895, 1916; Lehman, 1966.

TYPE SPECIES: *Cyprinus elvensis* De Blainville.

DISTRIBUTION: See Lehman, 1966, p. 160; Wang, 1974; Arratia, 1981; Gayet, 1982.

#### *Lepidotes* sp.

Figure 19

HORIZON AND LOCALITY: Stockade Beaver Member, Sundance Formation, Burnt Hollow, near Hulett, Crook County, Wyoming and Sundance Formation at mouth of Clark's Fork Canyon, Park County, Wyoming. For details see section on geologic occurrence.

REFERRED SPECIMENS: From the Sundance Formation, Stockade Beaver Shale Member, near Hulett, Wyoming: AMNH 11442, 11440. From Rierdon Formation, Clark's Fork Canyon, Wyoming: AMNH 11441.

DISCUSSION: The tentative identification of these specimens as *Lepidotes* is based primarily on the peglike, weakly tumid form and

relative size of the teeth on the premaxilla, maxilla, dentary, and dermopalatine (AMNH 11442). In this genus both the inner and outer teeth are generally obtuse, and in some species more tumid rather than acuminate, as in its probable sister genus *Semionotus*. Several anterior elements in the infraorbital series are preserved in AMNH 11442 and 11441 along with the c-shaped antorbital. The cheek area, including the suborbitals, is broken away. The short, posteriorly broadened and rounded maxilla is characteristic of both *Lepidotes* and *Semionotus* along with the robust premaxilla, which has an elongated, perforated nasal process. The short mandible with its articulation under the orbit is also characteristic of both taxa, as is the narrow, gently recurved preopercular. The scales in all three Sundance specimens are smooth and their posterior borders are not serrated.

At present there is no possibility of relating the Sundance *Lepidotes* to any of the 96 species of this genus listed by Woodward (1895), plus numerous others described since that time. Woodward (1895) concluded that the Rhaetic-Jurassic species tend to have styliform or weakly tumid, obtuse teeth with slender pedicles, whereas the known Cretaceous species have outer and inner teeth that are more robust with decidedly tumid to molariform crowns and relatively short pedicles. On the basis of Woodward's limited observations this appears to be plausible, but far more comparison is needed for substantiation.

#### HALECOMORPHI

#### CATURIDAE OWEN, 1860

#### GENUS *CATURUS*, AGASSIZ, 1834

**DIAGNOSIS:** A caturid genus distinguishable from other genera in this family (*Furo*, *Heterolepidotus*, and *Osteorachis*—see Patterson, 1973, 1975; Bartram, 1975) by the characters listed by Gardiner (1960, p. 293) plus the presence of multiple, irregular supraorbitals arranged in two or three rows.

**TYPE SPECIES:** *Caturus furcatus* Agassiz.

**DISTRIBUTION:** Lower Liassic to Wealden. Western Europe, Cuba, Brazil, eastern Greenland, western United States.

#### *Caturus dartoni* (Eastman)

Figures 20, 21

*Amiopsis* (?) *dartoni* Eastman, 1899b, p. 406.

*Amiopsis dartoni* Eastman; Boreske, 1974, p. 75.

**HORIZON AND LOCALITY:** Canyon Springs Sandstone Member, Sundance Formation near Hot Springs, South Dakota. Stockade Beaver Member, Sundance Formation, near Hulett, Wyoming. Todilto Limestone Member, Wanakah Formation, Bull Canyon, Guadalupe County, New Mexico. For additional details see section on geologic occurrence.

**HOLOTYPE:** NMNH 4792.

**REFERRED SPECIMENS:** From the Sundance Formation, Canyon Springs Sandstone Member near Hot Springs, South Dakota: NMNH 4793, 4794; MCZ 9696. From the Sundance Formation, Stockade Beaver Shale Member, near Hulett, Wyoming: AMNH 10975, 10994, 10996. From Wanakah Formation, Todilto Limestone Member, Bull Canyon area, New Mexico: BHI 953F.

**DISCUSSION:** The specimens from the Sundance Formation and the Todilto Limestone have been identified as *Caturus* based on the jaws, dentition, branchiostegal ray size and number (at least 24), the presence of hemichordacentra, the fusion of hypurals 1–3 (AMNH 10975), the relative size of the paired fins (pectorals much larger than pelvics, both with delicate fringing fulcra), and thin cycloidal scales that break up into sinuous rods (fig. 20B; Schultze, 1966, figs. 3, 51; Bartram, 1977, p. 219).

The pectoral fin has about 24 rays, the pelvic has eight to ten, the dorsal approximately 20 and the anal about 13. These counts are all within the range of the European species, including the type species *C. furcatus* from the Kimmeridgian (Woodward, 1895; Saint-Seine, 1949). The mostly complete Wanakah specimen has a standard length of about 30 cm, with the distance between the origin of the pectoral and pelvic fins measuring about 10 cm. In the Sundance individual this distance is about 13 cm.

According to Patterson (1973) and Bartram (1975), *Eoeugnathus*, *Sinoeugnathus*, *Allolepidotus*, *Eurycormus*, *Callopterus*, *Lophiostomus*, and *Macrepistius* should be removed from the Caturidae and assigned to

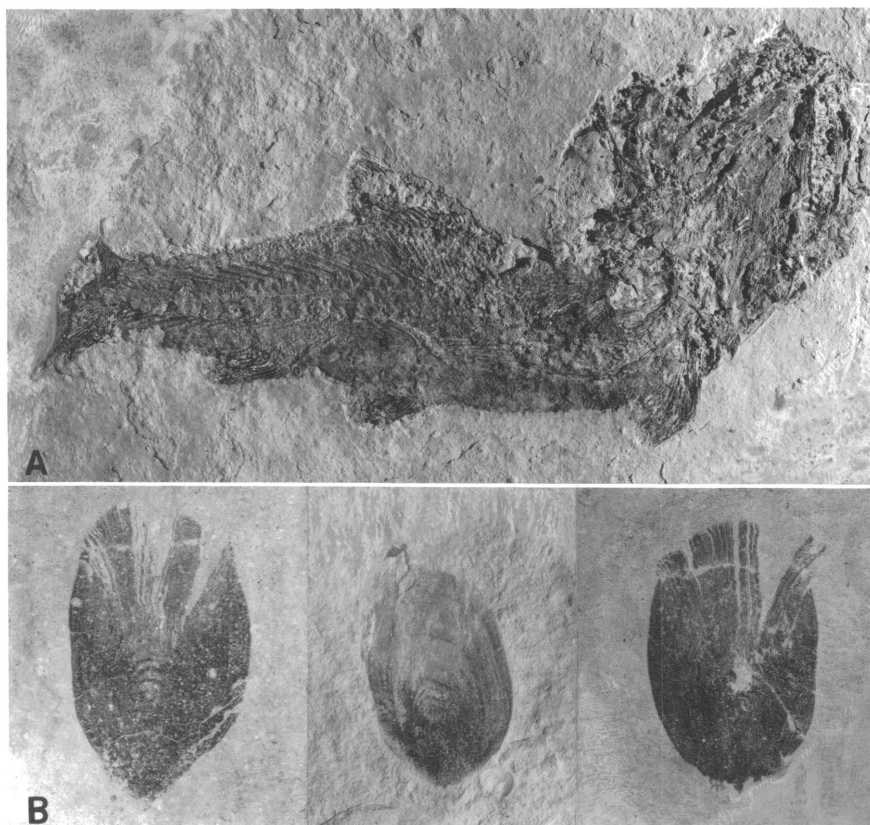


FIG. 20. *Caturus dartoni*. A. BHI 953F. From Bull Canyon, New Mexico.  $\times .38$ . B. AMNH 10994. Isolated scales from Hulett area, Wyoming.  $\times 3.25$ .

other families. The remaining five genera—*Caturus*, *Furo*, *Heterolepidotus*, *Osteorhachis*, and *Neorhombolepis*—may represent a grade group related to the amiids or the ophiopsids, or they may turn out to be a monophyletic group, if they all share with *Caturus* paired, blocklike ural-neural arches. *Caturus* is apparently distinguished from the other genera in this assemblage by having more than one row of supraorbitals, and sometimes a mosaic of extremely small ones (e.g., *C. porteri* Rayner, 1948, fig. 1; *C. drieri* Thiollière, Lehman, 1966, fig. 133). Unfortunately, the supraorbitals cannot be seen in the American specimens.

Although *C. dartoni* remains poorly known, it shares one derived character, fusion of hypurals 1–3, with the English Liassic *C. heterurus* (Patterson, 1973, fig. 21). We have also

observed fusion between the anterior hypurals in *C. smithwardi* White (1925) from the German Lias (Holzmaden). However, the first three hypurals are clearly separate in three Kimmeridgian species; *C. furcatus* (type-species), *C. pachyurus* Agassiz from the Bavarian lithographic limestone, and *C. drieri* from Cerin, France, and in one Lower Cretaceous species; *C. tarraconensis* Sauvage from Lerida, Spain. Among over 20 other nominal species of *Caturus*, the caudal skeleton is known in only five (*C. insignis* Kner, Upper Triassic, Austria; *C. giganteus* Wagner, *C. velifer* Thiollière and *C. bellicianus* [Thiollière] from the Kimmeridgian lithographic limestones of France and Germany; and *C. deani* Gregory from the Oxfordian of Cuba). We have not seen material of these five species. Pending a long overdue revision

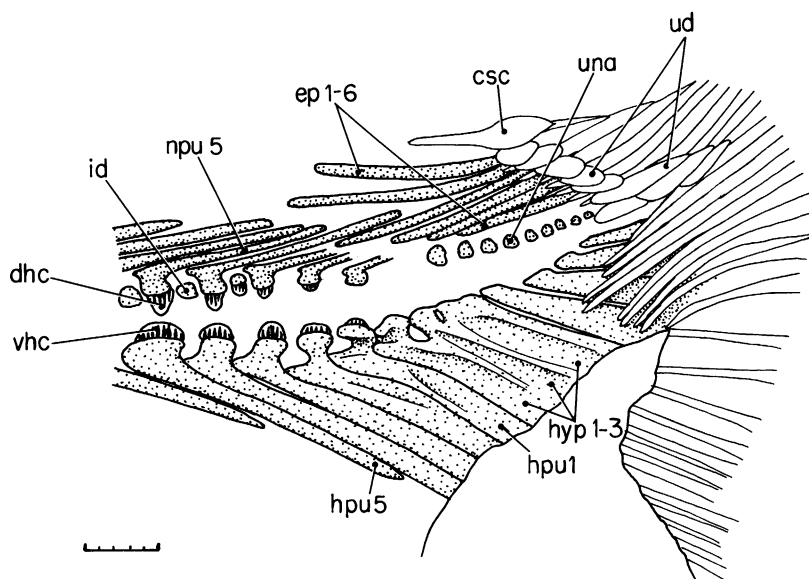


FIG. 21. *Caturus dartoni*. AMNH 10975. Caudal skeleton.  $\times 1.5$ . From Hulett, Wyoming.

of *Caturus*, we suggest that there may be two species-groups in *Caturus*—one characterized by fused anterior hypurals (including *C. heterurus*, *C. smithwoodwardi*, and *C. dartoni*), and the other by a mosaic of numerous very small supraorbitals (including *C. furcatus*, *C. porteri* and *C. drieri*).

#### TELEOSTEI

#### ICHTHYODECTIFORMES INCERTAE SEDIS *OCCITHRISSOPS*, NEW GENUS

TYPE SPECIES: *Occithrissops willsoni*, new species.

DISTRIBUTION: Upper Bathonian, Wyoming.

ETYMOLOGY: Refers to the occidental occurrence of the genus and its relationship to *Thrissops*.

DIAGNOSIS: Ichthyodectiform fishes in which the depth of head, length of snout, and size of mouth are intermediate between *Allothrissops* and *Thrissops*; chordacentra only, without perichordal ossification in individuals up to about 80 mm SL; uroneurals do not cover the lateral surfaces of preural centra, anterior tips of uroneurals 1–4 regularly spaced; supraneurals confined to abdominal vertebrae; anal fin strongly falcate, with 18–20 radials.

#### *Occithrissops willsoni*, new species

Figures 22–29

HOLOTYPE: AMNH 10964 (figs. 23A, 24A, 30), a large fish, 200 mm SL, lacking the tip of the snout and parts of the anal and caudal fins.

DISTRIBUTION: Same as for genus. All the specimens have been found in the lower part of the Sundance Formation.

ETYMOLOGY: In honor of the late Earl Willson of Hulett, Wyoming, on whose property most of the material was collected.

DIAGNOSIS: As genus, only species. Reaching about 200 mm SL; vertebrae 58 (33–34 + 22–23 + 2 uro); D iii, 10–11; A iv–v, 18–20; P ?, 14; V 9; C viii, I, 9, 8, I, vii.

REFERRED SPECIMENS: From the Sundance Formation, Stockade Beaver Shale Member, near Hulett, Wyoming: AMNH 10867, 10873, 10949, 10960, 10966, 10973, 10974, 10976, 10982, 10984, 10990, 10992, 10993, 11434, 11435, SDMS 54362.

#### DESCRIPTION

This species is described mainly by comparison with species of *Allothrissops* (Nybelin, 1964; Taverne, 1975a; Patterson and Rosen, 1977) and Jurassic species of *Thrissops* (Nybelin, 1964; Taverne, 1977), since the

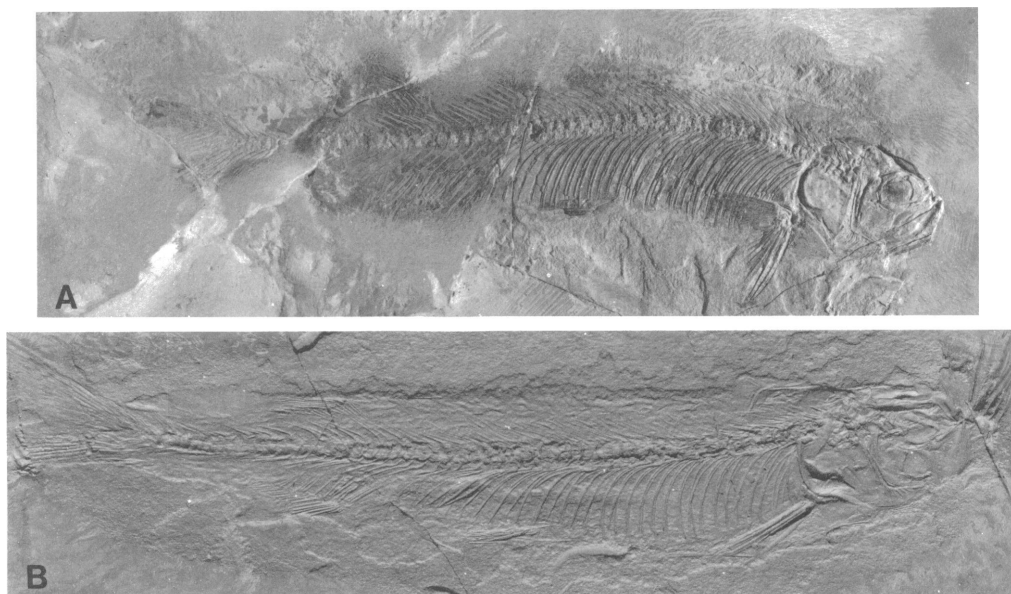


FIG. 22. *Occithrissops willsoni*. A. AMNH 10964. Holotype.  $\times 44$ . B. AMNH 10990.  $\times 0.78$ . From Hulett, Wyoming.

material of *Occithrissops* does not permit a comprehensive account.

**SKULL:** The skull of *Occithrissops willsoni* (fig. 23) is, so far as it is known, generally similar to that of *Allothrissops mesogaster* (Agassiz) (fig. 24A; Patterson and Rosen, 1977, figs. 5, 7–9), but resembles *Thrissops formosus* Agassiz (fig. 24B; Taverne, 1977, figs. 6, 7) in certain ways. The head of *O. willsoni* is proportionally deeper than that of *A. mesogaster*, the mouth is larger and more upturned, and the lower limb of the preopercular is shorter. In all these traits, *O. willsoni* tends toward the condition in *Thrissops formosus*. The ratio of head depth to head length is about 1.2–1.3 in *O. willsoni*, whereas in *Allothrissops mesogaster* this ratio is about 1.45–1.5, and in *Thrissops* it is 1.3 in *T. formosus*, 1.05 in *T. subovatus* v. Münster, and 1.0 in *T. cirinensis* Nybelin (measurements of *Thrissops* from figures in Taverne, 1977). The ratio of the lower limb of the preopercular to the upper limb (measured along the sensory canal) is about 1.75–1.9 in *O. willsoni*, 1.4–1.5 in *A. mesogaster*, 2.1 in *T. formosus*, 3.7 in *T. subovatus*, and 2.3 in *T. cirinensis* (*Thrissops* measured, as before, on Taverne's 1977 figures).

There is a marked difference in form of the antorbital and first two infraorbitals between

*Allothrissops mesogaster* and *Thrissops formosus* (fig. 24). In the specimens of *Occithrissops willsoni* these bones are not clearly visible, but SDSM 54362 suggests that they were like those in *Allothrissops*. The proportions and structure of the ethmoid region are also markedly different in *Allothrissops mesogaster* and *T. formosus* (cf. Patterson and Rosen, 1977, fig. 7A, and Taverne, 1977, fig. 9—the “rhinal” of Taverne is the “ethmopalatine” of Patterson and Rosen). The proportions, if not the details, of the ethmoid region of *O. willsoni* are traceable in AMNH 10873 (fig. 26A), and here again *O. willsoni* appears more like *Thrissops* than like *Allothrissops*. The length of the snout is approximately 75–80 percent of the diameter of the orbit in *A. mesogaster*, about 60–65 percent in *T. formosus*, and about 65–70 percent in *O. willsoni*. Nybelin (1964, p. 5) gives it as 60–80 percent in *T. formosus*.

