

LATE TRIASSIC FISHES FROM THE
WESTERN UNITED STATES

BOBB SCHAEFFER

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LATE TRIASSIC FISHES FROM THE WESTERN UNITED STATES

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INTRODUCTION

IT IS AN INTERESTING COMMENT on the Atomic Age that the search for uranium minerals led to the discovery of abundant and diversified fishes in the continental Upper Triassic rocks of the western United States. Prior to the 1950's specimens were rare, widely scattered, and, with a few exceptions, too fragmentary for meaningful study or identification. The first recorded remains (indeterminate scales and teeth) were found in 1879 by C. D. Walcott at Kanab, Utah, in what is now recognized as the Moenave Formation. Four years later Walcott collected additional specimens (discussed by Eastman, 1905) at the same locality, including the well-preserved examples of *Semionotus kanabensis* (Schaeffer and Dunkle, 1950). In 1880 R. C. Hills found some vertebrate remains in the Chinle (Dolores) Formation near San Miguel, Colorado, that he considered to be "near *Belodon priscus* [?phytosaur] and *Catopterus gracilis*."

Except for *Ceratodus* teeth, which have been found sporadically in both the Chinle Formation and Dockum Group, no other fishes were reported from the western Upper Triassic until 1928 when Warthin described a coelacanth quadrate (along with a *Ceratodus* tooth) collected from the Dockum Group in 1925 by E. C. Case. A few years later, Branson and Mehl (1931) recorded the presence of fish scales in the top of the Chugwater Formation (?Popo Agie Member) in Wyoming. Baker (1933) also reported isolated scales from the Chinle near Moab (Utah). A partial specimen of *Semionotus* cf. *gigas* was described by Hesse (1935, 1936) from a bone bed in Zion National Park that is now placed at the base of the Moenave Formation.

In the summer of 1953 Y. W. Isachsen (at that time with the Atomic Energy Commission) found well-preserved fishes near Big Indian Rock in Big Indian Valley, San Juan County, Utah. Gordon W. Weir of the United States Geological Survey obtained additional specimens shortly thereafter at other localities in Big Indian Valley and adjacent Little Valley. During the same field season a party from the Museum of Comparative Zoology collected several fish slabs in Little

Valley. The specimens found by Isachsen and Weir were sent to the United States National Museum in the fall of 1953 for preliminary study by D. H. Dunkle. The following summer Dunkle obtained additional specimens at many of these localities, and through his cooperation I was able to obtain a collection for the American Museum. Another promising Chinle locality was brought to my attention by G. L. Jepsen in the fall of 1954. This was discovered a few months earlier by J. O. Kalliokoski in the Dolores River Canyon near Bedrock, Colorado.

In 1956 Dunkle generously offered me the Chinle fishes at the United States National Museum for description. The excellent prospect of obtaining additional and possibly new kinds of fishes from both the Big Indian and Bedrock areas prompted further field work, which was undertaken between 1958 and 1964. Collecting at these localities was carried out with the assistance of Walter Sorensen of the American Museum Vertebrate Paleontology Laboratory. F. Earl Green of Texas Technological College joined the field party in 1960; Gilbert F. Stucker, of the American Museum, in 1962; and Richard Lund, in 1962 and 1964.

In the early 1940's fish remains were collected in the Dockum Group at *Trilophosaurus* Quarry No. 3 near Otis Chalk, Howard County, Texas. During the summer of 1954, Green and I prospected for additional remains in the Dockum. Although the possibilities were far from promising, we were fortunate in finding a small pond deposit filled with mostly dissociated fish remains near the *Trilophosaurus* localities. The matrix samples returned to the American Museum contained some identifiable fragments, but no specimens complete enough for detailed study. Another visit to this locality in 1963 produced one of the finest redfieldiid skulls yet discovered, as well as additional partly associated material.