In *Thrissops* (Taverne, 1977, and BMNH specimens) there is a large supraoccipital crest. *Occithrissops willsoni* (fig. 25) resembles *Allothrissops*, where the crest is small (Patterson and Rosen, 1977, fig. 5). According to Patterson and Rosen (1977, p. 100), another difference between *Allothrissops* and *Thrissops* is that there is a suborbital in the latter but none in the former. In *O. willsoni* no speci-

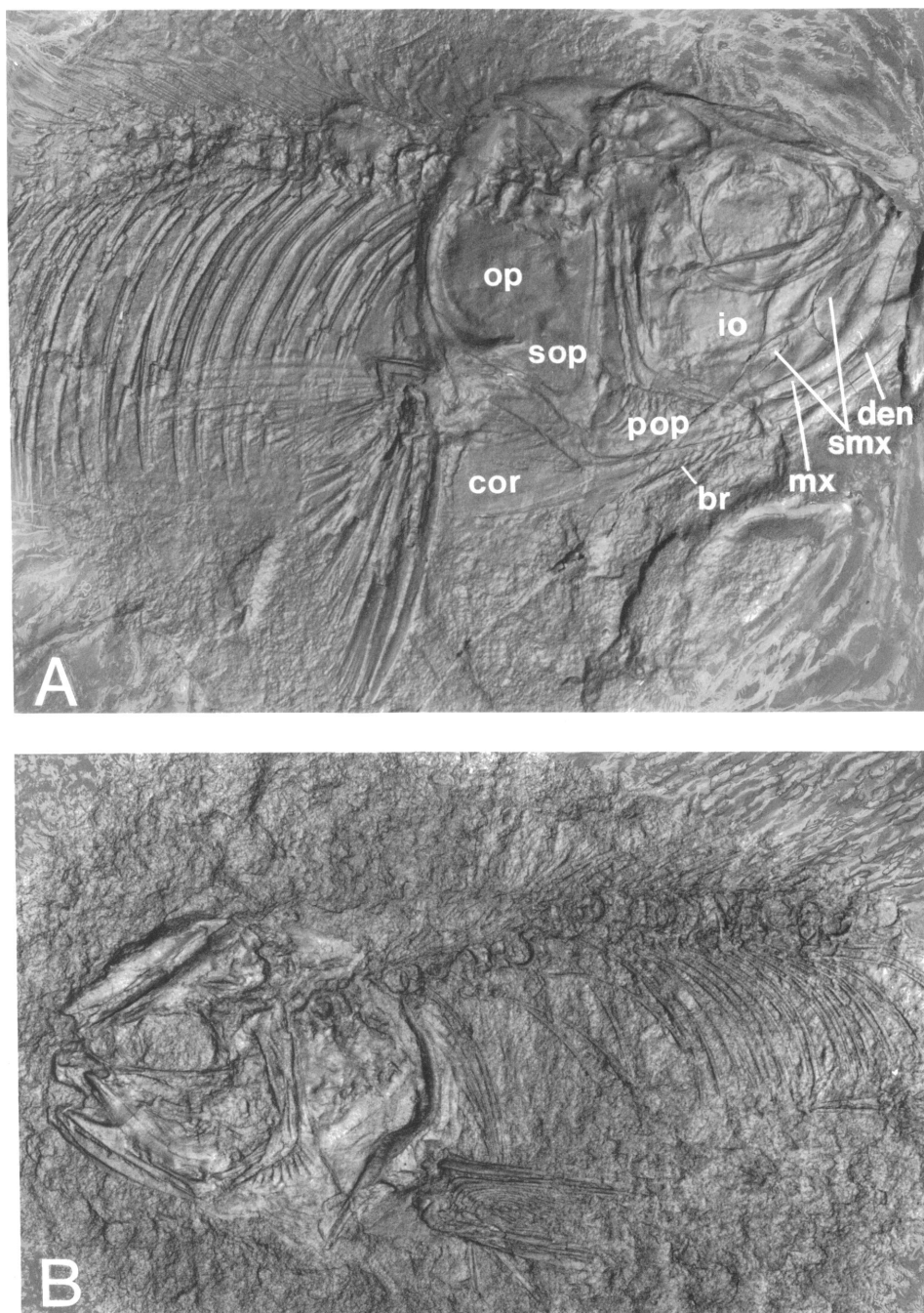


FIG. 23. *Occithrissops willsoni*. Skull in lateral aspect. A. AMNH 10964.  $\times 1.65$ . B. SDSM 54362.  $\times 2.5$ .

men is sufficiently well preserved to judge whether there was a suborbital. The quadrate

condyle lies beneath the posterior third of the orbit in *O. willsoni*, as in *A. mesogaster*; in

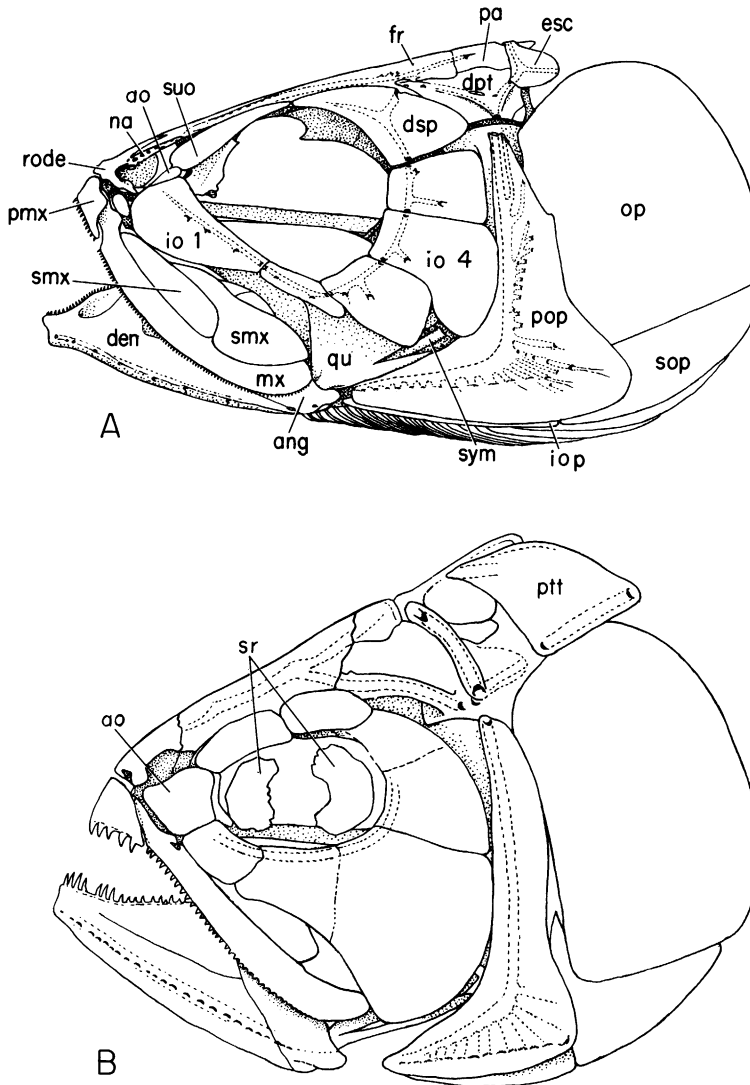


FIG. 24. Skull restorations. A. *Allothrissops mesogaster* (from Patterson and Rosen, 1977). B. *Thrissops formosus* (from Taverne, 1977).

*Thrissops* the condyle is situated farther forward, beneath or in front of the center of the orbit (Taverne, 1977).

Judging by illustrations in Nybelin (1964), Taverne (1975a, 1977), and Patterson and Rosen (1977), there is a marked difference in the jaws and dentition between *Allothrissops* and *Thrissops*. The former has small, *Lepidolepis*-like teeth and a lower jaw with a long, high coronoid process; *Thrissops* has larger, fanglike teeth set in long jaws (Taverne, 1977,

p. 17). Nybelin (1964) and Taverne (1977) noted that in *Thrissops* the teeth are smaller in *T. formosus* than in the other Jurassic species, and, in detail, it is not easy to distinguish the dentition of *T. formosus* from that of *Allothrissops* or *Occithrissops*. In *O. willsoni* (fig. 27A, B) there are about a dozen moderately large teeth on the premaxilla, and the bone has two dorsal processes, one at its medial border, and a larger one, more laterally placed. In *T. formosus* (fig. 27D) the

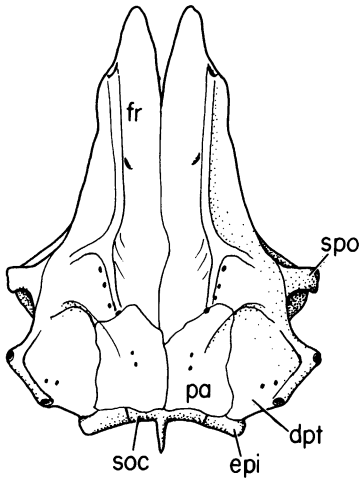


FIG. 25. *Occithrissops willsoni*. Sketch restoration of skull roof, based on AMNH 10973.  $\times 3.5$ .

premaxillary teeth are fewer (five to eight) and larger, and the bone is ovoid in outline, with a poorly marked dorsal process. In *Allothrissops* (fig. 27E–H) the premaxilla may have a medial process (*A. regleyi*, fig. 27E) or a broad dorsal process (*A. mesogaster*, fig. 27G), and the premaxillary teeth are variable

in size and number, but those of *A. mesogaster* may match those of *O. willsoni*.

The dentary teeth of *O. willsoni* (fig. 27C) are roughly equal in size along the margin of the bone, as they are in *Allothrissops* (fig. 27K, L), whereas in *T. formosus* (fig. 27I) they are somewhat enlarged in the middle of that margin. Although Taverne (1977) stated that *Thrissops* lacks a coronoid process on the dentary, none of the specimens recorded from the French or German lithographic stone shows the dentary margin in its entirety. Figure 28J shows an isolated *Thrissops* dentary which certainly possesses a coronoid process, and we assume that a similar process is present in the intact lithographic stone specimens. Thus the coronoid process is similar in *Thrissops*, *Allothrissops* and *Occithrissops*, but is placed farther back in *Thrissops* than in *Allothrissops*. In the position of the coronoid process and the length of the toothed border of the dentary, *Occithrissops* is intermediate between *Allothrissops* and *Thrissops*. In *A. mesogaster* (Patterson and Rosen, 1977, fig. 9A) the dentary tooth row is equal to about 40 percent of the length of the ventral border of the bone, whereas in *O. willsoni*

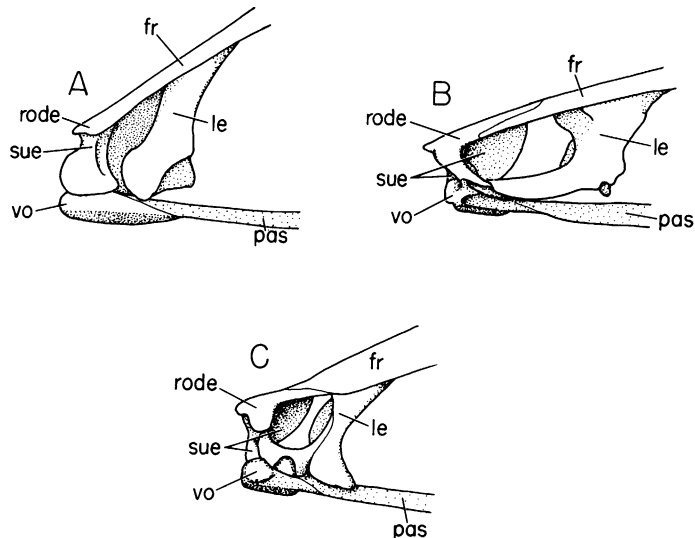


FIG. 26. Sketches to show proportions of the snout (ethmoid region of braincase) in A, *Occithrissops willsoni* (based on AMNH 10873); B, *Allothrissops mesogaster* (after Patterson and Rosen, 1977, fig. 7A); C, *Thrissops formosus* (based on Taverne, 1977, fig. 6), with additions after *Cladocyclus* (Patterson and Rosen, 1977, fig. 6A).



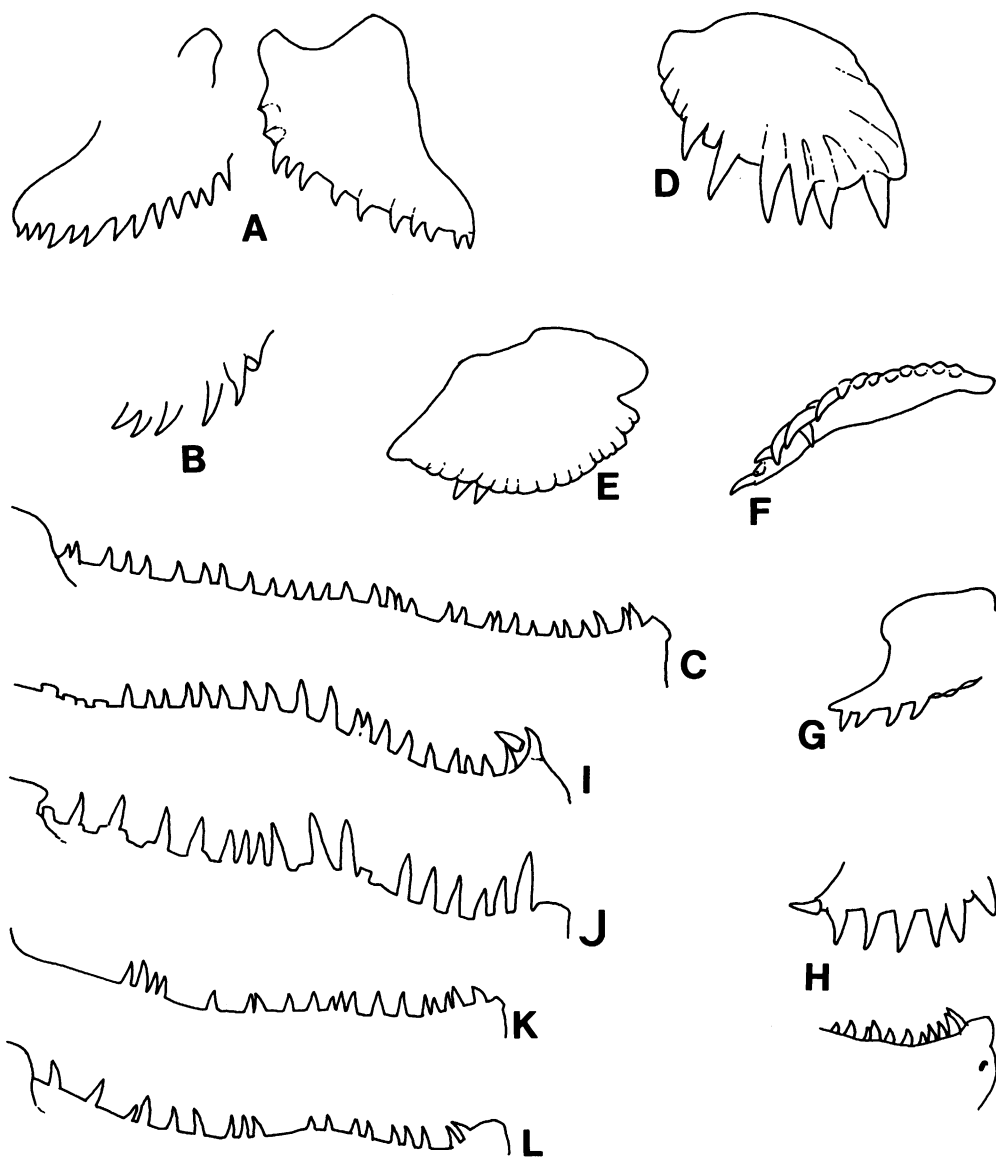


FIG. 27. Comparison of dentitions in ichthyodectiforms. A–C. *Occithrissops willsoni*: A, premaxillae of AMNH 10976; B, left premaxillary teeth of AMNH 10984; C, dentary margin of AMNH 10973. D. *Thrissops formosus*, right premaxilla (preserved in impression) of BMNH P. 3684. E. *Allothrissops regleyi*, right premaxilla of BMNH P. 918. F–H. *Allothrissops mesogaster*: F, right premaxillary teeth from below of BMNH P. 915; G, posterior part of right premaxilla of BMNH P. 3680b; H, right premaxillary teeth and anterior part of dentary margin of BMNH P. 3680a. I. *Thrissops formosus*, right dentary margin (medial view, reversed) of BMNH P. 3684. J. *Thrissops* sp., margin of isolated left dentary (reversed) of BMNH P. 54599. K, L. *Allothrissops mesogaster*: K, margin of right dentary (medial view, reversed) of BMNH P. 916; L, margin of left dentary (reversed) of BMNH P. 915. A–C, from Sundance Formation, Hulett, Wyoming; D, F–I, K, L, from Lithographic Stone, Bavaria; E, from Lithographic Stone, Cerin, Ain, France; J, from Kimmeridge Clay, Encombe, Dorset, England. Not to scale.

(fig. 28A) this ratio is about 45 percent and in *T. formosus* about 55 percent.

In both *Thrissops* and *Allothrissops* the distal ceratohyal is deep, with a large fenestra

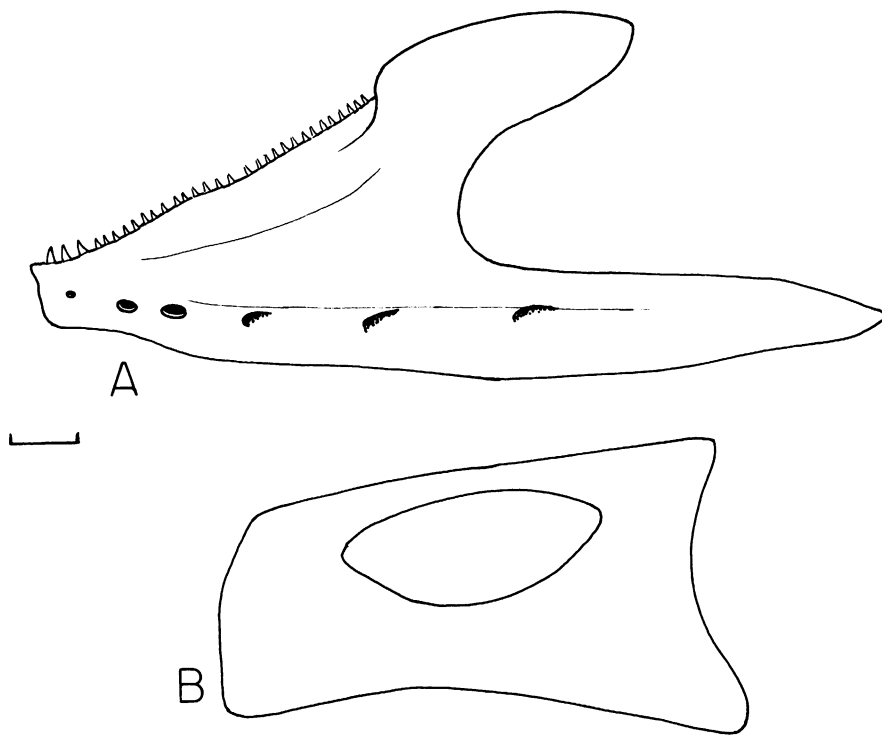


FIG. 28. *Occithrissops willsoni*. A. Left dentary in lateral view, based on AMNH 10973. B. Outline of distal ceratohyal, from AMNH 10962. Bar equals 1 mm.

(Patterson and Rosen, 1977, fig. 9B; Taverne's (1977, fig. 10) restoration of the ceratohyal of *T. formosus* lacking a fenestra is incorrect). *Occithrissops willsoni* also has a deep, fenestrated ceratohyal (fig. 28B). In *O. willsoni*, AMNH 11435 shows 17 branchiostegal rays, 13 on the distal ceratohyal, two or three on the gap between distal and proximal ceratohyals, and only one or two on the proximal ceratohyal (there may have been more branchiostegals posteriorly). The first 11 or 12 branchiostegals are slender and threadlike, and only the last three are spathiform. In *A. mesogaster* there are 18 branchiostegals, 11 on the distal ceratohyal, and the last three are spathiform (Patterson and Rosen, 1977, p. 102). *Thrissops formosus* has 20 branchiostegals (Taverne, 1977, fig. 10), 12 on the distal ceratohyal, and the last four are spathiform.

In the ventral limb of the preopercular, *O. willsoni* has eight to 10 sensory canal branches. *Thrissops formosus* also has about 10,

whereas *A. mesogaster* has 11–14 (Patterson and Rosen, 1977, fig. 5; Nybelin, 1964, pl. 9, fig. 3). As in both *Thrissops* and *Allothrissops*, there is a marked posterior expansion of the preopercular at the angle in *O. willsoni*.

**AXIAL SKELETON:** In the smallest available individual of *O. willsoni* (AMNH 10982, 49 mm SL) there are about a dozen ventral hemichordacentra extending from PU6 forward to the origin of the anal fin. The two ural chordacentra are also calcified, but there are no other centra. In somewhat larger specimens (AMNH 10873, 64.5 mm SL, and AMNH 11435, estimated SL 80 mm) there are cylindrical chordacentra throughout the column. In still larger specimens (SDSM 54362, 93 mm SL, and AMNH 10949, estimated SL 96 mm) there is evidence of perichondral bone on the surface of the chordacentra, and in the largest specimens (Holotype AMNH 10964, 200 mm SL, figs. 22A, 29) the centra are well ossified. In *Allothrissops* there are perichordal additions to the chor-

dacentra in specimens over about 30 mm SL; in the Jurassic *Thrissops* small individuals are not recorded (Nybelin, 1964).

In *O. willsoni* there are 58 vertebrae, 33–34 abdominal, 22–23 caudal, and two ural. In *Allothrissops mesogaster* there are 57–61 (31–33 + 24–27 + 2) vertebrae, and in *Thrissops formosus* there are 57–59 (33–35 + 24–26 + 2). In *O. willsoni* all the neural arches, haemal arches, and parapophyses are apparently autogenous. In *A. mesogaster* most of the caudal haemal arches are fused with the centra in large individuals. Patterson and Rosen (1977, p. 115) used this character as a synapomorphy to distinguish the suborder Allothrissopoidei (*Allothrissops* only) from the Ichthyodectoidei, including *Thrissops*. However, we suspect that some of the caudal haemal arches may fuse with the centra in large individuals of *T. formosus* and *T. subovatus*.

In *O. willsoni* there are long epineurals on the abdominal and first two or three caudal neural arches, a series of supraneurals from the occiput back to about the twenty-seventh vertebra, and the neural spines are paired from the occiput back to about the twenty-eight vertebra. In *A. mesogaster* and *T. formosus* the paired neural spines and supraneurals extend farther posteriorly. There are supraneurals back to the first or second caudal vertebra in *A. mesogaster*, and in BMNH 37043 the first median neural spine is on vertebra 35. *Thrissops formosus* has supraneurals back to vertebra 37 (Taverne, 1977, fig. 11). According to Nybelin (1964, p. 35), there is a difference between *Allothrissops* and *Thrissops* in the form of the ribs, which he believed are stout and thickened dorsally in *Thrissops* and slender throughout in *Allothrissops*. However, we are not convinced that there is a real difference here; the ribs appear to be similar in *Allothrissops*, *Thrissops*, and *Ocithrissops*.

**PAIRED FINS:** There are no notable differences between the pectoral girdle and fin of *A. mesogaster* (Patterson and Rosen, 1977, fig. 10) and *T. formosus* (Taverne, 1977, fig. 5). In *O. willsoni* the girdle is similar, so far as it is known, and shows the same massive coracoid as in *Allothrissops* and *Thrissops*. The pectoral fin of *O. willsoni* contains at least 14 rays, the first three of which are stout

and segmented only toward the tip, where the second and third rays split up into fine branches. The pectoral fin occupies about half the distance between its insertion and that of the pelvic.

In *O. willsoni* the pelvic fin originates beneath vertebra 26–28, and contains nine rays which extend over the length of five or six vertebrae. The pelvic is similar in *A. mesogaster* and *T. formosus*.

**UNPAIRED FINS:** The dorsal fin of *O. willsoni* originates behind the anal, opposite vertebra 39–40, and with its first radial ending proximally behind neural spine 36. The fin contains three unbranched, and 10 or 11 branched rays that insert on 10 or 11 radials. The first is bifid proximally and has an anterior process extending from its head. The dorsal fin is not significantly different in *A. mesogaster* and *T. formosus* (Nybelin, 1964; Taverne, 1977).

The anal fin of *O. willsoni* originates beneath vertebra 37–38, with its first radial ending proximally in front of the haemal spine of vertebra 34–35. The fin contains four or five unbranched, and 18–20 branched rays that insert on 18–20 radials. The fin is falcate, with the longest ray equal in length to seven or eight caudal vertebrae. In *A. mesogaster* the anal contains four or five unbranched rays and about 25 branched rays, inserting on 24–27 radials. The first radial ends in front of the haemal spine of vertebra 32–33, and the fin originates under vertebra 36–37. In *T. formosus*, the anal contains four or five unbranched rays and about 30 branched rays, which insert on 29–32 radials. The first radial ends in front of the haemal spine of vertebra 33–35, and the fin originates under vertebra 38–42 (Taverne, 1977). The anal is falcate in both *Allothrissops* and *T. formosus*, but more strongly so in the latter (Nybelin, 1964): the longest anal ray is equal in length to about eight caudal vertebrae in *T. formosus* and to about four in *A. mesogaster*, *A. salmoneus*, and *A. regleyi*. The anal fin of *O. willsoni* (18–20 radials) is therefore shorter than that of *Allothrissops* (24–30 radials) and *T. formosus* (29–32 radials), but closer in form to that of *T. formosus*, since its longest rays are equal in length to seven or eight vertebrae.

**CAUDAL SKELETON AND FIN:** The caudal skeleton of *O. willsoni* is best preserved in

the holotype (AMNH 10964, fig. 29), but parts of it are also visible in AMNH 10873, 10949, and 10990. The caudal skeleton is generally similar to that of *A. mesogaster* (Taverne, 1975a, fig. 14; Patterson and Rosen, 1977, figs. 17, 18) and *T. formosus* (Patterson and Rosen, 1977, fig. 14; Taverne, 1977, figs. 14, 15) except for a striking difference in the form of the uroneurals. One synapomorphy of the Ichthyodectiformes recognized by Patterson and Rosen (1977, p. 115) is described as "six or seven uroneurals, the first three or four extending anteroventrally to cover the entire lateral surface of the first, second, or third preural centra." As figure 29 shows, this condition is not found in *O. willsoni*, for the lateral surface of the preural centra is exposed beneath the uroneurals, which occupy the dorsolateral position normal in leptolepids and other generalized teleosts (Patterson and Rosen, 1977). Among the four specimens of *O. willsoni* showing the uroneurals, there is one (AMNH 10949) in which the anterior ends of the first four uroneurals do cover the lateral surfaces of U1–PU2, but the bones appear to be disarticulated post mortem. The other two specimens show the same configuration as in figure 29. In all four specimens the tips of the first four uroneurals are regularly spaced, each ending close to the anterior margin of a centrum in the sequence U1 and PU1–3 (fig. 29). This condition also contrasts with that in *Allothrissops* and *Thrissops*, where three or four bunched uroneurals extend forward to PU2. Regular spacing of the tips of the uroneurals is general in leptolepids and in *Pachythrissops* (Patterson and Rosen, 1977, figs. 33, 35, 45, 46, 51).

The neural arches of the ural and last few preural centra are poorly preserved in *O. willsoni*, and only AMNH 10964 (fig. 29) shows them at all completely. In that specimen these neural arches are difficult to assign to centra since the last three (labeled NPU1–NPU3) appear to end above the junctions between centra. In *Allothrissops* and *Thrissops* the neural arches and spines are variable in this region (Patterson and Rosen, 1977, p. 110; Taverne, 1977, p. 26), but since there is never a full-length neural spine on PU1, we assign the last such spine in AMNH 10964 to PU2, and assume that this centrum (or PU3) bore two neural arches.

In *O. willsoni* the two lower hypurals show the configuration typical in ichthyodectiforms (cf. fig. 29 and Patterson and Rosen, 1977, p. 106). AMNH 10964 has eight hypurals (fig. 29), again as in *Allothrissops* and *Thrissops*, and there are three epurals as in those genera.

The caudal fin of *O. willsoni* contains 19 principal rays, of which 17 are branched. There are eight upper and seven lower procurrent rays (fig. 29). The fin formula is similar to that in *Allothrissops* and *Thrissops*. There is a single urodermal in *O. willsoni* (AMNH 10966), as in *T. formosus* and some individuals of *A. mesogaster* (Patterson and Rosen, 1977, p. 113). According to Nybelin (1964), the caudal fin is larger and more deeply forked in *Thrissops* than in *Allothrissops*, and the lower lobe is longer than the upper in *Thrissops*, whereas the two lobes are equal in *Allothrissops*. In *O. willsoni* the caudal fin is weakly forked as in *Allothrissops*, but in all five specimens where the tail is intact, the lower lobe is longer than the upper. The excess length of the lower lobe is only 2–4 percent that of the upper in AMNH 10992 and 10966, but is 13–15 percent in AMNH 10960, 10974, and 10993. However, in *Allothrissops* we find a similar excess of 10–15 percent in the length of the lower caudal lobe.

**SQUAMATION:** The scales of *O. willsoni* are not particularly well preserved, but show nothing to differentiate them from those of *A. mesogaster* and *T. formosus*. As in those species, *O. willsoni* had one scale row to each vertebra.

**DIET:** Gut contents are preserved in several specimens of *O. willsoni*. As in *Allothrissops* (Patterson and Rosen, 1977, p. 115), they are in the form of amorphous phosphatic matter, suggesting a microphagous diet. Swallowed prey are known in *Thrissops* (Nybelin, 1958), indicating a predatory habit.

#### RELATIONSHIPS OF *OCCITHRISOPS*

Patterson and Rosen (1977, p. 115) have defined the order Ichthyodectiformes by five characters: (1) floor of nasal capsule with an ethmo-palatine ossification that articulates with the palatine; (2) six or seven uroneurals with the first three or four extending anteroventrally to cover the sides of the first to third

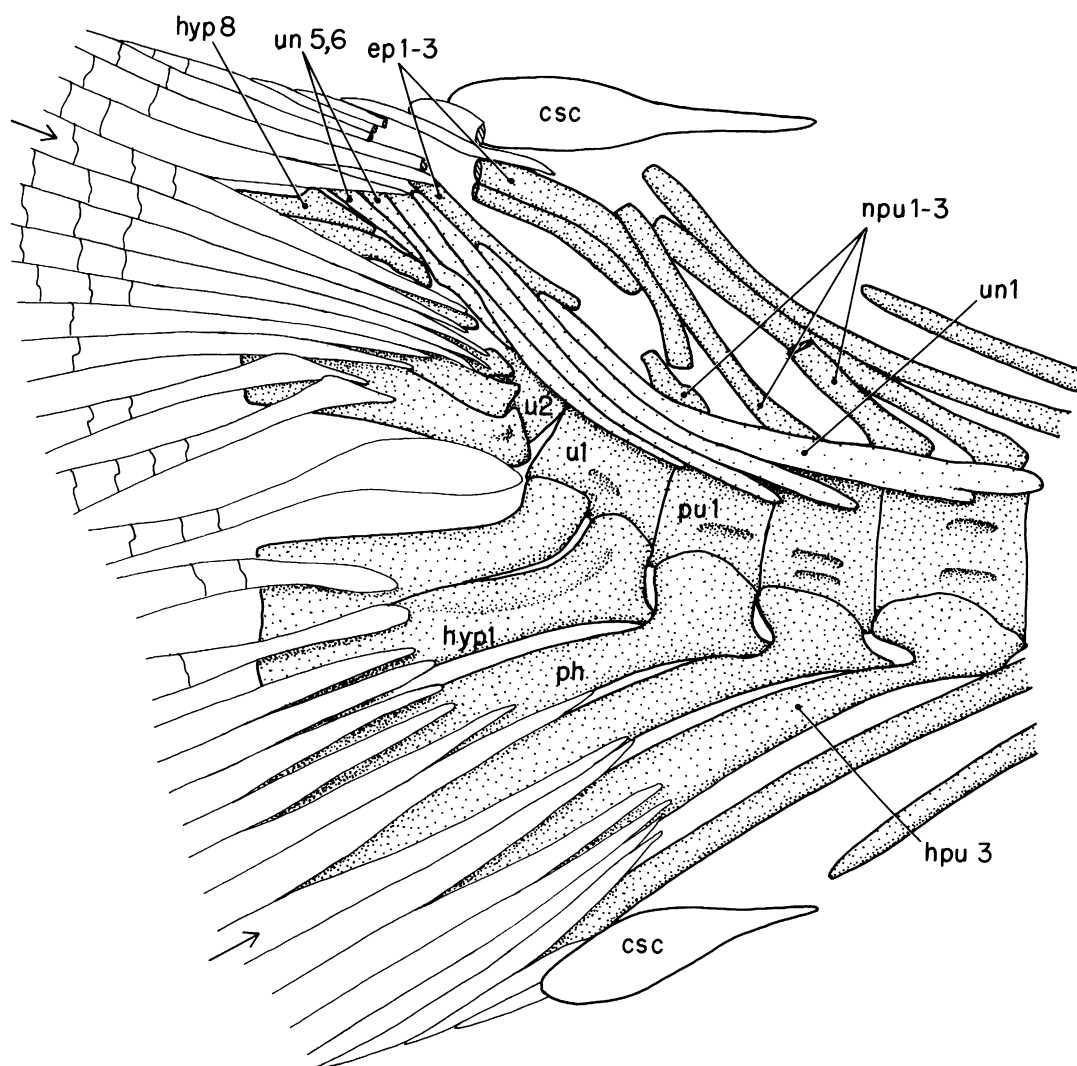


FIG. 29. *Occithrissops willsoni*. Caudal skeleton as preserved in the holotype, AMNH 10964.  $\times 7.5$ . From Hulett, Wyoming.

preural centra; (3) teeth in a single series in the jaws; (4) coracoid enlarged and meeting its fellow in a midventral symphysis; and (5) anal fin long, falcate, and opposed by a short, remote dorsal fin. *Occithrissops willsoni* shares characters 3, 4, and 5 with the ichthyodectiforms, but lacks character 2. The condition of character 1 remains unknown. Unfortunately, the characters shared by *Occithrissops* and the ichthyodectiforms are not unique to these fishes and thus do not demonstrate that *Occithrissops* is an ichthyodectiform. There are, however, detailed resemblances between

*Occithrissops*, *Allothrissops*, and/or *Thrissops* in the dentition (fig. 27) and fin structure, which provide evidence that *Occithrissops* is, in fact, an ichthyodectiform.

Within the ichthyodectiforms Patterson and Rosen (1977) have established two suborders, the Allothrissopoidei (the Upper Jurassic *Allothrissops* only) and the Ichthyodectoidei (Upper Jurassic-Cretaceous *Thrissops* and 10 other Cretaceous genera). If these two suborders are sister groups, there are only three possible positions for *Occithrissops* within Ichthyodectiformes: it is an



*cithrissops* and *Allothrissops*, but characters 1 and 6 imply that *Occithrissops* may be closer to *Thrissops* and the ichthyodectoids than is *Allothrissops*, whereas characters 3, 4, 5, and perhaps 2, suggest that *Allothrissops* may be closer to *Thrissops* and other ichthyodectoids than is *Occithrissops*, or, in other words, that *Occithrissops* is the sister group of *Allothrissopoidei* + *Ichthyodectoidei*. The presence of character 4 in *Thrissops curtus* indicates that this feature is not universal in ichthyodectoids (*T. curtus* appears to be an ichthyodectoid because it has a triangular supraoccipital crest and a serrate-margined basal sclerotic bone; cf. Patterson and Rosen, 1977, p. 115). Character 2 (persistence of chordacentra) can hardly be considered a primitive feature in *Occithrissops*, as this evaluation would imply that perichordal centra arose independently in ichthyodectiforms and other teleosts. If characters 2 and 4 are excluded, we have two characters relating *Occithrissops* to ichthyodectoids (proportions of head and falcate median fins), and two relating *Allothrissops* to ichthyodectoids (long series of supraneurals and long anal fin). The first pair of characters seems more likely to be significant, but we are unwilling to resolve the incongruence without more knowledge of *Occithrissops* and of other Late Jurassic and Early Cretaceous ichthyodectiforms. For the present, we place *O. willsoni* as *Ichthyodectiformes incertae sedis*. We justify erection of the new genus *Occithrissops* for the reason that it shows no indication of close relationship to any other ichthyodectiform genus, and differs from all by the characters given in the diagnosis above.

#### TELEOSTEI INCERTAE SEDIS

##### TODILTIA, NEW GENUS

TYPE SPECIES: *Leptolepis schoewei*.

DISTRIBUTION: Lower Callovian, Colorado, and New Mexico.

ETYMOLOGY: For the Todilto Limestone.

DIAGNOSIS: Middle Jurassic teleostean fishes of leptolepid grade, but differing from similar fishes in having only chordacentra until late in growth. The chordacentra receive perichordal additions only in the midcaudal region, and only in the largest specimens. About 50 vertebrae, 30 abdominal. Dorsal

fin in the middle of the back with about 16 rays; anal originates beneath posterior edge of dorsal, with about 14 rays; pelvics beneath dorsal origin, with about 12 rays. No bone-enclosed rostral commissure or rostral pit-line; supraorbital sensory canal not meeting infraorbital, and with three medial and two lateral branches above the rear of the orbit. Anterior pit line on parietal, but probably no middle pit line. Infraorbital sensory canal with four branches in lacrimal, none in second infraorbital, two or three in third, two in fourth, and one in fifth. No suborbital. Eight to 12 sensory canal branches in preopercular. Maxilla toothed throughout its length; teeth larger on premaxilla than on maxilla. In lower jaw, dentary with a few teeth and a high coronoid process; angular and retroarticular fused; sensory canal enters medial face of postarticular process. About 15 branchiostegal rays, no gular. No pelvic splint. Paired neural spines and unpaired supraneurals present from occiput back to beneath dorsal fin, so that supraneurals lie between the first few dorsal radials; epineurals on abdominal and first few caudal neural arches; five to seven pairs of epipleurals present in region of abdominal/caudal transition. Caudal skeleton with two free ural centra, six uroneurals, eight or nine hypurals, three epurals, one dorsal fringing fulcrum and two urodermals. Two scale rows to each vertebra.

##### *Todiltia schoewei* (Dunkle)

Figures 31–36

*Leptolepis schoewei* Dunkle, 1942, p. 62, pl. 6.

"*Leptolepis*" *schoewei* Dunkle; Schultze and Enciso, 1983, p. 1053, fig. 3.

HOLOTYPE: KUMVP No. 784, a juvenile fish 36 mm in SL from Felch Creek, 15 m (24 km) north of Canon City, Colorado.

DIAGNOSIS: As for genus; only species.

REFERRED SPECIMENS: From Wanakah Formation, Pony Express Limestone Member, Piedra River Canyon, Colorado: AMNH 11457. From Wanakah Formation, Todilto Limestone Member, near Hot Springs, New Mexico: AMNH 9832, 11489, 11490. From Wanakah Formation, Todilto Limestone Member, Bull Canyon area, New Mexico: NMNH 8551, 17899, 17903, 17907; BHI P3, P4, P5, 951. From Wanakah Formation, To-

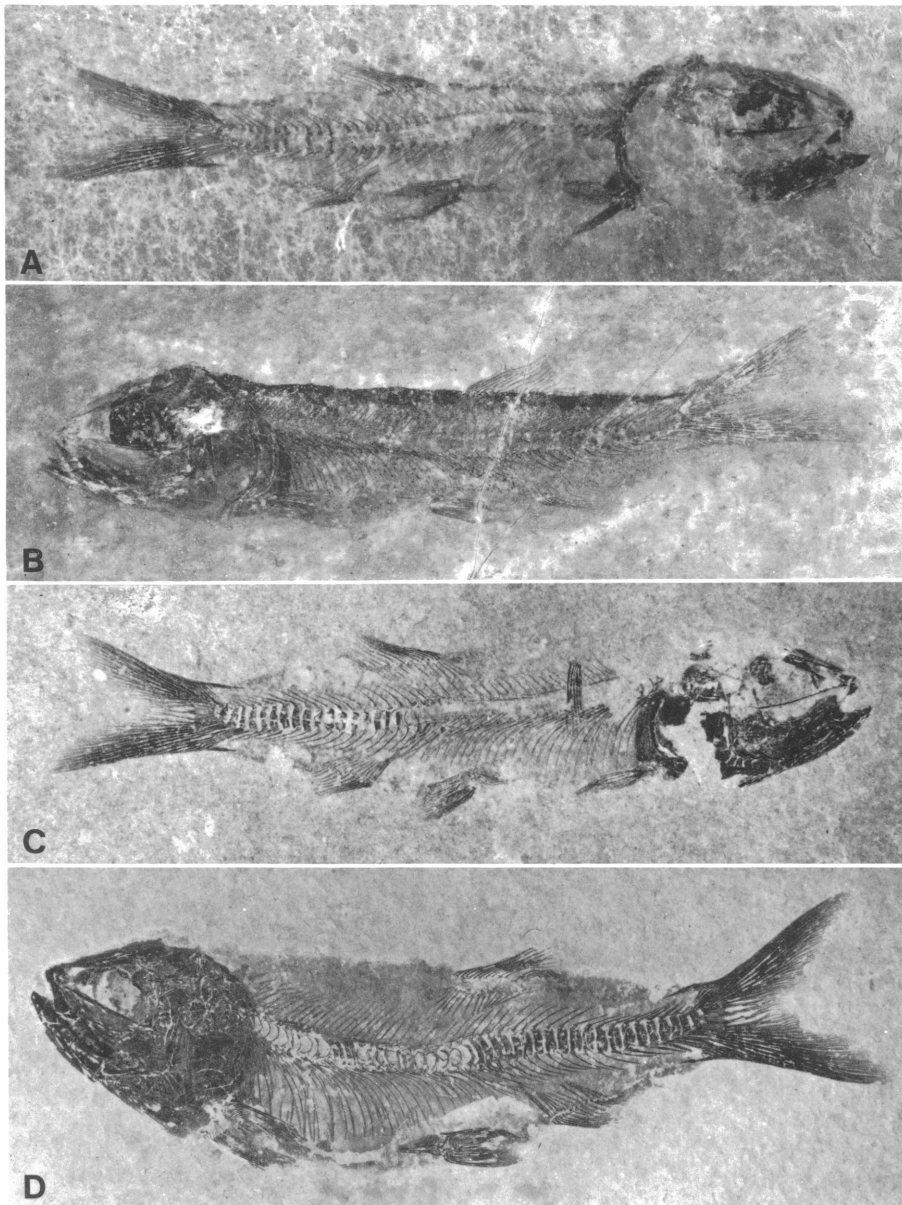


FIG. 31. *Todiltia schoewei*. Growth series (SL). A, AMNH 17899, 40 mm; B, NMNH 9832, 37 mm; C, AMNH 11487, 48 mm; D, AMNH 11488, 66 mm. A, from Bull Canyon, N.M.; B, from Hot Springs, N.M.; C and D, from Merrill Ranch, N.M.

dilto Limestone Member, Merrill Ranch, New Mexico: AMNH 11487, 11488, 14495, 11496, 11508, 11516.