As the bone of both the Chinle and Dockum fishes is consistently softer than the surrounding matrix, the Airbrasive machine could not be used to expose the specimens. The long and frequently tedious manual

preparation was accomplished by Walter Sorensen, Martin Cassidy, and Michael Insinna. In order to obtain a sharp impression of the entire body, dilute hydrochloric and acetic acid were used to remove the bone fragments in several specimens with badly comminuted skulls and scales. "Smooth-on" peels made from these specimens have been particularly informative.

The photographs were taken with incandescent illumination or with ultraviolet radiation (at 3660 Å) by Chester Tarka. The drawings by Michael Insinna are based on opaque projections of selected specimens, on photographs provided by Tarka, and, for the redfieldiid skulls, on sheet wax reconstructions. Dorsal views of the redfieldiid skulls have been drawn without foreshortening to show the shape and relative size of the roofing elements.

I am greatly indebted to Dr. Gordon W. Weir and Dr. John H. Stewart, both of the United States Geological Survey, for locality and, particularly, stratigraphic data based on their extensive knowledge of the Upper Triassic sequence in the Colorado Plateau; and to Dr. F. E. Green, Dr. J. T. Gregory, and Mr. Glen L. Evans for information on the Dockum Group. The location and stratigraphic position of an Upper Triassic bone bed in Zion National Park were clarified through the cooperation of the Park Superintendent, Dr. Frank R. Oberhansky. Professor A. S. Romer kindly lent the Chinle specimens at the Museum of Comparative Zoology. I am also obligated to Drs. J. T. Gregory and J. Ostrom for the loan of remains in the Peabody Museum that Gregory collected in the Redonda Member of the "Chinle" in Quay County, New Mexico, and to Dr. J. A. Wilson for the opportunity to study the fishes from the *Trilophosaurus* Quarry. Dr. E. I. White

and Dr. Colin Patterson kindly permitted me to examine pertinent collections in the British Museum (Natural History); Dr. Brian Gardiner has generously provided additional data on the Australian and South African redfieldiids in that institution. Dr. A. W. Crompton and Dr. T. H. Barry arranged for the loan of the *Ischnolepis* specimens in the South African Museum (Natural History).

The purpose of the present paper is to describe the recently discovered fishes from the Chinle Formation and the Dockum Group, and to consider in more general terms the fish occurrences in the continental Upper Triassic rocks of western North America. Because the redfieldiids are of particular interest, a separate section is devoted to the morphology and distribution of the family Redfieldiidae.

ABBREVIATIONS

The following abbreviations are used to designate institutional collections:

- A.M.N.H., the American Museum of Natural History
- A.N.S.P., Academy of Natural Sciences of Philadelphia
- M.C.Z., Museum of Comparative Zoology, Harvard University
- P.U., Princeton University, Princeton, New Jersey
- S.A.M., South African Museum, Cape Town
- T.T.C.M., Texas Technological College Museum, Lubbock
- U.M.M.P., University of Michigan, Museum of Paleontology
- U.S.N.M., United States National Museum, Smithsonian Institution
- U.T.B.E.G., University of Texas, Bureau of Economic Geology, Austin
- Y.P.M., Peabody Museum, Yale University

GEOLOGIC OCCURRENCE

IN THIS SECTION an attempt is made to summarize the stratigraphy of the Upper Triassic fish localities in Colorado, Utah (text fig. 1), New Mexico, and Texas. Localities that have yielded the specimens described in this paper are discussed in some detail; others are mentioned only in regard to their stratigraphic allocation. The correlation chart (text fig. 2) is based in part on Reeside *et alii* (1957), and on unpublished data provided by F. E. Green, E. H. Colbert, and J. T. Gregory.

CHINLE FORMATION

In southeastern Utah the Upper Triassic Chinle Formation is divided into seven members: Temple Mountain, Shinarump, Monitor Butte, Moss Back, Petrified Forest, Owl Rock, and Church Rock (Stewart, 1956, 1957; Stewart *et al.*, 1959; Schultz, 1963). Throughout this area and in southwestern Colorado, the Chinle overlies the Moenkopi Formation (probably Lower and Middle Triassic), or, where the Moenkopi is absent, the Cutler Formation (Permian). It is overlain by the eolian, cross-bedded Wingate Sandstone (Upper Triassic).