COMMENTARY: Throughout the following description and discussion of *Todiltia* we compare *Todiltia schoewei* with leptolepids

and with “*Leptolepis*” species. Our usage needs explanation. The Leptolepididae are known to be a polyphyletic grade taxon (e.g., Patterson and Rosen, 1977). Traditionally, *Leptolepis* and the leptolepids are generalized Jurassic and Early Cretaceous teleosts, with



small, feebly-toothed mouths, thin, cycloid scales, and unmodified fins. At least 50 nominal species of *Leptolepis* have been described. During the last two decades, the trend has been toward assigning these species to new or revived genera, mostly monotypic, including: *Aethalionopsis* Gaudant, *Ascalabos* Münster, *Clupavus* Arambourg, *Leptolepides* Nybelin, *Nybelinoides* Taverne, *Paraclupavus* Saint-Seine and Casier, *Pattersonella* Taverne, *Pholidolepis* Nybelin, *Proleptolepis* Nybelin, *Pseudoleptolepis* Taverne, *Seefeldia* Nybelin, *Tharsis* Blainville, and *Wenzichthys* Taverne. Some of these genera have been shown to be related to higher teleosts (*Clupavus*, *Leptolepides*, *Nybelinoides*, *Pattersonella*, *Tharsis*, *Wenzichthys*). Others are less closely related to Recent teleosts than is the type species of *Leptolepis*, the Toarcian *L. coryphaenoides* Bronn (*Pholidolepis*, *Proleptolepis*, *Seefeldia*). There remains a residue of nominal species of *Leptolepis*, comprising two suites. The first includes comparatively well-known species (reviewed by Nybelin, 1974; Taverne, 1975a, 1975b; Patterson and Rosen, 1977) whose relationships are "somewhere in the region" of *L. coryphaenoides*. Yet even in this restricted sense, *Leptolepis* remains polyphyletic (Patterson and Rosen, 1977). Finally, there is a second suite of poorly known *Leptolepis* species whose relationships are unknown. Our study of *L. schoewei* removes it from this second suite, but shows that it falls into the first, *Leptolepis sensu* Nybelin (1974). Since we believe that genus to be polyphyletic, we have two alternatives. The first is to refer to *L. schoewei* and other members of *Leptolepis sensu* Nybelin (apart from the type species) as "*Leptolepis*"; the second is to continue the trend of dismembering "*Leptolepis*" into monophyletic or monotypic genera. We have decided to make the new genus *Todiltia* for *L. schoewei*, and to refer only *L. coryphaenoides* (and the closely related or synonymous *L. normandica*) to *Leptolepis sensu stricto*. We will refer to *Leptolepis sensu* Nybelin as "*Leptolepis*," and to *Leptolepis sensu lato* as "leptolepids." Nybelin (1974) restricted the Leptolepididae to the three genera *Leptolepis sensu* Nybelin, *Proleptolepis*, and *Tharsis*. That assemblage is, however, polyphyletic (Patterson and Ro-

sen, 1977, p. 54), and, in our view, serves no useful purpose. By "leptolepid," we do *not* mean Leptolepididae *sensu* Nybelin, or *sensu* Taverne (e.g., 1975a, 1975b).

Summarizing our usage:

1. *Leptolepis* = *L. coryphaenoides* and *L. normandica*.
2. "*Leptolepis*" = other species of *Leptolepis sensu* Nybelin (1974) and Taverne (1975a, 1975b).
3. leptolepid = *Leptolepis sensu lato*, not Leptolepididae *sensu* Nybelin or Taverne.

## DESCRIPTION

MEASUREMENTS AND PROPORTIONS: See table 1.

SKULL: A sketch restoration of the head is shown in figure 32. Nothing is known of the braincase, except that there were separate pterospheneoids and an orbitospheneoid, a well-ossified lateral ethmoid, and a mesethmoid of typical leptolepid form (Patterson, 1975, figs. 127, 128, 130, 131). The dermal component (rostrodermethmoid) has a pair of strong posterolateral processes forming the anterior wall and the floor of the nasal pit. There is no sign of a rostral commissure or pitline. It is not known whether the parasphenoid bore teeth and a basipterygoid process, as it does in other leptolepids.

The skull roof is imperfectly known, but appears similar to that of other leptolepids (Cavender, 1970, fig. 1; Nybelin, 1974, figs. 1, 4, 23, 29; Patterson, 1975, fig. 147; Patterson and Rosen, 1977, figs. 34, 49). The supraorbital sensory canal in the frontal runs to the posterior margin of the bone, as is usual in leptolepids. Above the posterior part of the orbit the canal gave off three medial and two lateral branches. These are fewer branches than in *Tharsis dubius* (Patterson and Rosen, 1977, fig. 147) or in the Callovian "*Leptolepis*" (Patterson, 1975, fig. 147), but more than in *Leptolepides sprattiformis* (Patterson and Rosen, 1977, fig. 49). There was evidently no postorbital connection between the infra- and supraorbital canals. On the parietal, the line of the supraorbital canal is continued by a shallow anterior pit line groove. There is no sign of a middle pit line but the

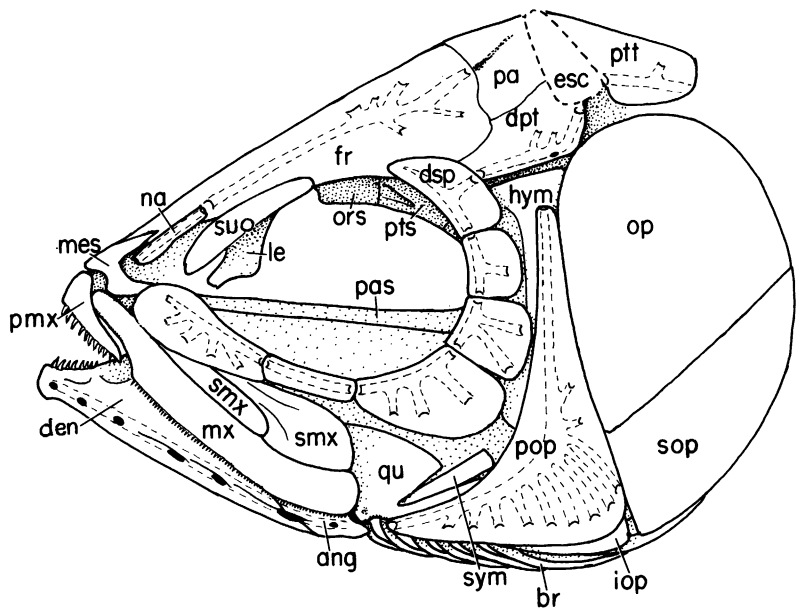


FIG. 32. *Todiltia schoewei*. Restoration of skull in lateral aspect.

preservation in this area is poor. The nasal is a slender, tubular bone.

The circumorbital bones are fairly well preserved in several specimens, and follow the standard pattern of a triangular dermosphenotic (dsp), three broad infraorbitals (io 3–5) behind the orbit, a slender one (io 2) below it, a triangular lacrimal (io 1), and a single large supraorbital (suo). The small antorbital present between the supraorbital and lacrimal in other leptolepids has not yet been recognized in *Todiltia*. The infraorbital sensory

canal has one bone-enclosed branch in io 5, two in io 4, two (USNM 17907) or three (AMNH 11508) in io 3, none in io 2, and four in the lacrimal. There is no indication of a suborbital behind io 5, and we assume that this bone was absent.

The upper jaw also follows the usual leptolepid pattern, with a small premaxilla and a long, curved maxilla, each with teeth along the oral margin. The teeth are larger on the premaxilla than on the maxilla. There are two supramaxillae, the anterior long and slender,

TABLE 1  
*Todiltia schoewei*, Counts and Measurements  
(SL in millimeters, other measurements as percentage of SL.)

Specimen	SL	Total length	Max. trunk depth	Head length	Head depth	Abdominal vertebrae	Caudal vertebrae	Number of epipleurals	Dorsal fin-rays	Dorsal radials	Anal fin-rays	Anal radials
NMNH 17899	37	124	18	35	24	?30	18+2	5	iv, 13	13	iii, 11	12
AMNH 11487	48	123	24	32	22	—	18+2	7	iv, 12	13	iii, 11	12
AMNH 11508	60	123	25	34	25	28+	18+2	8	iv, 13	14	iii, 11	12
AMNH 11488	66	120	29	32	23	30	18+2	8	iv, 13	14	iii, 11	12
NMNH 17907	78.5	118	22	31	24	—	18+2	7	iv, 13	—	—	12

and the posterior with a pointed process above the anterior. The visible parts of the palate show nothing remarkable. No teeth are evident on the palate, but preservation may be inadequate. In the lower jaw, the dentary bears a few teeth, about equal in size and number to those on the premaxilla. Behind these teeth, the dentary rises in the long, high coronoid process normal in leptolepids. The mandibular sensory canal opens by three pores on the lateral surface of the anterior part of the dentary, two large pores on the ventral surface of the tube in the dentary, a pore at the suture between dentary and angular, and one small pore on the angular. The angular has a well-developed postarticular process, and the point of entry of the sensory canal is on the medial face of this process (cf. Patterson and Rosen, 1977, fig. 32). The retroarticular and angular appear to be fused in the only specimen in which the inner face of the lower jaw is partially visible (AMNH 11488, a large individual, SL 66 mm). We assume that this fusion was ontogenetic (cf. Patterson and Rosen, 1977, fig. 32).

Nothing is known of the hyoid or gill arches. There are at least 13 branchiostegal rays (AMNH 11488) and possibly as many as 16 (AMNH 11508). There is no indication of a gular, despite Dunkle's (1942, p. 62) mention of "a relatively large median gular plate." The shape of the preopercular and opercular bones is shown in figure 32. The number of branches of the preopercular sensory canal is variable, probably in part as the result of ontogenetic multiplication of branches, as inferred by Nybelin (1974) in other leptolepids, and as described by Allis (1889) in *Amia*. In NMNH 17899 (37 mm SL) there are eight branches, six of them on the lower limb of the bone, and in AMNH 11487 (48 mm SL) there are also six branches on the lower limb. In AMNH 11508 (60 mm SL) there are 11 branches in all, eight on the lower limb, whereas in AMNH 11488 (66 mm SL) there are also 11 branches in all, but nine on the lower limb. NMNH 8551 (64 mm SL) also has nine branches on the lower limb, and NMNH 17907 (78.5 mm SL), the largest specimen, has 10 branches on the lower limb. There is no indication of a suprapreopercular bone.

**AXIAL SKELETON:** Whereas the skull and fin skeleton of *Todiltia* show nothing remarkable in comparison with leptolepids, the axial skeleton differs strikingly from that of most species ascribed to "*Leptolepis*." In two specimens where the vertebrae are accurately countable (AMNH 11488 and NMNH 17907), there are 50 vertebrae, 30 abdominal, 18 caudal, and two ural centra. All specimens show 18 caudal vertebrae. There is marked variation, assumed to be ontogenetic, in the vertebral centra. In the smallest specimens, such as AMNH 11495 (SL 28 mm) there are no centra at all. In slightly larger specimens, such as AMNH 9832 and NMNH 17899, both SL 37 mm long, only the second ural centrum in AMNH 9832 is calcified. There are two cylindrical ural centra in NMNH 17899 plus separate dorsal and ventral hemicentra in PU1, a slender centrum or hemicentrum tapering dorsally above HPU3 (fig. 34), and eight delicate centra extending from PU5 to PU12. Those of PU7-8 are the widest of this series.<sup>4</sup> AMNH 9832 (fig. 31A) (SL 40 mm) has slender ventral hemicentra extending forward from the ural centra to PU 11, but has no obvious dorsal hemicentra, except perhaps in PU6. AMNH 11487 (fig. 31C) (SL 48 mm) has cylindrical centra forward from U2 to PU16. Those of PU6-8 are the widest centra in this series, and as preserved, PU3-9 or 10 show a vertical split in the middle of the centrum. Also in this specimen, PU17 is represented by two hemicentra, preserved as left and right, and in PU18 there are two minute, spindle-shaped hemicentra, again preserved as left and right. In all these small individuals, the uncalcified part of the vertebral column was occupied by a wide, unconstricted notochord. From the mode of calcification of the centra (which occurs long after ossification of the neural and haemal arches in the form of crescentic hemicentra), and their dense, acellular structure,

<sup>4</sup> It is possible that the pattern of centra in NMNH 17899, with a gap between PU1 and PU5 occupied only by one incomplete centrum, is abnormal, since the neural and haemal arches are "out-of-step" (fig. 34). The centrum above HPU3 passes toward a neural arch, which shows features of both NPU2 and NPU3 in other specimens and has a gap behind it, so that it counts as NPU2.

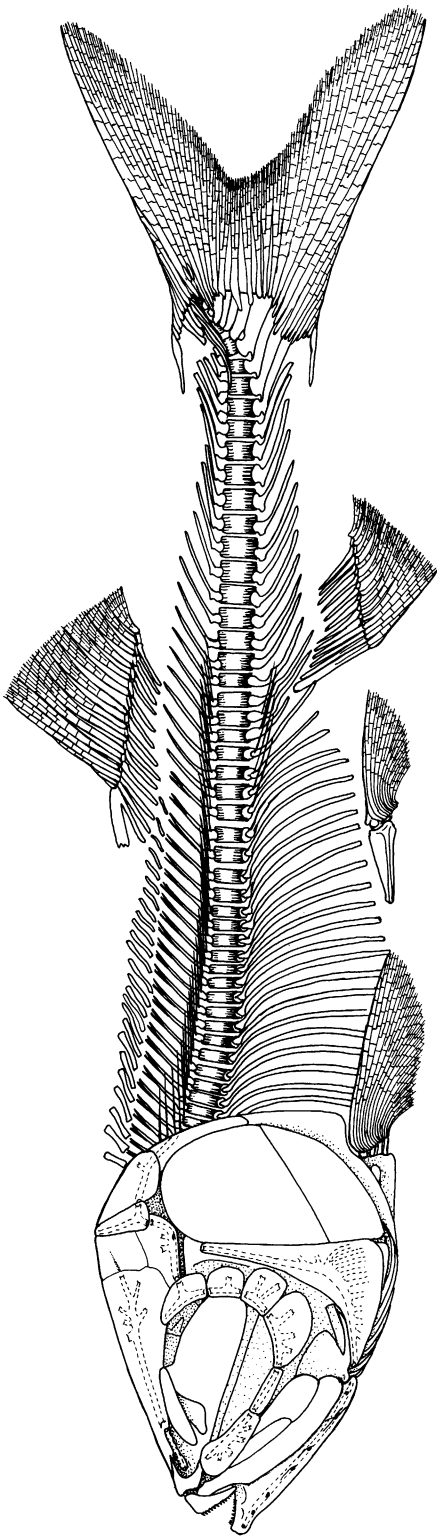


FIG. 33. *Todiltia schoewei*. Restoration of entire skeleton.

we assume that they are chordacentra (cf. François, 1966, on *Salmo*).

In larger specimens (59–78 mm SL) (e.g., fig. 31D) the whole vertebral column is occupied by cylindrical chordacentra, and at least those in the caudal region (those first calcified) are slightly hourglass-shaped, so that the notochord was slightly constricted in the middle of each centrum. As noted, the centra in the midcaudal region, roughly PU3–10, usually show a vertical split in the middle, evidently accentuated by crushing in preservation. In AMNH 11508 (SL 60 mm) there is a double first ural centrum, the first and second hypurals articulating with separate cylindrical chordacentra. In the largest specimens, such as NMNH 17907 (SL 78.5 mm) the midcaudal centra, about PU3–15, show perichordal ossification in the form of cellular bone with surface relief, superficial to the smooth, acellular chordacentra.

Vertical splits in the midcaudal centra, similar to those in *Todiltia*, have also been reported in "*L.*" *talbragarensis* Woodward by Cavender (1970, p. 23), who suggested that a groove was present even in uncrushed centra. We have observed splits in crushed midcaudal centra of several other "leptolepids" (e.g., young *Tharsis dubius* (Blainville) and *Ascalabos voithii* Munster). Cavender took the splits in the centra as "possibly indicating an original diplospondylous mode of formation," comparable with the midcaudal diplospondyly of pholidophorids.

Similar divisions in crushed centra are best known in the Late Jurassic and Early Cretaceous lycopterids, where they occur throughout the column (Gaudant, 1968, p. 24). Following Saito (1936), lycopterid vertebrae are interpreted as diplospondylous, the precentra carrying the neural and haemal arches in young fishes, and the pre- and postcentra fusing more or less completely in fishes over about 50 mm SL (Greenwood, 1970, p. 273). Lycopterids would be unique among actinopterygians if their centra developed by the formation of separate pre- and postcentra throughout the column. From observations on BM(NH) specimens of *Lycoptera*, the vertical splits in the crushed centra look the same as in leptolepids and, as in the leptolepids, they are most conspicuous in the midcaudal

centra (about PU4–13, cf. Saito, 1936, pl. 4, fig. 2), which are the longest rostrocaudally. In *Lycoptera* the neural and haemal arches do not articulate with the "precentrum," but often bridge the split in the centrum.

We suggest that conditions in leptolepids and lycopterids can be explained by comparison with ontogenetic events in Recent teleosts, without postulating a unique developmental pattern for lycopterid vertebrae. François (1966, 1967) has shown that in *Salmo* the centrum first appears as a ventral hemichordacentrum that extends dorsally to form a cylindrical chordacentrum (cf. Cavender, 1970, fig. 6—*Hiodon* and *Coregonus*). The perichordal centrum develops from two annular centers, one at the anterior and the other at posterior end of each chordacentrum. These perichordal rings extend toward one another and fuse, forming a cylindrical perichordal centrum. The chordacentrum is later resorbed or suppressed in the middle of the centrum. These events will explain observations in leptolepids and lycopterids. According to this interpretation, the vertical splits in the centra are a plane of weakness caused either by resorption of the chordacentrum, beginning in the middle of the centrum, or by resorption plus the gap between the perichordal rings encroaching from either end.

The only difference between the pattern in *Salmo* and in the leptolepids and lycopterids is that these, as in *Todiltia*, may show traces of dorsal hemichordacentra (also present in pholidophorids). In *Salmo* and the gymnotoid *Eigenmannia* the gradient of centrum formation is anteroposterior (François, 1966; Meunier and Kirschbaum, 1978), whereas in *Todiltia* the first centra to calcify are the ural centra, followed by those in the midcaudal region implying a caudo-rostral gradient. From the dimensions of the centra in other leptolepids and in *Lycoptera* (Saito, 1936, pl. 4, fig. 2), which are longest rostrocaudally in the midcaudal region, as in *Todiltia*, it appears that the gradient was also caudo-rostral in other leptolepids and in lycopterids.

In *Todiltia* the neural arches are autogenous throughout the vertebral column, and the neural spines are paired from the occiput back to the middle of the dorsal fin. In AMNH 11488, the first median neural spine is the

twenty-eighth, ending beneath the proximal end of the seventh dorsal fin radial. Median supraneurals lie distal to the neural spines from the occiput back to the anterior part of the dorsal fin. In AMNH 11488, supraneurals coexist with dorsal radials for three vertebrae, and in AMNH 11487 for four. The supraneurals are slightly sigmoid in shape, and are largest immediately behind the occiput, decreasing in size posteriorly. Long epineurals are present on the neural arches throughout the abdominal region and on the first two or three caudal neural arches. Most of the epineurals are outgrowths of, or continuous with, the neural arches, but the last few may be independent.

Beneath the centra, the parapophyses and haemal arches are autogenous throughout the column. The abdominal parapophyses bear long pleural ribs, extending to the ventral margin of the body. It is impossible to say whether or not the first two centra bore ribs. The last three or four pairs of ribs decrease in length, and the last three abdominal parapophyses show marked successive increase in length. There are slender epipleural intermuscular bones originating on the last five or six parapophyses and on the first one or two caudal haemal arches, making a total of five (in the smallest specimens) to seven or eight pairs of epipleurals (table 1).

**PAIRED FINS AND GIRDLES:** In the shoulder girdle the usual teleostean complement of dermal bones is present: extrascapular, post-temporal (suprascapular), supracleithrum, cleithrum, and at least two platelike post-cleithra. No details of the supratemporal can be observed. The post-temporal (pt, fig. 32) is large and platelike, penetrated by the main lateral line which gives off one dorsal branch. The supracleithrum and cleithrum (fig. 33) show nothing remarkable. All that is visible of the endoskeletal girdle is the outline of the coracoid and four pectoral radials, increasing in size downward (AMNH 11488). The pectoral fin contains 17 rays and extends about halfway to the pelvic origin.

The pelvic girdle occupies a length of about four vertebrae; the pelvic fin is situated beneath the origin of the dorsal fin. The girdle resembles those of *Leptolepis coryphaenoides* and *Tharsis dubius* (Nybelin, 1974, pls. 10, 23). There appears to be at least one ossified

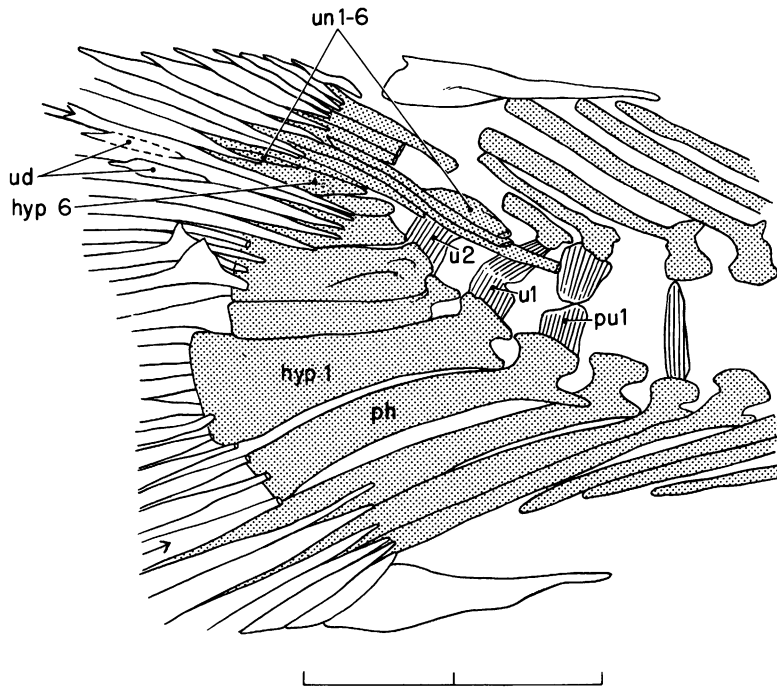


FIG. 34. *Todiltia schoewei*. NMNH 17899. Caudal skeleton. Bar equals 2 mm.

pelvic radial. The pelvic fins are best preserved in AMNH 11488, where the left fin contains 12 rays and the right 11; the first ray is unbranched, and all are segmented. There is no pelvic splint. The pelvic fin extends about three-fourths the distance between the pelvic and anal origins.

**UNPAIRED FINS:** The dorsal fin originates behind the pelvic fin origin and above the twenty-seventh or twenty-eighth vertebra. The fin base occupies the length of nine vertebrae. The fin contains four unbranched rays, the first unsegmented, and 12 or 13 branched rays, supported by 13 or 14 radials (table 1). The first radial is bifid, with a platelike anterior limb divided into finger-like processes. This radial supports the first three unbranched rays. Ossified middle segments are present distal to the third and succeeding radials in larger individuals (fig. 33).

The anal fin arises opposite the hind end of the dorsal fin base, and its base occupies the length of five or six vertebrae. The fin contains three unbranched rays, the first unsegmented, and 11 branched rays, supported

by 12 radials. The first two radials lie in front of the first caudal haemal spine, and support the three unbranched rays. Ossified middle segments are present distal to the fourth and succeeding radials.

**CAUDAL SKELETON AND FIN (figs. 34–36):** The neural spines of PU2–4 are broader distally than their predecessors, and decrease progressively in length. The neural spine of PU2 is about two-thirds as long as that of PU3. PU1 bears a normal but reduced neural arch with a short neural spine except in NMNH 17899, fig. 34, where the neural arches are “out-of-step,” and U1 bears an even smaller arch and spine. Also in NMNH 17899 the arch and spine of U1 resemble those of PU1 in other specimens. The haemal spines of PU1–3 are long, broad and in contact with each other: they support the ventral procurrent rays, and the parhypural (haemal spine of PU1) supports the lowermost four principal rays.

There are two ural centra, the first supporting hypurals 1 and 2, as usual, and the second hypurals 3–5, except in AMNH 11508,

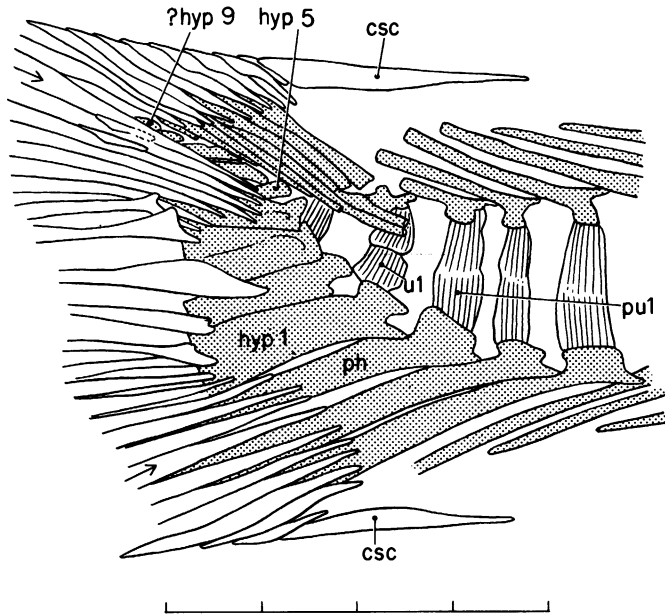


FIG. 35. *Todiltia schoewei*. AMNH 11487. Caudal skeleton. Bar equals 4 mm.

where the first ural centrum is double. There are six uroneurals: the first extends forward to PU2 and ends posteriorly over U2; the second extends from PU1 to above the head of the seventh hypural; the third extends forward to U1; the fourth reaches U2; and the fifth and sixth are small, slender and largely hidden by the fin-rays. In AMNH 11488 (fig. 36B) and third uroneural appears to be divided into two roughly equal parts by an oblique suture, which seems to be natural and not an artifact. Patterson and Rosen (1977, p. 129) noted a differentiation of the uroneural series in certain leptolepids and in higher teleosts where the first four uroneurals are elongate (e.g., *Tharsis dubius*, *ibid.*, fig. 35), and the last three uroneurals are shorter and more horizontal, forming a series that lies lateral to the hind ends of the anterior uroneurals. In *Todiltia* there is no such differentiation in NMNH 17899 (fig. 34) or in AMNH 11487 (fig. 35), but in AMNH 11488 (fig. 36) the last two uroneurals appear to be more horizontal than, and differentiated from, the anterior four uroneurals. This might represent intraspecific variation, but since the condition in figure 36 could be due to post-mortem disturbance, and that in figures 34

and 35 could not, we will assume that the undifferentiated state is representative of the species. There are eight or nine hypurals (figs. 35, 36B) and three epurals (fig. 36B).

The caudal fin contains 19 principal rays with nine branched in the upper lobe and eight in the lower. This is the generalized teleost condition. The bases of the first six upper branched rays form a bundle that extends across several hypurals. The bases of the seventh and eighth rays have dorsal processes. The broad, elongate base of the ninth, which reaches hypural 3, is typical of leptolepids and certain pholidophorids (Patterson and Rosen, 1977, figs. 31, 35). The upper principal rays are preceded by 10 procurent rays, the last three segmented distally. There is one dorsal fringing fulcrum (fig. 36A). The lower principal rays are preceded by six procurent rays, all but the first segmented. There are no ventral fringing fulcrum. Two elongate urodermals (figs. 34, 35) lie on the two uppermost branched principal rays. There is a large caudal scute in front of the upper and lower procurent rays.

The caudal fin is deeply forked, and its length is about 24 percent of the standard length.

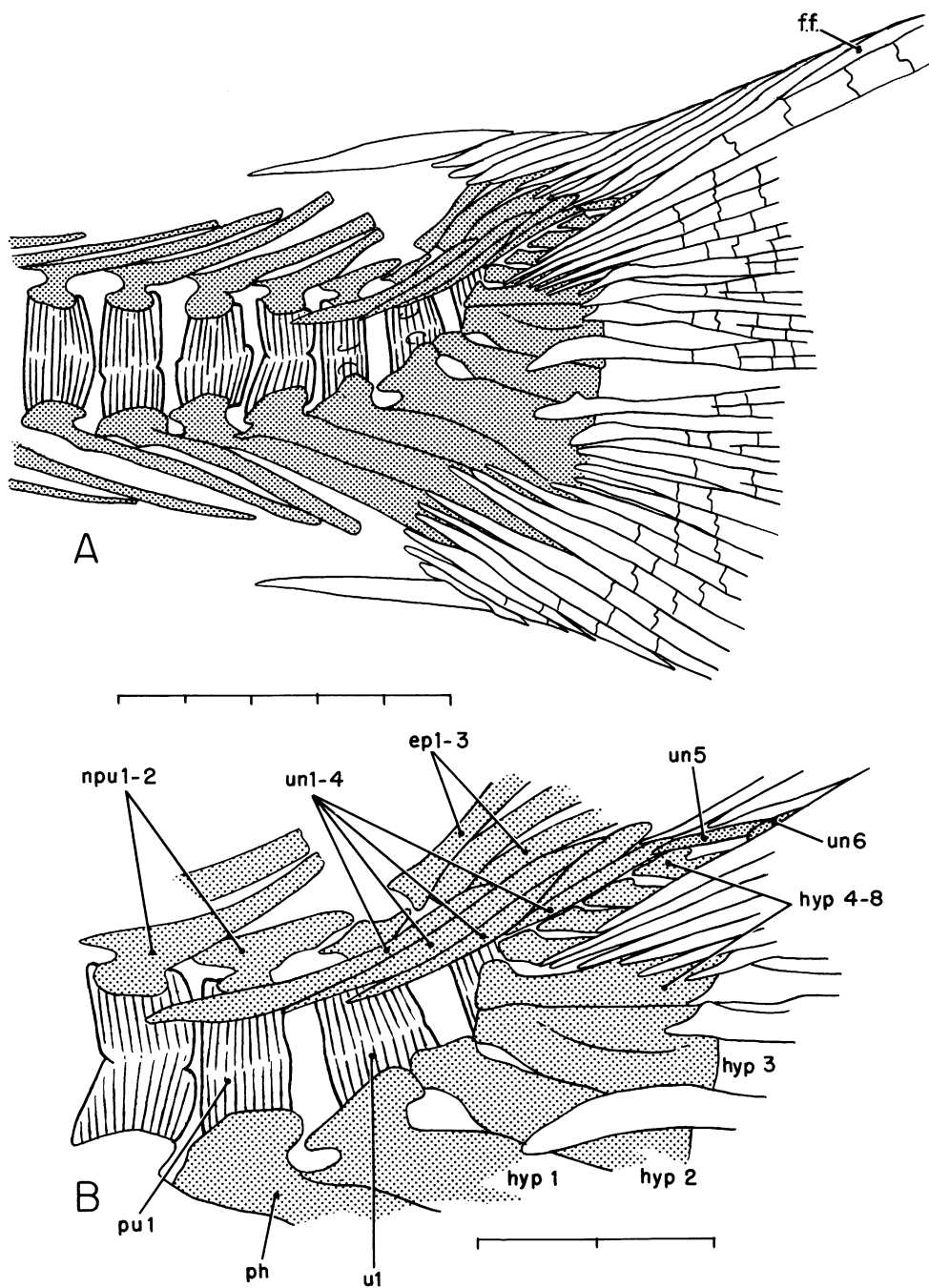


FIG. 36. *Todiltia schoewei*. AMNH 11488. A. Caudal skeleton. B. Enlarged portion of caudal skeleton with basal fulcra omitted. Bar for A equals 5 mm; for B 2 mm.

**SQUAMATION:** The scales are preserved as a uniform film, in which circuli are occa-

sionally visible, but it is impossible to count circuli or scales with any accuracy. The lateral



line scales, visible in the region of the uncalcified notochord of NMNH 17899, appear to outnumber the vertebrae two to one, suggesting that there were about 90 scale rows.

**SOFT ANATOMY:** In NMNH 17903, much of the epaxial and caudal hypaxial musculature is preserved as a yellowish mass within which fibers and their alignment are clearly visible. In the small NMNH 17899 (fig. 31A) and in AMNH 9832 (fig. 31B), pigment is preserved (in addition to the retinal pigment preserved in most specimens) in the form of dark spots, assumed to be chromatophores. There is a dark band of pigment along the dorsal midline, and an even sprinkling of chromatophores over the head and anterior part of the abdomen, with a denser patch around the pectoral fin.

The gut content is preserved in nearly all specimens, as a white or yellowish, featureless, phosphatic mass. This suggests a microphagous diet. The combined information on gut form from all specimens, shows that there was a large stomach anteriorly, separated by a sphincter from an intestine which looped ventrally, rose dorsally again above the pelvic fins, then passed obliquely down to the anus, in front of the anal fin.

#### RELATIONSHIPS OF *TODILTIA*

Dunkle (1942) distinguished *Leptolepis schoewei* from other leptolepids by "an exceptionally weak vertebral development," and by five other features that are either general in leptolepids, such as autogenous neural and haemal arches and caudal scutes, or are shown by better material to have been misinterpreted. The relatively late calcification of the chordacentra in *Todiltia* (at about 30 mm SL), their absence in the abdominal region below about 50 mm SL, and the feeble development of perichordal centra in the largest individuals (about 80 mm SL), remain the most striking characters of the species. These characters are discussed again in comparing *Todiltia* with "*L.*" *talbragarensis*.

In an outline classification of certain pholidophorids, leptolepids, and other Mesozoic lower teleosts, Patterson and Rosen (1977) listed 48 characters which specified previously unrecognized monophyletic groups. Comparing *Todiltia* with that list, it has all

the characters of *L. coryphaenoides* and lower forms (nos. 1–24), three of the characters of *Tharsis dubius* and higher teleosts (nos. 31, 32, and 34): no middle pit line groove on dermopterotic, no suborbital and epipleurals present in the middle part of the trunk. Among the other characters of *Tharsis dubius* and higher groups, *Todiltia* is known to lack sculptured centra constricting the notochord, differentiated anterior and posterior uro-neurals (cf. figs. 34–36 with Patterson and Rosen, 1977, fig. 35), and all subsequent characters in their list. The main purpose of the Patterson-Rosen scheme was to determine the relationships of the Mesozoic ichthyodectiforms. Those fishes were found to lack three of the characters of *Tharsis dubius* and higher groups: absence of the suborbital bone, presence of epipleurals, and the uroneurals in two series.

Thus *Todiltia*, on the basis of present knowledge, has two derived characters not found in the ichthyodectiforms—absence of the suborbital and presence of epipleurals, and lacks one derived character present in these fishes—well-developed perichordal centra. However, the ichthyodectiform *Oc-cithrissops*, as noted above, also lacks well-developed perichordal centra until it exceeds the apparent maximum size of *Todiltia*. Among the leptolepids, Patterson and Rosen (1977) found two taxa, the poorly known "*Leptolepis*" *macrophthalmus* Egerton and "*Leptolepis*" *talbragarensis* Woodward, which have approximately the same character combination as *Todiltia*. The monotypic *Ascalabos voithii* Munster was also found to fit at about this level. "*Leptolepis*" *caheni* (Saint-Seine and Casier, 1962), which Taverne (1975c) has compared with "*L.*" *talbragarensis*, also requires further comment.

"*Leptolepis*" *macrophthalmus*, "*L.*" *talbragarensis*, *Ascalabos voithii*, and *Todiltia schoewei* have a broadly similar caudal skeleton (cf. figs. 24–36 with Patterson and Rosen, 1977, figs. 45, 46, 53). *Todiltia* and "*L.*" *macrophthalmus* have an "empty triangle" beneath the dorsal caudal scute and above the epurals that is partly or completely filled in both "*L.*" *talbragarensis* and *Ascalabos* by elongate preural neural spines. This same empty triangle occurs in *L. coryphaenoides* (Taverne, 1982, fig. 5), "*L.*" *caheni* (Taverne,

1975c, figs. 10, 11), and in *Tharsis* (Patterson and Rosen, 1977, fig. 35; Taverne, 1975a, fig. 9). "*L.*" *macrophthalmus* and "*L.*" *talbragarensis* apparently lack epipleurals, although these elements are present in *Todiltia* and *Ascalabos*.<sup>5</sup> Little has been learned about the detailed structure of "*L.*" *macrophthalmus*, but with its long, slender body, numerous preopercular sensory canal branches (Patterson and Rosen, 1977, fig. 35b), and well-ossified centra, it shows no particular similarity to *Todiltia*. In vertebral structure, "*Leptolepis*" *talbragarensis* is like *Todiltia*. The smallest specimens of *L. talbragarensis* available to us are about 30–35 mm SL. The earliest stages of vertebral development show ventral hemichordacentra in the first few vertebrae (7–8 in BMNH P. 12426, 33 mm SL) and in the midcaudal region (PU5–8 in P. 12426). In larger specimens, ca. 40 mm SL, most centra are rings rather than hemicentra, but there is still a gap in vertebral calcification at the rear of the abdominal region and in the last few caudal centra (e.g., BMNH P. 37972a, ca. 39 mm SL, lacks PU21–29 and PU4–U1; P. 12447b, 41 mm SL, lacks the last five abdominal centra and PU1–3). By about 50 mm SL, all centra are represented by rings, but PU1 is the last to calcify. The pattern and sequence of vertebral calcification as estimated from SL in "*L.*" *talbragarensis* thus matches that in *Todiltia*.