Several members of the Chinle Formation pinch out or grade out to the north across southeastern Utah in the direction of Moab. In the Big Indian Valley area (San Juan County) a sandstone unit, correlated in part at least with the Moss Back Member, lies at the base of the Chinle. The overlying portion consists predominantly of red beds that are in part laterally continuous with the Church Rock Member. The lower part of these beds may grade into the Owl Rock Member, even though the two units are not lithologically similar.

In the Paradox Valley (and adjacent parts of the Dolores River Canyon), Montrose County, Colorado, the upper part of the Chinle (Dolores Formation of some authors) unconformably overlies the Moenkopi Formation. The Moss Back equivalent is absent, and the Chinle section is represented mainly by a lateral continuation of the Church Rock Member (see above; Stewart *et al.*, 1959, p. 551), which is overlain by the Wingate Sandstone. These units extend eastward to the

ancestral Uncompahgre Highland where they finally pinch out.

The Chinle fish localities in the northern part of the Colorado Plateau have been plotted on a sedimentary facies map kindly supplied by J. H. Stewart (see Stewart and Wilson, 1960). They all occur in a predominantly very fine-grained sandstone and siltstone facies, about 25 to 30 miles wide, which extends in a southeast direction from the vicinity of Castledale through Moab to Telluride and southward from there to the Colorado-New Mexico line. The lithology suggests deposition by a stream network; a major flow to the northwest is indicated by the cross strata (Stewart *et al.*, 1959, p. 523). The grain size and degree of sorting imply slow erosion in the source areas and deposition in a subsiding basin. The environment was probably an alluvial plain with streams and shallow-water ponds, or mud flats. Daugherty (1941) and Van Houten (1961) believed that the Chinle sediments were deposited in a tropical to subtropical climate, with an alternation of wet and dry seasons.

In both Big Indian Valley and the Dolores River Canyon, fish occur in channel deposits, and in laminated siltstones and mudstones indicating lacustrine deposition. The reason for this apparent restriction of the fishes to the sandstone and siltstone facies is obscure, particularly since the streams, ponds, and lakes of the alluvial plain must have supported large fish populations throughout Chinle time. The most reasonable conclusion is that the conditions for preservation were generally more favorable in certain sub-environments.

The Big Indian Valley-Little Valley section¹ has been studied in detail by G. W. Weir, and the following comments are based mainly on his unpublished data. In the Little Valley section measured by him (sects. 29, 32, T. 30 S., R. 25 E., S.L.P.M.), the upper part of the Chinle, from the Wingate contact to the top of the Moss Back equivalent,

¹ Little Valley is a southeast continuation of Big Indian Valley. See United States Geological Survey Mt. Peale 4 NW. Quadrangle, Utah, San Juan County, or Lisbon Valley 15-minute quadrangle, Utah-Colorado.

is 356 feet thick. This sequence is composed of alternating units of mudstone (28%), siltstone (24%), fine-grained sandstone (40%), and conglomerate (6%), and includes one layer of limestone (2%).

In Big Indian Valley and Little Valley the fish zone lies 125 to 150 feet below the base of the Wingate cliff, but the occurrences are spotty. At one locality (NW. $\frac{1}{4}$, sect. 30, T. 30 S., R. 25 E., S.L.P.M.) fish were found in a channel deposit of very fine-grained gray sandstone. This deposit, now covered with rubble from a prospector's road, is approximately 40 feet wide and 6 feet thick. The fishes are concentrated in a zone about 1 foot thick near the bottom. Dissociated remains are common, and complete specimens occur either massed together without orientation or are more or less scattered. Other occurrences in the vicinity of Big Indian Rock (e.g., sect.

24, T. 30 S., R. 24 E., S.L.P.M.) indicate that fish concentrations are fairly common in this area.