However, there are other differences between "*L.*" *talbragarensis* and *Todiltia*. According to Cavender's (1970) and Nybelin's (1974) accounts, "*L.*" *talbragarensis* has: a

<sup>5</sup> Taverne (1975b) published an account of *Ascalabos voithii* based principally on a specimen in the Rijksuniversiteit, Gent, Belgium. This individual differs from those described by Nybelin (1974) and Patterson and Rosen (1977) in lacking epipleural bones, in having 43 vertebrae (including the ural centra) rather than 38–39, in having four rather than three uroneurals extending forward to PU1, and in a few other details. Taverne's specimen is small, 43 mm SL. BMNH P. 3671, labeled "*Leptolepis polyspondylus* Agassiz" by von Münster (Nybelin, 1974, p. 174), is about 32 mm SL, and shows the same features as Taverne's specimen. Nybelin refers to the BMNH specimen as "too badly preserved to allow a safe identification," but we suggest the possibility that neither Taverne's specimen nor BMNH P. 3671 may be *A. voithii*.

supraorbital-infraorbital sensory canal junction behind the orbit (absent in *Todiltia*), one branch of the infraorbital sensory canal in infraorbital 3 (two or three in *Todiltia*), no canal branch in infraorbitals 4 or 5 (two in infraorbital 4, and one in 5 in *Todiltia*), a pelvic splint (absent in *Todiltia*), about three fewer vertebrae than in *Todiltia*, and three or four upper caudal fringing fulcra (one in *Todiltia*). The significance of most of these features is unknown, but together with the absence of epipleurals in "*L.*" *talbragarensis*, they distinguish the two species. We have found no special similarities to justify a sister group relationship between them.

*Ascalabos voithii* (Nybelin, 1974; Patterson and Rosen, 1977) differs from *Todiltia* in having annular chordacentra throughout the column (at 35 mm SL), larger teeth, longer jaws, about 10 fewer vertebrae, and a predatory habit (swallowed prey observed by Nybelin [1974, p. 180], and by us in BMNH specimens). According to Nybelin, one of the most striking features of *A. voithii* is that the distance between the origins of pelvic and anal fins is only 62–70 percent of that between the pectoral and pelvic origins. In *Todiltia* this ratio is even lower—52–62 percent. Although *Todiltia* shares with *A. voithii* such features as epipleurals, a similar number of preopercular sensory canal branches, and a single dorsal caudal fringing fulcrum (contra Nybelin, 1974, p. 179), there seems to be no good reason for regarding the two species as related, or for including *schoewei* in the genus *Ascalabos*.

"*Leptolepis*" *caheni*, from the Kimmeridgian of Zaire, differs from *Todiltia* and resembles "*L.*" *talbragarensis* in having a supraorbital/infraorbital canal junction and no epipleurals. "*Leptolepis*" *caheni* has some differentiation of the uroneurals into anterior and posterior series, approaching the condition in *Tharsis* and higher teleosts. The centra of "*L.*" *caheni* were described by Taverne (1975c, p. 837) as lacking relief, but their composition is unknown (chordal or perichordal).

These comparisons are summarized in table 2. As the table shows, at our current level of knowledge of these five species, comparisons are restricted to superficial features, are

Comparison Between *Todiltia schoewei* and Other Leptolepids

	Number of vertebrae	Form of centra	Epipleurals	so/to canal junction	pop canal branches	Total to canal branches	Number of uroneurals	Number of hypurals	Number of urodermals	Number of caudal fringing fulcra	Dorsal fin-rays	Anal fin-rays	Pectoral fin-rays	Pelvic fin-rays
<i>Todiltia schoewei</i>	50	chordal	+	-	8-12	9-10	6	8-9	2	1	16-17	14	17	11-12
"Leptolepis"	44-45	chordal	-	+	6	4-5	6-7	9	2	3-4	14-15	11-12	13-14	10
<i>talbragarensis</i>														
"Leptolepis"	ca. 44	perichordal	?-	?	ca. 18	?	6	8	2	?	ca. 15	12-13	18	9
<i>macrophthalmus</i>														
"Leptolepis"	37-40	"without relief"	-	+	4	?	7 <sup>a</sup>	8	1 <sup>a</sup>	2	13-14	12-13	13	14
<i>caheni</i>														
<i>Ascalabos voithii</i>	38-40	one lateral ridge	+	?-	?12	?	7	9	2	1	17	14	15-16	11
<i>L. coryphenoides</i>	43-44	perichordal	-	-	10-19	10-16	7	8-9	2	1-2	15-16	11	16	11-13

<sup>a</sup> The seventh uroneural of "L." *caheni* (Taverne, 1975c, figs. 10, 13) may be a displaced second urodermal.

conflicting, and are rendered questionable by individual variation within species and by problems with inadequate preservation and/or observation. So our conclusion, that we cannot specify the nearest relative of *Todiltia*, is in part only a reflection of our ignorance of this and other leptolepids.

## DISCUSSION AND SUMMARY

In comparing the Sundance and Wanakah fishes with those from other areas, we will treat them as a single assemblage.<sup>6</sup> This can be justified in our present state of knowledge on the grounds of paleogeography (fig. 1), and by the general distribution of *Hulettia* from southern Montana to New Mexico. The apparent restriction of *Caturus* and *Occithrissops* to the Sundance and of *Todiltia* to the Wanakah may have some unresolved paleoecological basis, as noted in the section on geological occurrence.

The Sundance-Wanakah assemblage includes:

*Hybodus* sp.

*Ischyodus* sp.

*Hulettia americana* (Eastman)

*Lepidotes* sp.

*Caturus dartoni* (Eastman)

*Occithrissops willsoni* new genus, new species

*Todiltia schoewei* (Dunkle)

This list is obviously limited in comparison to assemblages from rocks of comparable age and area in Europe (table 3). There are several possible explanations for this. One is that exploration for Jurassic fishes in North America is still inadequate by European standards. Representatives of most taxa listed above were found before 1900 (excepting *Occithrissops* and *Todiltia*) and no concerted effort was made to improve this situation before 1959, although several collections were

<sup>6</sup> The term fauna is hardly applicable here. We are concerned at best with biased samples of the fish fauna that occupied the western interior sea and possibly some of the surrounding drainages during the Middle Jurassic. There is no way of knowing how representative any fossil fish assemblage may be in terms of the original diversity or the original habitats.

obtained later from the Todilto. Intensive prospecting at the Hulett Sundance fish localities during eight field seasons failed, for reasons unknown, to increase the diversity. Another is that suitable preservation environments for Jurassic fishes were seemingly more restricted on this continent than in Europe. But regardless of this apparent low diversity, these specimens must be regarded as a valid and meaningful sample of the fishes that inhabited the western interior sea area during mid-Jurassic times.

Perhaps the most striking aspect of this assemblage is the inclusion of four familiar genera (*Hybodus*, *Ischyodus*, *Lepidotes*, and *Caturus*), plus three new monotypic genera (*Hulettia*, *Occithrissops*, and *Todiltia*) whose relationships are obscure. The first four taxa are represented only by one or a few fragmentary specimens, whereas the last three are known from relatively abundant and complete material. This spectrum of occurrence and degree of completeness is related to different levels of resolution in our understanding of these fishes. These levels are manifest in terms of preservation, relative abundance, diversity and, of course, the evident problems in systematic interpretation.

The chondrichthyan genera *Hybodus* and *Ischyodus* are undoubtedly form genera with long temporal and wide geographic ranges. Unfortunately, they are usually represented by isolated teeth. *Lepidotes* and *Caturus* also have long temporal and wide geographic ranges, but their representation in the fossil record is considerably better. Certain species are well-known anatomically, and there is abundant, well-preserved material in the British Museum (Natural History) and a few other collections. *Lepidotes* is not a form genus in the sense that *Hybodus* and *Ischyodus* are, and in our opinion the only question about its monophyly concerns possible synonymy with *Semionotus* (Olsen and McCune, ms.). At present, the many nominal species of *Lepidotes* and/or *Semionotus* are monophyletic at some undetermined level, and are interrelated in unknown ways.

We also suspect that *Caturus* is a form genus, either para- or polyphyletic. But the caudal skeleton of *C. dartoni* implies that it belongs to a monophyletic subgroup comprising at least *C. heterurus*, *C. smithwoodwardi* and

*C. dartoni*. All of these taxa are characterized by having fused lower hypurals, as discussed above. The relationships of this subgroup to other nominal *Caturus* species remain unknown. Thus in identifying new fossils as members of genera such as these, and in comparing them with their presumed occurrence elsewhere, one must be careful not to draw unwarranted inferences that go beyond the anatomical and systematic data. Names alone, without supporting data, are a poor guide to relationship.

The three new monotypic genera, *Hulettia*, *Occithrissops*, and *Todiltia* in themselves represent three different levels of resolution—that is the descending categorical level at which each must be regarded as *incertae sedis*: *Hulettia* in the Halecostomi, *Todiltia* in the Teleostei and *Occithrissops* in the Ichthyodectiformes. Analogous examples are also cited in the comparisons of Jurassic fish assemblages in the Appendix.

Stratigraphically and geographically, the closest assemblage to the Sundance-Wanakah one is that from the Oxfordian of Cuba (Gregory, 1923; White, 1942; Dunkle, personal commun.; see Appendix). Here we are immediately faced with the problem of trying to evaluate assemblage resemblances—related mostly to inadequate description and comparison. Although this Cuban assemblage has been known for more than 60 years, and several collections of fish-containing nodules exist in museums, no detailed study of the fishes has yet been made. Apart from the pycnodont *Gyrodon*, Gregory's (1923) identifications (*Caturus*, ?*Sauropsis*, the new "pachycormid" genus *Eugnathides* and *Lep-tolepis*) seem as likely to mislead as to inform, if taken at face value. White's (1942) monotypic "leptolepid" genus *Luisichthys* may be a synonym of *Pachythrissops*, but critical details are lacking in his description. Until a modern, systematic study is published, it appears that the Cuban assemblage differs mainly from that of the Sundance/Wanakah in including pycnodonts and in lacking chondrichthyans.

South America (see Appendix) is less well explored than North America in regard to Jurassic fishes. To date, the only coherent knowledge from this continent concerns the Oxfordian assemblage from Domeyko, in

eastern Chile (Arratia, 1982). This contains undescribed *Lepidotes*, pycnodonts and amioids, and the teleosts *Pholidophorus domeykanus* Arratia et al. (1975a), "*Leptolepis*" *opercularis* Arratia et al. (1975c), and three monotypic endemic genera, *Protoclupea* Arratia et al. (1975b), *Varasichthys* Arratia (1981) and *Chongichthys* Arratia (1982). Here we have a problem similar to that represented by the Sundance/Wanakah assemblage. *Lepidotes*, *Pholidophorus* and "*Leptolepis*" are widespread and long-ranging "phenetic abstractions." As the last two are certainly non-monophyletic, they are essentially valueless for assemblage comparison. Among the three monotypic genera, *Varasichthys* and *Chongichthys* have been well described, so far as the material allows, and their structure has been thoroughly compared with that of other Jurassic fishes by cladistic analysis. The conclusion reached by Arratia (1981, 1982) is that both taxa are *incertae sedis* within the Teleostei; that is, their relationships are unknown. They therefore pose the same systematic problem as *Hulettia* and *Todiltia*—as comparatively well-known fossil neopterygians that are valueless for purposes of assemblage comparison because each is, at present, unique and without known relatives.

Discrimination of these two sets of taxa (wide-ranging, non-monophyletic, and unique monotypic) is a result of the introduction of cladistics into paleontology. Before cladistics, fossil fishes such as *Varasichthys*, *Chongichthys*, and *Todiltia* would have been treated as members of a grade taxon, probably designated as *Leptolepis* or Leptolepididae. They could have been used in faunal comparisons, perhaps as stratigraphic indicators, and as contributions to the phylogeny and historical biogeography of teleosts. But those comparisons, and the conclusions drawn from them, would have been as devoid of phylogenetic meaning as the statement that *Varasichthys*, *Chongichthys*, and *Todiltia* are teleosts of unknown relationship. Para- or polyphyletic grade taxa, like *Leptolepis sensu lato*, and the Leptolepididae, are taxonomic artifacts, and opinions on stratigraphy, phylogeny, or biogeography based on them are equally artificial.

The problem outlined above is a growing one, and one that will not disappear. Cladistic

analysis has shown, or suggested, that traditional Mesozoic actinopterygian groups such as the parasemionotids, semionotids, caturids, pholidophorids, and leptolepids are non-monophyletic, as are many of their included genera. Other traditional groups, such as the macrosemiids (Bartram, 1977), pachycormids and aspidorhynchids (Patterson, 1977; Mainwaring, 1979), are found to be monophyletic, but of unknown or uncertain relationship even at a very high taxonomic level. Given the cladistic method, the tendency, with increasing knowledge of morphology, is to divide extinct para- or polyphyletic groups (form taxa) into smaller monophyletic or monotypic units. These may be left in limbo, either temporarily or permanently. Examples in this paper are the species group of *Caturus* proposed above, as well as the genera *Hulettia*, *Todiltia*, *Varasichthys*, and *Chongichthys*.

One could take this situation to mean that paleontological critics of cladistics, such as Campbell (1975) or Van Valen (1978), are correct in stating that the cladistic method is unsuited to the study of fossils, in which significant characters may be difficult or impossible to find. But alternatives to cladistic hypotheses of relationship, however fragile, are "horizontal groups," which are acknowledged to be para- or polyphyletic (Campbell, 1975, p. 95), or "segments of clades bounded by adaptive changes" (Van Valen, 1978, p. 293). As is now evident, vague concepts like these guided most of us in pre-cladistic days in assigning fossil fishes to form genera such as *Hybodus* and *Leptolepis*, or in judging that fossils previously assigned to these genera merited new generic status. Campbell (1975, p. 95) claims that taxa conceived in this way "cannot be used for detailed biogeographical work," but "can be used as indicators of similar climatic belts, broad geographic provinces, and comparable habitats." As the tables in the Appendix show, however, *Hybodus*, *Lepidotes* or *Leptolepis sensu lato*, imply virtually cosmopolitan distribution, and so are not helpful. To date, we lack criteria by which *Hybodus*, *Lepidotes*, or *Leptolepis* might be broken up into more useful (in Campbell's sense) subgroups.

In systematics, the two horns of the paleontologist's dilemma are cladistic analysis

versus the traditional or evolutionary method (e.g., Mayr, 1982). The first leads to uncertainty, expressed in liberal use of *incertae sedis*. The second leads to spurious certainty, when phenetic or "adaptive" groupings are treated as real.

As for "detailed biogeographical work" (Campbell's 1975 phrase), it begins for the cladist with the question "what is the sister-group, and where does it live?" The question is asked for many taxa in a diversified fauna. In our Sundance/Wanakah assemblage, the question cannot be answered for any taxon, and analytical biogeography cannot be started. For the traditionalist, biogeography can be sketched out with a broader brush. For

example, the Sundance endemic *Occithrissops willsoni* is the earliest ichthyodectiform known, and could be treated as ancestral to other members of the group, or at least to the ichthyodectoids. Ancestry is thus one way of interpreting the meaning of a monotypic taxon in a trichotomous cladogram like figure 30C. One could then develop a narrative of ichthyodectiform dispersal, with the Sundance Sea as the center of origin. But just as evolutionary systematics may lead to spurious certainty, so evolutionary biogeography may lead to spurious stories. Our inability to resolve the relationships of *Occithrissops* is surely no basis for an inferred center of origin.

#### APPENDIX: THE DISTRIBUTION OF JURASSIC FISHES

A résumé of Jurassic fish distribution has been included in this Appendix in the form of two tables, one for marine (table 3) and the other for nonmarine (table 4), and by a series of paleogeographic maps (figs. 37–39) showing most of the areas in which Jurassic fishes have been found. In our present state of knowledge, this compilation must be regarded as tentative. The reasons for this have been set forth in the preceding discussion, which emphasizes some of the problems that arise in analyzing and comparing any fossil fish assemblages of about the same age from different areas or parts of the world. Our justification for including these tables is simply that no effort of this sort has been attempted before, and that the tables will provide a summary of current information about both the systematics and the distribution of Jurassic fishes.

The preparation of worldwide taxonomic, stratigraphic, and geographic records of extinct animals, such as are represented in these tables, necessarily involves data compression and various arbitrary decisions. If such compilations are uncritical, they cease to be informative. Doubtful or questionable identifications, which are often perpetuated in tables such as these, can mislead the specialist as well as the non-specialist. On the other hand, to omit a record because of doubt about provenance or identification can also lead one astray. We have tried to steer a middle course, using specialist knowledge judiciously, checking specimens where possible, and omitting records only when we believe that they lack any real factual basis.

The distinction between the marine and non-marine tables has been based on the literature, on paleogeography, and on our own opinion and/or field experience of the associated fauna and flora.

Forcing all Jurassic fish localities into either a marine or a nonmarine setting involved some judgments that may be incorrect, but in our view that possibility is preferable to lumping all occurrences, or to introducing a third set of tables for indeterminate or possible brackish-water occurrences.

The basis for the classification is necessarily a combination of the "classical" and phylogenetic approaches. For the Chondrichthyes, the recent studies of Thies (1983), Maisey (personal commun.), and Patterson (1965) have been utilized. The actinopterygian classification is mostly based on Gardiner (1967) for the chondrosteans, on Patterson (1973) for the non-teleost neopterygians, and on Patterson and Rosen (1977) for the teleosts. Taxa of unknown or uncertain status are framed by quotation marks or are placed in an *incertae sedis* category.

The abbreviations in the marine and non-marine tables represent the stages of the Jurassic, as follows:

Upper	Portlandian	Po
	Kimmeridgian	K
	Oxfordian	Ox
Middle	Callovian	Ca
	Bathonian	Bt
	Bajocian (incl. Aelenian)	Bj
Lower	Toarcian	T
	Pliensbachian	Pl
	Sinemurian	S
	Hettangian	H

In some areas, and particularly for nonmarine deposits, the Jurassic has been divided only into Lower (L), Middle (M) and Upper (U), and in a few places only a Jurassic age (J) has been recog-

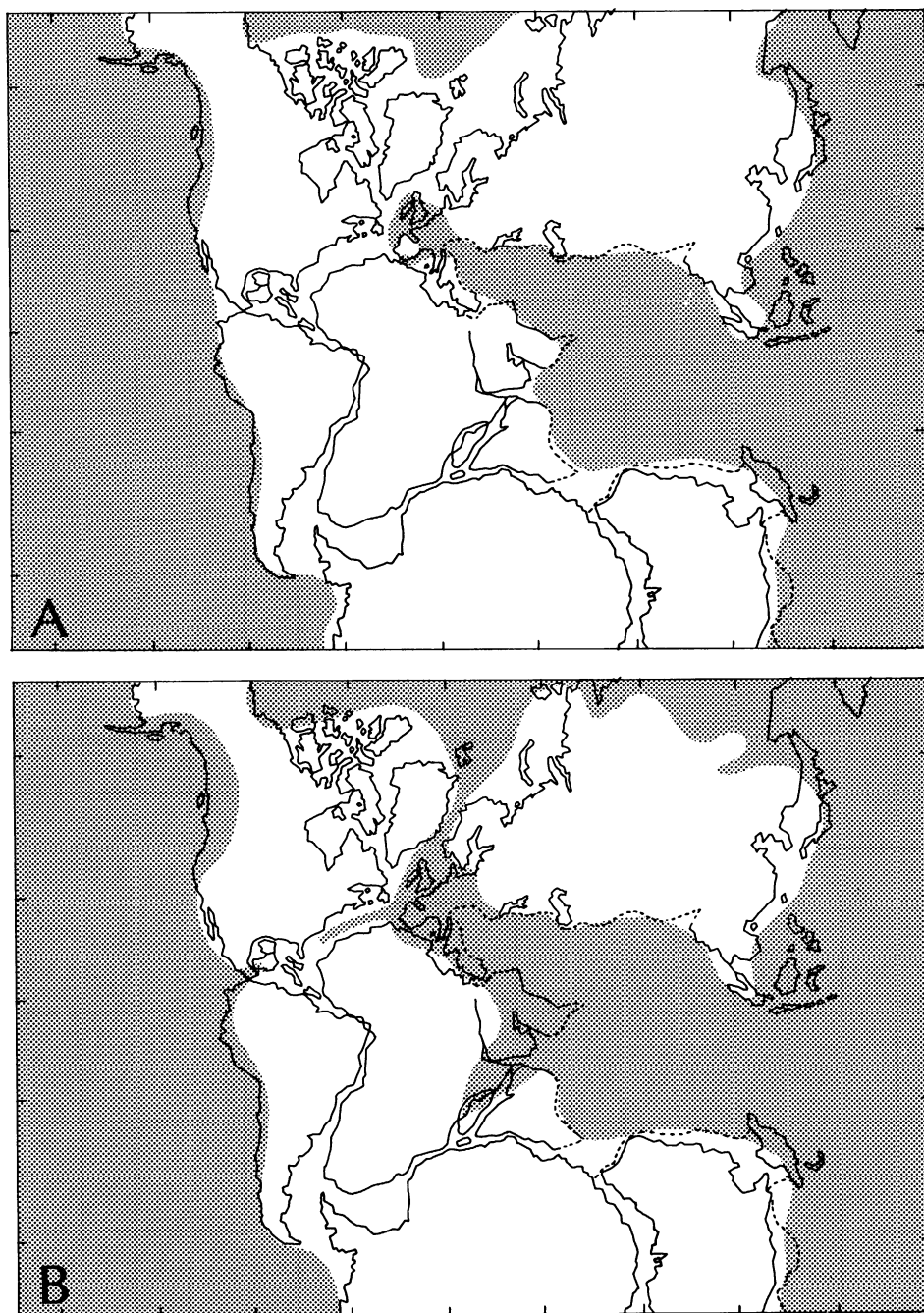


FIG. 37. A. Paleogeographic map showing approximate distribution of land and sea during the Hettangian and Sinemurian. B. Same for the Pliensbachian and Toarcian. Modified after Hallam (1975). Geographic areas in tables 3 and 4 are shown in figure 39.

nized. In the Lower and Middle Jurassic, stages are non-controversial, except that we have not distinguished the Aalenian, including it as (Lower)

Bajocian. There are problems toward the end of the Jurassic, where, as Rawson et al. (1978, p. 7) put it, "Ammonite provincialism had reached such

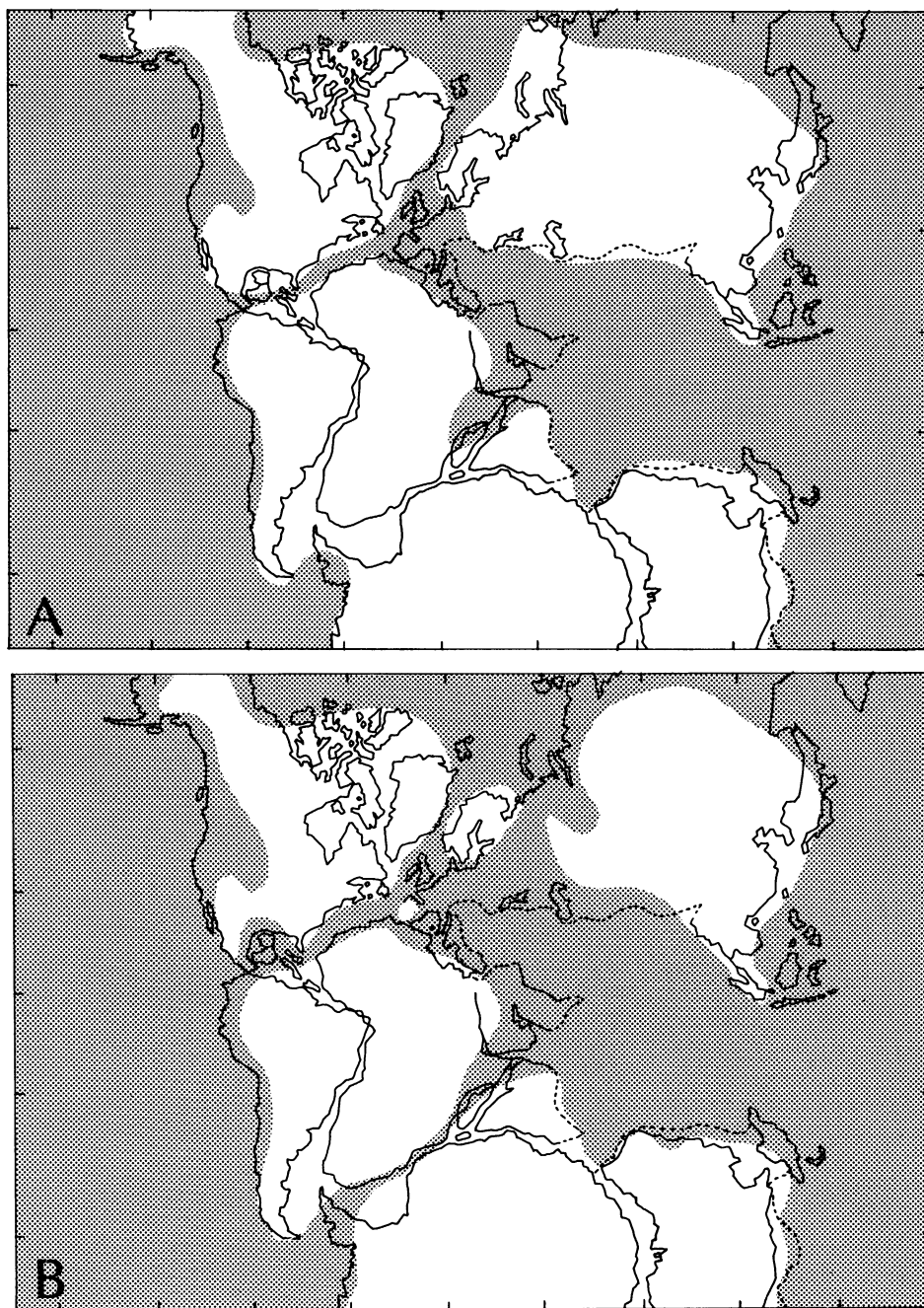


FIG. 38. A. Paleogeographic map showing approximate distribution of land and sea from the Bajocian to the early Callovian. B. Same for the late Callovian to Kimmeridgian. Modified after Hallam (1975). Geographic areas in tables 3 and 4 are shown in figure 39.

a peak . . . that it is extremely difficult to correlate the Tethyan and boreal ammonite sequences near

the Jurassic/Cretaceous boundary. Hence a three-fold stage terminology has evolved for the top of



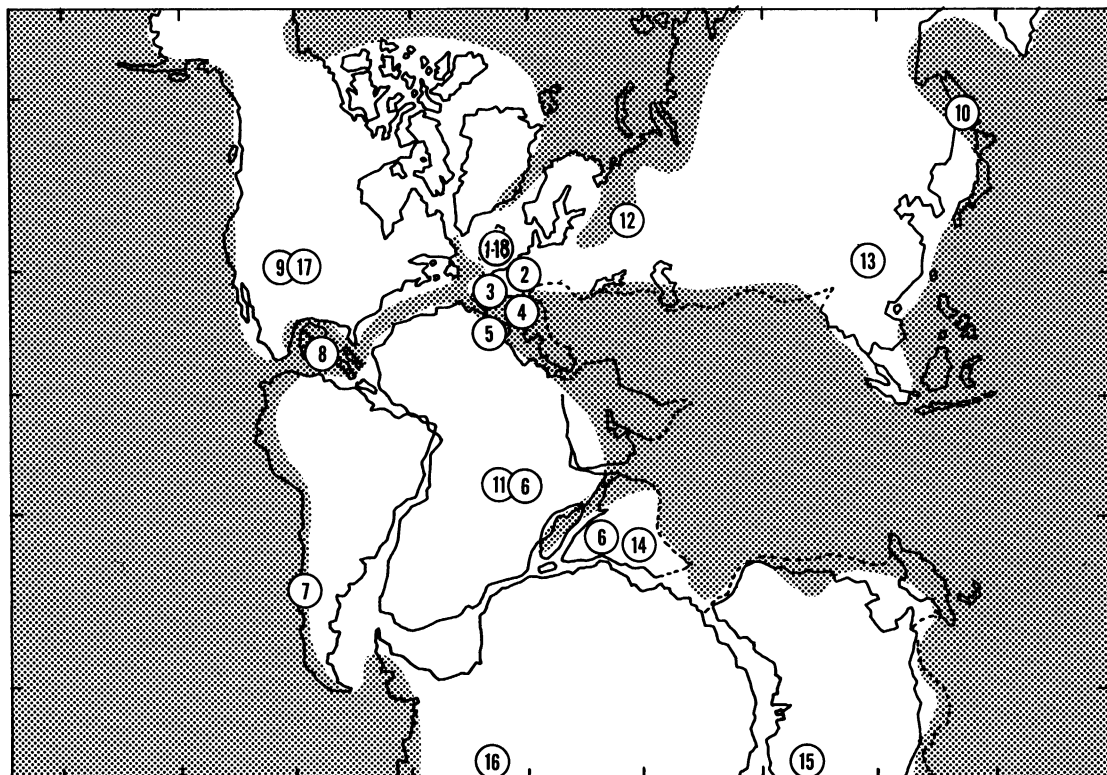


FIG. 39. Paleogeographic map showing approximate distribution of land and sea during the Portlandian. Modified after Hallam (1975). Numbers refer to geographic areas in tables 3 and 4.

the Jurassic: Tithonian for the 'standard' Tethyan sequence and Volgian or Portlandian for the boreal regions."

There is also a problem with the Purbeckian, traditionally regarded as the terminal stage of the Jurassic in Britain. We follow Casey (1973) and Rawson et al. (1978) in taking the mid-Purbeck Cinder Bed as the base of the Cretaceous. The lower (Jurassic) half of the old Purbeckian is now named the Lulworth Beds, and the upper (Cretaceous) half the Durlston Beds. In attempting a world survey of Jurassic fishes, our selection of Upper Jurassic stage names is influenced by the fact that we have used the British Museum (Natural History) collections, and their catalogues and records, as an up-to-date and verified list of Jurassic taxa that will serve as a standard for the identification and composition of assemblages from other areas. We have therefore followed the Upper Jurassic correlation chart recently published by the Geological Society of London (Cope et al., 1980), and used Kimmeridgian and Portlandian as the last two Jurassic stages. This means that the well-known European Tithonian assemblages (e.g.,

Solnhofen, Cerin) appear as Kimmeridgian, and the Lulworth Beds (formerly Purbeckian) appear as Portlandian.

The earliest Cretaceous fish assemblages from Great Britain have also been included in the tables, to emphasize their close identity with the Late Jurassic ones, as follows:

Wealden and Purbeckian above the Cinder Bed (freshwater)	We
Marine equivalents of Wealden	Ne

The geographic subdivisions in tables 3 and 4 are based on regional or paleogeographical considerations. The numbered paragraphs in the discussion below refer to these subdivisions, as do the numbers in figure 39. The paleogeographic maps (figs. 37-39) should be examined in connection with the remarks on occurrence.

#### Marine Occurrences (Table 3)

1. Great Britain is treated separately because, as noted above, the extensive collections of Jurassic

TABLE 3  
World Distribution of Jurassic Fishes-Marine<sup>a</sup>

	1 Great Britain	2 Northern Europe	3 Portugal Spain	4 Italy Sicily	5 North Africa	6 Erythraean Trough Zaire	7 Argentina Chile	8 Mexico Cuba	9 USA Canada	10 USSR Japan
Chondrichthyes										
Elaosobranchii										
Hybodontidae										
<i>Acrodus</i>	S, Bj-Bt	S, Bj	K							
<i>Hybodus</i>	S-Ne	S, T-Bj, Ox-Po	K	S, Bj	U	Bj-Po?			Bj	?Po
<i>Asteracanthus</i> (= <i>Strophodus</i> )	Bj-Po	T-Po	Ca, K	Bj, K-Po		Bj-Po?				
<i>Neoselachii</i> inc. sed.										
<i>Synechodus</i>	Ne	K		S						
<i>Palaeospinax</i>	S	H, Bj, Ox								
<i>Sphenodus</i>	P, Ca	P, Bj-Po		Bj, Ox-Po		M-U				Po
(= <i>Orthacodus</i> )										
Heterodontidae										
<i>Heterodontus</i>	Ca, K-Po	T-Bj, K								
<i>Paracestracion</i>	Ca, K	K								
Hexanchidae										
<i>Hexanchus</i>	Ca	P, Bj, Ox-Po				K				
Orectolobidae										
<i>Palaeocarcharias</i>		K								
<i>Agaleus</i>	S									
<i>Corysodon</i>		K								
<i>Crossorhinops</i>		K								
<i>Orectoloboides</i>	Ca									
? <i>Orectolobus</i>		K								
(= <i>Crossorhinus</i> )										
<i>Phorcynis</i>		K								
<i>Paleobrachaelurus</i>	Ca	T, Bj								
<i>Annea</i>		Bj								
Scapanorhynchidae										
<i>Scapanorhynchus</i>	Ne									

TABLE 3—(Continued)

	1 Great Britain	2 Northern Europe	3 Spain	4 Italy	5 North Africa	6 Erythraean Trough	7 Argentina	8 Mexico	9 USA	10 USSR
Scylorhinidae										
<i>Palaeoscyllium</i>	.	K	.	.	.	.	.	.	.	.
<i>Pristiurus</i>	.	K	.	.	.	.	.	.	.	.
Squatinae										
<i>Squatina</i>	Ne	Ox-K	.	.	.	.	.	.	.	.
Protospinacidae										
<i>Protospinax</i>	Ca	Ox-K	.	.	.	.	.	.	.	.
(= <i>Squalogaleus</i> )										
Rhinobatidae										
<i>Spathobatis</i>	Ca	T-Bj, K	.	.	.	.	.	.	.	.
(?= <i>Aellopos</i> )										
<i>Asterodermus</i>	.	K	.	.	.	.	.	.	.	.
<i>Belemnobatis</i>	.	K	.	.	.	.	.	.	.	.
Batoidei incer. sed.										
<i>Jurobatus</i>	.	T	.	.	.	.	.	.	.	.
? <i>Cyclarthrus</i>	S	S	.	.	.	.	.	.	.	.
<i>Breviacanthus</i>	Bt	.	.	.	.	.	.	.	.	.
Holocephali										
Squalorajidae										
<i>Squaloraja</i>	S	.	.	S	.	.	.	.	.	.
Myriacanthidae										
<i>Agkistracanthus</i>	.	H	.	.	.	.	.	.	.	.
<i>Alethodontus</i>	.	H	.	.	.	.	.	.	.	.
<i>Myriacanthus</i>	S, Bj	H	.	.	.	.	.	.	.	.
<i>Metopacanthus</i>	S	T	.	S	.	.	.	.	.	.
Chimaeropsidae										
<i>Chimaeropsis</i>	.	?S, K	.	.	.	.	.	.	.	.
Acanthorhinidae										
<i>Acanthorhina</i>	.	T	.	.	.	.	.	.	.	.
Chimaeridae										
<i>Ganodus</i>	Bj-Bt,	K	.	.	.	.	.	.	.	.
(= <i>Leptacanthus</i> )	K-Po									
<i>Ischyodus</i>	Bt-Ne	Bt, Ox-Po	.	.	.	.	.	.	Bt	.

TABLE 3—(Continued)

	1 Great Britain	2 Northern Europe	3 Portugal Spain	4 Italy Sicily	5 North Africa	6 Erythraean Trough Zaïre	7 Argentina Chile	8 Mexico Cuba	9 USA Canada	10 USSR Japan
<i>Brachymylus</i>	Ca, K	.	.	.	.	.	.	.	.	.
<i>Pachymylus</i>	Ca	.	.	.	.	.	.	.	.	.
<i>Elasmodectes</i>	K	.	.	.	.	.	.	.	.	.
? <i>Pristacanthus</i>	Bt	Bt	.	.	.	.	.	.	.	.
Osteichthyes										
Actinopterygii										
Cosmolepidae										
<i>Cosmolepis</i>	H-S	.	.	S	.	.	.	.	.	.
(=Oxygnathus)										
Centrolepidae										
<i>Centrolepis</i>	S, Bt	.	.	.	.	.	.	.	.	.
Coccolepidae										
<i>Coccolepis</i>	S, Bt-Ca, Po	K	.	.	.	.	.	.	.	.
cf. <i>Pteroniscus</i>	.	.	.	S	.	.	.	.	.	.
<i>Brownieichthys</i>	H	.	.	.	.	.	.	.	.	.
Peltopleuridae										
<i>Placopleurus</i>	.	.	.	S	.	.	.	.	.	.
Platysiagidae	S	.	.	.	.	.	.	.	.	.
<i>Platysiagum</i>										
Saurichthyidae										
<i>Saurorhynchus</i>	S, T	P-T	.	.	.	.	.	.	.	.
(=Belonorhynchus)										
Ptycholepidae										
<i>Ptycholepis</i>	H, S, T	S, T	.	.	.	.	.	.	.	.
Chondrosteidae										
<i>Gyrosteus</i>	T	T	.	.	.	.	.	.	.	.
<i>Chondrosteus</i>	H-S	T	.	.	.	.	.	.	.	.
Halecostomi incer. sed.										
<i>Huletia</i>	.	.	.	.	.	.	.	.	Bt-Ca	.
<i>Songanella</i>	.	.	.	.	.	K	.	.	.	.
Semionotidae										
<i>Lepidotes</i>	T-Ne	T, Bt-Po	Ca, K	P-Po	U	T-Bt, K	Ox-Po	Ox-K?	Bt	Po

TABLE 3—(Continued)

	1 Great Britain	2 Northern Europe	3 Portugal	4 Italy	5 North Africa	6 Erythraean Trough	7 Argentina	8 Mexico	9 USA	10 USSR
<i>Austrolepidotus</i>	.	.	.	.	.	.	T?	.	.	.
Dapediidae										
<i>Heterostrophus</i>	Ca	K	.	.	.	.	.	.	.	.
<i>Dapedium</i>	H-T	S, T-Bj	.	S	.	.	.	.	.	.
<i>Tetragonolepis</i>	T	T	P?	.	.	.	.	.	.	.
<i>Paradapedium</i>	.	.	.	.	.	.	.	.	.	.
Gyrodontidae										
<i>Eomesodon</i>	H <sub>1</sub>	H?, Bt,	.	.	.	.	.	.	.	.
	Bj-Po	K-Po	.	.	.	.	.	.	.	.
<i>Macromesodon</i>	Bj-Bt,	Ox-Po	.	.	.	.	.	.	.	.
(= <i>Mesodon</i> , <i>Gyron-</i>	K-Po									
<i>chus</i> , <i>Scaphodus</i> )										
<i>Gyrodus</i>	Ox-Ne	Ox-Po	K, Po	Bj, Ox, Po	.	.	.	Ox-K?	.	Po
<i>Mesturus</i>	Ca, K	T, Ca,	.	.	.	.	.	.	.	.
		K-Po								
<i>Proscinetes</i>	Bt,	Ox-Po	Ca, K	.	.	.	.	.	.	.
(= <i>Microdon</i> )	K-Po									
<i>Athrodon</i>	Po	K	.	.	.	.	.	.	.	.
<i>Coelodus</i>	Po	Po	.	?Po	.	.	.	.	.	.
Macrosemiidae										
<i>Macrosemius</i>	?Bt	K	.	.	.	?K	.	.	.	.
(= <i>Disticholepis</i> )										
<i>Histonotus</i>	Po	K	.	.	.	.	.	.	.	.
<i>Enchelyolepis</i>	Po	Po	.	.	.	.	.	.	.	.
<i>Notagodus</i>	.	K	.	.	.	.	.	.	.	.
<i>Propterus</i>	.	K	K	.	.	.	.	.	.	.
? <i>Eusemius</i>	.	K	.	.	.	.	.	.	.	.
Oligopleuridae										
<i>Oligopleurus</i>	.	K	.	.	.	.	.	.	.	.
Ionoscopidae										
<i>Ionoscopus</i> ( <i>Oenoscopus</i> )	Po	K	.	.	.	.	.	.	.	.
<i>Callopterus</i>	.	K	.	.	.	.	.	.	.	.