In Little Valley, abundant fish remains occur in a fine-grained, pale green siltstone unit about 10 inches thick, which is overlain by a greenish, mud-pellet conglomerate of about the same thickness. The unit is about 150 feet below a prominent cliff-forming spur of Wingate Sandstone on the southeast side of the valley (NW. $\frac{1}{4}$, sect. 32, T. 30 S., R. 25 E., S.L.P.M.). On the northwest side of this spur the unit can be followed for a distance of more than 1500 feet. About 1000 feet from the nose of the spur, the under surface of the fish-bearing layer has been exposed by slumping in the unit below. In the vicinity of the resulting overhang, the fish are concentrated in one bedding plane near the middle of the layer. Mass mortality in a sedi-

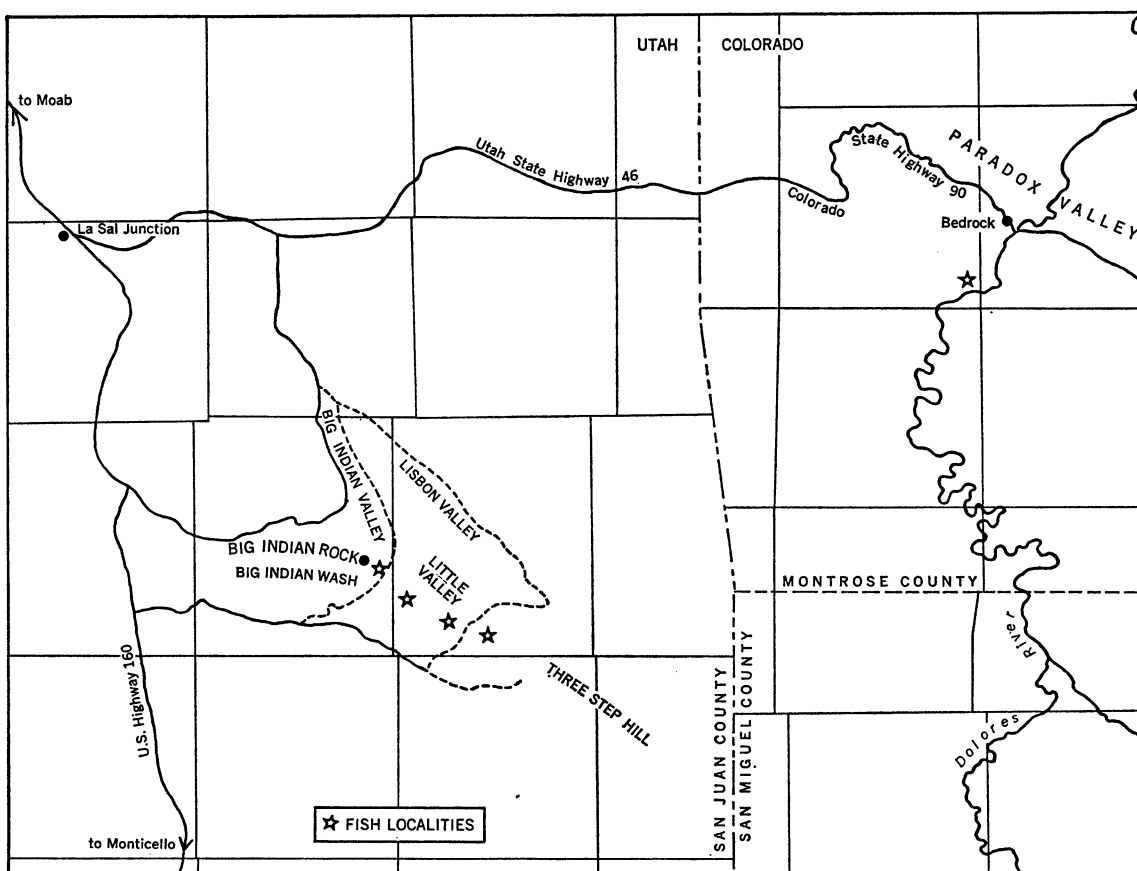


FIG. 1. Map of Chinle fish localities (indicated by stars) in San Juan County, Utah, and Montrose County, Colorado.

ment-laden or desiccated stream channel is the most reasonable explanation for this local abundance, which averages 25 to 30 individuals per square foot. Most of the known genera in the Chinle fish fauna are included here. Fishes have also been found at several places along the ridge (Three Step Hill) in sect. 33, T. 30 S., R. 25 E., S.L.P.M.

The Chinle fish localities in the Dolores River Canyon (about 22 airline miles northeast of Big Indian Rock) lie southwest of Bedrock, Montrose County, Colorado, about 2.8 miles up the canyon from the intersection of the canyon road with Highway 90. The fish zone is exposed in two dry washes, roughly 1000 feet apart, on the north side of the river. Locality A, the shallower wash, is east of, and Locality B, the deeper and more extensive wash, is south of, the center of sect. 36, T. 47 N., R. 19 W., S.L.P.M.

The stratigraphic position of the fish zone in the Dolores River Canyon is difficult to determine because the Chinle-Wingate contact is not sharp, as it is in southeastern Utah. Stewart (1956) has pointed out that, in parts of west-central Colorado, this contact is transitional, involving a lateral gradation of the Wingate Sandstone into the siltstone at the top of the Chinle. In the section immediately north of the fish localities, the typically massive, cross-bedded Wingate overlies a 50-foot-thick sequence of partly cross-bedded, sandy siltstone, and fine-grained sandstone units with thin, intercalated units of siltstone and mudstone. This sequence must represent interfingering and lateral gradation between the Wingate and Chinle as suggested by Stewart's fence diagram (1956, fig. 2, locality 21). Below the base of the transitional sequence there are about 40 feet of slope-forming, platy, fissile mudstones. The cliff-forming units in the canyon are invariably above the platy mudstone, but, depending on local conditions, the entire transitional sequence may either have a vertical face or be weathered into slopes with partly or completely isolated knobs and spurs.

A highly resistant red, gray, or greenish sandy siltstone about 1 foot thick, containing isolated bones of redfieldiids, semionotids, coelacanths, and phytosaurs, underlies the platy siltstone. As it is exposed in a generally east-west direction in most of section 36, this

"upper bone bed" forms a useful local horizon marker. Below the upper bone bed there is another 30-foot bed of fissile mudstone, with thin, intercalated units of siltstone, which forms gentle slopes to the canyon floor.

The main fish zone is exposed in the washes eroded below the general level of the canyon floor. At Locality A, fish have been found only in and immediately below a resistant, deep red, ripple-laminated siltstone that appears to be a channel deposit. The top of this unit is about 45 feet below the upper bone bed. A coelacanth skull (A.M.N.H. No. 5653) in a siltstone concretion was discovered on the floor of this wash near the canyon road. It had obviously been transported, but the source bed is unknown. At Locality B, the main fish horizon is capped by a ledge-forming unit of fine-grained sandstone 2 to 3 feet thick containing some fish and phytosaur fragments. It is approximately 128 feet below the base of the massive Wingate Sandstone, or 78 feet below the base of the transitional sequence.

Beneath the sandstone there is a dark reddish brown to purplish or greenish chunky mudstone 4 to 10 inches thick. Fish are present but rare in this unit. A partial coelacanth skeleton was found in the mudstone and another specimen in a siltstone concretion within the mudstone. Below the mudstone a 2-inch layer of greenish, nodular siltstone or mudstone, with a mud-pellet conglomerate base, contains abundant fishes. Underlying the greenish siltstone, another reddish brown to purple mudstone unit about 25 feet thick has fishes concentrated near the base. This lies above other mudstone and siltstone layers that could not be adequately prospected.

The entire fish zone in the Dolores Canyon, as described above, is roughly 30 feet thick. It probably includes concentrations of fishes at many levels covered by talus or unexposed in the canyon floor. It rests on a reddish brown silty sandstone unit approximately 35 feet thick that is cross-bedded in the upper half. This unit is exposed in the wash of Locality B where it runs to the Dolores River to the south of the canyon road. The change in lithology suggests local replacement of a broad stream channel by a shallow-water mud flat with more transient streams and ponds. Within the fish zone, rapid lateral

changes in lithology reflecting channel, pond, and mud-flat deposition are evident. The sequence detailed above (for Locality B) is not exactly repeated at Locality A, although the same general alternation of claystone and siltstone is evident.