TABLE 3—(Continued)

	1 Great Britain	2 Northern Europe	3 Portugal Spain	4 Italy Sicily	5 North Africa	6 Erythraean Trough Zaire	7 Argentina Chile	8 Mexico Cuba	9 USA Canada	10 USSR Japan
Halecomorphi										
Caturidae										
<i>Caturus</i>	S, T, Bt-Po	T K-Po	Ca	.	.	?K	.	Ox-K?	Bt-Ca	.
(= <i>Strobilodus</i> )										
<i>Furo</i>	H-S, T, ?Bt, K-Po	T-Bj, K-Po	.	S	.	T	.	.	.	.
(= <i>Eugnathus</i> )										
<i>Eugnathides</i>	.	.	.	.	.	.	.	Ox-K	.	.
<i>Osteorachis</i>	S, Ca	.	.	.	.	.	.	.	.	.
<i>Heterolepidotus</i>	H-S, Bj, K	T, K	.	.	.	.	.	.	.	.
" <i>Eurycormus</i> "	Ca, K	Ca	.	.	.	.	.	.	.	.
Ophiopsidae										
<i>Ophiopsis</i>	Bj, Po	K	.	.	.	K	.	.	.	.
Amiidae										
<i>Amiopsis</i>	Po	.	.	.	.	.	?Ox-K	.	.	.
(= <i>Megalurus</i> , <i>Urocles</i> )										
<i>Liodesmus</i>	.	K	.	.	.	.	.	.	.	.
Teleostei										
Pholidophoridae								?Ox, K	.	.
<i>Pholidophorus</i>	H-Po	S, T-Bj, K	.	S-T	.	K	Po	.	.	.
<i>Pholidolepis</i>	S	.	.	S	.	.	.	.	.	.
<i>Pholidophoroides</i>	S	.	.	.	.	.	.	.	.	.
<i>Pholidophoropsis</i>	S	.	.	.	.	.	.	.	.	.
<i>Pholidophoristion</i>	Po	K	.	.	.	.	.	.	.	.
<i>Ankylophorus</i>	.	K	.	.	.	.	.	.	.	.
<i>Eurycormus</i>	.	K	.	.	.	.	.	.	.	.
Ichthyokentemidae										
<i>Ichthyokentema</i>	Po	.	.	.	.	.	.	.	.	.
? <i>Ceramurus</i>	Po	.	.	.	.	.	.	.	.	.
Pachycormidae										
<i>Asthenocormus</i>	Ca	K	.	.	.	.	.	.	.	.
<i>Euthynotus</i>	T	T-Bj	.	.	.	.	.	.	.	.

TABLE 3—(Continued)

	1 Great Britain	2 Northern Europe	3 Portugal	4 Italy	5 North Africa	6 Erythraean Trough	7 Argentina Chile	8 Mexico Cuba	9 USA Canada	10 USSR Japan
<i>Pachycormus</i>	T, ?Bj	T	.	T	.	.	.	.	.	.
<i>Saurostomus</i>	T	T	.	.	.	.	.	.	.	.
<i>Hypocormus</i>	Ca, K	K-Po	.	.	.	.	.	.	.	.
<i>Orthocormus</i>	.	K	.	.	.	.	.	Ox-K	.	.
<i>Sauropsis</i>	.	T, K	.	.	.	.	.	.	.	.
(= <i>Prosauropsis</i> )										
<i>Leedsichthys</i>	Ca	.	.	.	.	.	.	.	.	.
? <i>Ohmdenia</i>	.	T	.	.	.	.	.	.	.	.
Aspidorhynchidae										
<i>Aspidorhynchus</i>	Bt-Ca, K-Po	K-Po	.	.	.	.	.	Ox-K	.	.
<i>Belonostomus</i>	Bt, K, Ne	K-Po	.	.	.	.	.	.	.	.
Pleuropholidae										
<i>Pleuropholis</i>	Po	K-Po	.	.	.	K-Po?	.	.	.	.
? <i>Ligulella</i>	.	.	.	.	.	K	.	.	.	.
Leptolepidae										
<i>Proleptolepis</i>	S	.	.	.	.	.	.	.	.	.
<i>Leptolepis</i>	T, Bt	T	.	T	T	.	.	.	P	.
Leptolepidae inc. sed.										
<i>Varasichthys</i>	.	.	.	.	.	.	Ox?	Ox-K?	.	.
<i>Luisichthys</i>	.	.	.	.	.	.	.	.	.	.
Ichthyodectiformes inc. sed.										
<i>Occlithrissops</i>	.	.	.	.	.	.	.	.	Bt	.
Allothrissopidae										
<i>Allothrissops</i>	K	K	.	.	.	.	.	.	.	.
Ichthyodectidae										
<i>Thrissops</i>	K-Po	.	.	.	.	.	Ox-K?	.	.	.
Ichthyodectiformes-Osteo-										
glossomorpha inc. sed.										
" <i>Leptolepis</i> "										
<i>macrophthalmus</i>	Ca	.	.	.	.	.	.	.	.	.
<i>Todilia</i>	.	.	.	.	.	.	.	.	Ca	.
" <i>Leptolepis</i> " spp.	Po	K	.	.	.	K	Po	Ox-K?, Po	.	.
<i>Pachythrissops</i>	Po	K	.	.	.	.	Ox-K?	.	.	.

TABLE 3—(Continued)

	1 Great Britain	2 Northern Europe	3 Portugal Spain	4 Italy Sicily	5 North Africa	6 Erythraean Trough Zaire	7 Argentina Chile	8 Mexico Cuba	9 USA Canada	10 USSR Japan
<i>Ascalobos</i>	.	K	.	.	.	.	.	.	.	.
<i>Tharsis</i>	K	K	.	.	.	.	.	.	.	.
<i>Chongichthys</i>	.	.	.	.	.	.	Ox-K?	.	.	.
<i>Neolycoptera</i>	.	.	.	.	.	.	U?	.	.	.
<i>Elopocephala</i> inc. sed.	.	K	.	.	.	.	.	.	.	.
<i>Anaethalion</i>	.	.	.	.	.	.	.	.	.	.
<i>Clupeocephala</i> inc. sed.	.	.	K	.	.	.	.	.	.	.
<i>Leptolepides</i>	.	.	.	.	.	.	Ox-K?	.	.	.
<i>?Protoclupea</i>	.	.	.	.	.	.	.	.	.	.
<i>Sarcopterygii</i>										
<i>Actinistia</i>										
<i>Coelacanthidae</i>										
<i>Holophagus</i>	S	T	Po	.	.	.	.	.	.	.
(= <i>Trachymetopon</i> )										
<i>Undina</i>	?H, Po	K	.	.	.	.	.	.	.	.
<i>Libys</i>	.	K	.	.	.	.	.	.	.	.
<i>Coccoderma</i>	.	K	.	.	.	.	.	.	.	.
<i>Bunoderma</i>	.	.	.	.	.	.	Po	.	.	.

<sup>a</sup> In tables 3 and 4 “?” means a question about systematics and “S?” means a question about age or stratigraphy.



fishes in the British Museum (Natural History), along with their systematic catalogues and stratigraphic records, have provided an updated, verified, or verifiable, list of Jurassic taxa that can serve as a standard for the identification of Jurassic assemblages from other areas. Assignment of genera to stage is frequently based on our assessment of these collections.

2. Northern Europe includes France and Germany with their diversified faunas, as well as Austria, Poland, Denmark, and Spitzbergen, which have relatively few reported taxa.

3. Spain and Portugal are grouped separately mainly to emphasize their Tethyan connections. All of these areas in western Europe were covered during most of the Jurassic by the transgressive eastern extension of the Tethys Sea (figs. 37–39). It should be noted here that the famous Montsech, Lérida locality in Spain, long regarded as Kimmeridgian-Portlandian, has proved to be Lower Cretaceous or Valanginian (Brenner, Geldmacher, and Schroeder, 1974).

4. Italy and Sicily were part of, or close to, the African plate in the Mesozoic and were also covered by the Tethys Sea. The entries for the Sinemurian in column 4 are based on preliminary determinations of a collection from Osteno, Lake Lugano, Lombardy (Pinna, 1967; Arduini, Pinna, and Teruzzi, 1981) now under study by B. G. Gardiner and C. Patterson.

5. North Africa is represented in table 3 to include Morocco, Algeria, and Tunisia. These areas were also covered by the transgressive Tethys.

6. The so-called Trans-Erythrean Trough (Hallam, 1975, p. 167 and fig. 10.2) was an extensive gulf-like transgression from the Tethys Sea that covered parts of Arabia, Baluchistan (India), East Africa, and Madagascar prior to their separation. As noted in table 3, some marine Jurassic fish remains have been found in each of these areas. The occurrence of Jurassic marine sediments and fishes in the Songa Limestone of Zaïre close to the equator and about 25°E longitude, can be most readily explained in terms of a limited, transitory, marine transgression that extended westward from the Trans-Erythrean Trough during the Late Jurassic (Cahen, 1954; Saint-Seine and Casier, 1962).

7. The western coastal areas of the South American plate were covered by transgressive seas during most of the Jurassic (Weeks, 1947, figs. 7, 8). As listed in table 3, fishes have been found in Argentina and Chile.

8. The separation of the North American and African plates began in the Early Jurassic. The North Atlantic ocean extended southward between these continents and, in effect, continued westward as an epicontinental seaway that sepa-

rated North and South America by the Early Bajocian (figs. 37–39). This seaway was responsible for the marine, fish-bearing deposits in Cuba and Mexico.

9. The western margin of the North American plate was covered by a transgressive sea during the Early Jurassic (fig. 37A, B). By the mid-Jurassic that sea extended into the western interior as a vast embayment (figs. 1 and 38). The Fernie Group of western Canada (Friebold, 1957), the Pliensbachian Nicely Formation of Oregon (Imlay, 1980), the Sundance and possibly all or part of the Wana-kah Formation were deposited in, or marginal to, this transgressive sea. As discussed earlier, all of these rock units contain fishes. The Greenland portion of the North American plate was covered by the sea along a restricted part of its eastern border during much of the Jurassic (figs. 38A, B, 39). One fish specimen has been described from Tithonian deposits on this island (Aldinger, 1932).

10. A single Late Jurassic marine fish occurrence has been reported from the island of Honshu, Japan (Yabe, 1902), probably on the southeast side where most of the marine facies are located. Russian marine (or presumably marine) fish localities have been reported in Upper Jurassic, probably Portlandian (Middle Volgian) deposits that are mostly west of the Ural Mountains (figs. 38B, 39).

#### Non-marine Occurrences (Table 4)

11. The entire Jurassic marine and continental rock sequence in Zaïre has been dated only to the Upper Jurassic, mostly on the basis of presumably marine fishes (Saint-Seine and Casier, 1962). This nearly unique nonmarine fish assemblage provides little aid in this regard.

12. The lacustrine deposits in the USSR reported to contain fishes have been approximately located on the basis of comments in Obruchev (1967): Karatau, Kazak, lat. 40–45°N, long. 70°E; Semipalatinsk, Kazak, lat. 50°N, long. 80°E; Bogoslovsk, Sverdlovsk, lat. 60°N, long. 60°E; Irkutsk, Irkutsk, lat. 51°N, long. 105°E. The fish assemblage for each of these localities has also been compiled from Obruchev (1967) which includes most of the primary references.

13. In China, Jurassic fishes have been found in continental, presumably lacustrine deposits in a number of provinces. They are listed here on the basis of updated information kindly supplied by Dr. Hsient'ing Liu (personal commun.), plus recent opinions regarding their affinities.

14. In India, the Kota Formation contains a Lower Jurassic assemblage recently reviewed by

TABLE 4  
World Distribution of Jurassic Fishes-Non-marine<sup>a</sup>

	11 Zaire	12 USSR	13 China	14 Thailand India	15 Australia	16 Antarctica	17 North America	18 Great Britain
<b>Chondrichthyes</b>								
Elasmobranchii								
Hybodontidae	.	.	.	L	.	.	.	.
<i>Hybodus</i>	.	.	M	.	.	.	.	We
<i>Acrodus</i>	.	.	M	.	.	.	.	.
<i>Lissodus</i>								
(= <i>Lonchidion</i> )	.	.	.	.	.	.	.	Bt, We
<i>Asteracanthus</i>	.	.	U	.	.	.	.	.
<i>Bdellodus</i>	.	.	.	L	.	.	.	.
<i>Hylaeobatis</i>	.	.	.	.	.	.	.	We
<b>Osteichthyes</b>								
Actinopterygii								
Holuridae								
<i>Palaeoniscinotus</i>	.	M	.	.	.	.	.	.
Coccolepidae								
<i>Pteroniscus</i>	.	U	.	.	.	.	.	.
<i>Coccolepis</i>	.	U	.	.	M	.	.	We
<i>Plesiococcolepis</i>	.	.	L	.	.	.	.	.
Ptycholepidae								
<i>Ptycholepis</i>	.	.	.	.	.	.	H-S	.
<i>Chungkingichthys</i>	.	.	M	.	.	.	.	.
<i>Yuchoulepis</i>	.	.	M	.	.	.	.	.
Redfieldiidae								
<i>Redfieldius</i>	.	.	.	.	.	.	S	.
Chondrosteidae								
<i>Peipiaosteus</i>	.	.	U	.	.	.	.	.
<i>Stichopterus</i>	.	M	.	.	.	.	.	.
Halecostomi								
Semionotidae								
<i>Semionotus</i>	.	.	.	.	.	.	H-S	.
<i>Lepidotes</i>	U	.	L	L-U?	.	.	.	Po, We
Dapediidae								
<i>Paradapedium</i>	.	.	.	L	.	.	.	.
<i>Tetragonolepis</i>	.	.	.	L	.	.	.	.
Gyrodontidae								
? <i>Tibetodus</i>	.	.	J	.	.	.	.	.
<i>Coelodus</i>	.	.	.	.	.	.	.	Po, We
Uarbryichthyidae								
<i>Uarbryichthys</i>	.	.	.	.	M	.	.	.
Halecomorphi								
Caturidae								
<i>Caturus</i>	.	.	.	.	.	.	.	We
Ophiopsidae								
<i>Neorhombolepis</i>	.	.	.	.	.	.	.	We
Amiidae								
<i>Sinamia</i>	.	.	U	.	.	.	.	.
<i>Ikechaoamia</i>	.	.	U	.	.	.	.	.

TABLE 4—(Continued)

	11 Zaïre	12 USSR	13 China	14 Thailand India	15 Australia	16 Antarctica	17 North America	18 Great Britain
Teleostei inc. sed.								
<i>Catervariolus</i>	U	.	.	.	.	.	.	.
<i>Galkinia</i>	.	U	.	.	.	.	.	.
<i>Ligulella</i>	U	.	.	.	.	.	.	.
<i>Majokia</i>	U	.	.	.	.	.	.	.
Pholidophoridae								
<i>Pholidophorus</i>	.	M-U	.	.	.	.	.	.
<i>Baleiichthys</i>	.	M	M	.	.	.	.	.
<i>Hungkiichthys</i>	.	.	J	.	.	.	.	.
<i>Hengnania</i>	.	.	L	.	.	.	.	.
<i>Aetheolepis</i>	.	.	.	.	M	.	.	.
<i>Aphnelepis</i>	.	.	.	.	M	.	.	.
<i>Madariscus</i>	.	.	.	.	M	.	.	.
<i>Archaeomaene</i>	.	.	.	.	M	.	.	.
<i>Oreochima</i>	.	.	.	.	.	M	.	.
Ichthyokentemidae								
<i>Ichthyokentema</i>	.	?M	.	.	.	.	.	.
Pleuropholidae								
<i>Pleuropholis</i>	U	.	.	.	.	.	.	.
<i>Parapleuropholis</i>	U	.	.	.	.	.	.	.
<i>Austropleuropholis</i>	U	.	.	.	.	.	.	.
Ichthyodectiformes-Osteoglossomorpha inc. sed.								
<i>Pachythrissops</i>	.	.	.	.	.	.	.	We
" <i>Leptolepis</i> " <i>talbragarensis</i>	.	.	.	.	M	.	.	.
<i>Aethalionopsis</i>	.	.	.	.	.	.	.	We
" <i>Leptolepis</i> " sp.	.	.	.	.	.	.	.	We
<i>Fuchunkiangia</i>	.	.	U	.	.	.	.	.
<i>Mesoclupea</i>	.	.	U	.	.	.	.	.
<i>Huashia</i>	.	.	U	.	.	.	.	.
Hiodontidae								
<i>Lycoptera</i>	.	.	U	.	.	.	.	.
<i>Tongxinichthys</i>	.	.	U?	.	.	.	.	.
<i>Sinolycoptera</i>	.	.	U?	.	.	.	.	.
Elopocephala inc. sed.								
" <i>Anaethalion</i> "	.	.	U	.	.	.	.	.
Clupeomorpha inc. sed.								
<i>Paraclupea</i>	.	.	U	.	.	.	.	.
Sarcopterygii								
Actinistia								
Coelacanthidae								
<i>Lualabaea</i>	U	.	.	.	.	.	.	.
<i>Indocoelacanthus</i>	.	.	.	L	.	.	.	.
<i>Diplurus</i>	.	.	.	.	.	.	S	.
Dipnoi								
Ceratodontidae								
<i>Ceratodus</i>	.	.	L, U	.	.	.	Pl, Po	Bt?

<sup>a</sup> See footnote on p. 76.

Jain (1980). Dr. Philippe Janvier (personal commun.) has provided information on the Jurassic fishes of Thailand.

15. The age of the well-known non-marine fish locality at Talbragar, New South Wales, Australia remains uncertain. It is regarded here as Middle Jurassic (White, 1981; Long, 1982).

16. The single actinopterygian known from Antarctica is probably of Middle Jurassic age (Schaeffer, 1972) and is apparently related to the pholidophorid *Wadeichthys* (Waldman, 1971) from the continental Lower Cretaceous of Victoria, Australia.

17. In regard to Jurassic non-marine fishes from North America, the Pliensbachian Kayenta Formation (Imlay, 1980) of Utah and Colorado has yielded only *Ceratodus* teeth. The Tithonian Morrison Formation also contains *Ceratodus* teeth plus some scrappy remains that suggest *Ophiopsis* (Prothero, 1981). Fishes from the Hettangian and Sinemurian zones of the Newark Supergroup are discussed by Olsen, McCune, and Thomson (1982). As interpretation of the depositional environment of the Todilto and Pony Express limestones remains equivocal (see section on Geologic Occurrence), the fishes from these units are included in the marine list along with the taxa from the Sundance Formation.

18. The British Purbeck and Wealden fishes (Woodward, 1916, 1919) are included here either under Portlandian (Purbeck below the Cinder bed) or Wealden (Purbeck above the Cinder Bed, Wealden).

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