Fish remains from other areas and members of the Chinle Formation are rare, but I suspect that scales, at least, have been found more frequently than published evidence indicates. In addition to the occurrences mentioned above in the Introduction, *Ceratodus* and *Semionotus* are known from the upper part of the Petrified Forest Member of the Chinle Formation in northern Arizona (Colbert and Gregory, 1957). A palaeonisciform of uncertain affinity and a coelacanth were found in association with *Coelophysis*, also in the upper part of this member, at Ghost Ranch, New Mexico. Isolated scales were recovered by C. L. Camp in the Upper Chinle about 10 miles south of Canjilon, New Mexico. Joseph T. Gregory has discovered *Ceratodus* teeth and catopterid remains in a red siltstone unit in the upper part of the Redonda Member of the "Chinle" Formation (the Redonda Formation of Griggs and Read, 1959) in North Apache Canyon, Quay County, New Mexico.

MOENAVE FORMATION

The Upper Triassic Moenave Formation has been described by Harshbarger, Repenning, and Irwin (1957) as a predominantly sandstone unit in northeastern Arizona and the adjacent part of Utah. It conformably overlies the Upper Triassic Wingate Sandstone, where present, and conformably underlies the ?Triassic Kayenta Formation. Two members have been recognized in the Moenave: the basal Dinosaur Canyon Sandstone and the overlying Springdale Sandstone. The latter is present only in the northern half of the Moenave depositional area.

Fish remains occur in the upper part of the Dinosaur Canyon Sandstone or the Springdale Sandstone (or both) at Kanab, Utah. In this area the Wingate Sandstone is absent and the Moenave overlies the Petrified Forest Member of the Chinle Formation. There are two bone beds at the Kanab locality, both with abundant *Semionotus* or *Lepidotus* remains in reddish brown argillaceous shale. The lower one, about 1 foot thick, is 260 feet

above the contact with the Chinle. The upper one, of the same thickness, is 43 feet above the lower bone bed. These distinctive units have been traced by E. H. Colbert from Kanab northeastward along the Vermilion Cliffs to Paria, a distance of 40 miles. The exact horizon from which Walcott obtained *Semionotus kanabensis* (Schaeffer and Dunkle, 1950) is not known, but his field notes (*in* Cross, 1908) suggest that it may be a fine-grained sandstone layer near the lower bone bed. According to Harshbarger, Repenning, and Irwin (1957, pp. 16-29), fish remains (not identified) have also been found in the upper part of the Dinosaur Canyon Sandstone Member at many localities between Kanab and Lees Ferry, Arizona, and particularly in the Vermilion Cliffs north of United States Highway 89 between House Rock and Marble Canyon.

A sparse, thin *Semionotus* bone bed is present in shales of the Springdale Sandstone Member in Zion Park near the mouth of Pine Creek Canyon. The Moenave here also overlies the Petrified Forest Member of the Chinle Formation. Presumably the partial specimen of *Semionotus* cf. *gigas* described by Hesse (1935) came from this locality.

DOCKUM GROUP

Separation of the Upper Triassic Dockum Group into the Tecovas Formation and the overlying Trujillo Formation is well defined in the Texas Panhandle (Reeside *et al.*, 1957). In the adjacent part of New Mexico the Trujillo may be represented by channel sandstones in a red shale unit overlying the Santa Rosa Sandstone. The red shale unit and the Redonda Member above it have been assigned to the "Chinle" Formation. South of the Panhandle, between Crosby and Howard counties, the Trujillo is presumably absent. According to some Dockum students, sandstone units, probably incorrectly referred to as Santa Rosa, separate a thick sequence of claystones and siltstones into an overlying "Chinle" and an underlying "Tecovas." The latter rests either directly on the Permian, or locally on a basal unit of the Dockum called the Camp Springs Conglomerate.

The relative ages of the various Dockum units (including the so-called "Chinle") and their correlation with the subdivisions of the Chinle and Chugwater formations to the

north and west have been elucidated by Gregory's (1957, 1962a, 1962b) analysis of their tetrapod faunas, particularly the phytosaurs. As fish remains have also been found in many of the units, a summary of this evidence is necessary.

In northeastern New Mexico, the Redonda Member of the "Chinle" has yielded advanced phytosaurs that indicate an age similar to the top of the Chinle in Utah. The red beds below the Redonda and above the Santa Rosa contain phytosaurs that are comparable to those from the upper part of the Petrified Forest Member of the Chinle in Arizona. These phytosaurs are more advanced than those from any part of the Dockum Group in Texas.

Phytosaurs from the Tecovas in the Texas Panhandle and from equivalent beds southward to Crosby County resemble forms from the lower part of the Petrified Forest Member of the Chinle. The Camp Springs Conglomerate in Scurry County, and the Dockum claystones and siltstones in Howard and Borden counties, contain the phytosaurs *Paleorhinus* and *Angistorhinus*. As these genera are more primitive than those from the Petrified Forest Member of the Chinle, the Dockum here can be regarded as possibly equivalent to the lower part of the Chinle in Utah, Arizona, and northwestern New Mexico. It can also be considered equivalent to the Popo Agie Member of the Chugwater Formation in Wyoming, which contains *Paleorhinus* and *Angistorhinus*. The tetrapod assemblage from the three *Trilophosaurus* quarries in Howard County includes these phytosaurs and is regarded by Gregory (personal communication) as "the earliest known [assemblage] from the Upper Triassic in North America." The phytosaur evidence thus indicates that the Dockum Formation transgresses time from south to north, and that there is a critical transition in Crosby County.

The fishes collected by Gregory in the Redonda and in the Upper "Chinle" of western New Mexico (discussed above) are closest in age to the fish faunas from the Upper Chinle in Big Indian Valley, Utah, and in the Dolores River Canyon, Colorado. The coelacanth skull described by Schaeffer and Gregory (1961) from the upper part of the Tecovas in Palo Duro Canyon, Randall County, Texas, and the coelacanth remains

discussed by Warthin (1928) from Crosby County, are from rocks probably equivalent to the Petrified Forest Member of the Chinle. *Ceratodus* teeth and isolated actinopterygian scales (in the Texas Technological College Museum) have been collected by F. E. Green in Crosby and Garza counties. Some of the Crosby County specimens are from beds containing *Rutiodon perfecta* and *R. ["Leptosuchus"] crosbiensis*, indicating an age equivalent to the lower part of the Petrified Forest Member in Arizona. Others occur in the *Paleorhinus* zone, which may be equivalent to the lower part of the Chinle. One of Green's localities, between Crosbyton and Kalgary, Crosby County, has also yielded fragments of *Trilophosaurus*.

The only Dockum locality that has produced abundant fish remains is southeast of Big Spring, Howard County, about 3 miles north of a settlement called Otis Chalk, on State Highway 821.¹ This small, apparently isolated, dark red siltstone lens is replete with partly and completely dissociated dermal bones and scales of redfieldiids. The nature of the preservation suggests maceration in a pond that was contracted during intervals of desiccation. As this deposit produced one of the best redfieldiid skulls ever found, it is frustrating to note that additional fish localities were not discovered in the extensive surrounding exposures.

In this area the red shales and intercalated sandstone layers are essentially horizontal, and the field evidence indicates that the fish locality is at about the same level as the nearby *Trilophosaurus* quarries. Quarry 3, about 0.5 mile to the east, has yielded several partial redfieldiid specimens, including the only known braincases that can be assigned to this family. On the basis of the evidence cited above, these are the oldest undoubted redfieldiids from North America. The Dockum here is 500 feet thick, which means only that these localities are close to the southeastern border of the geosyncline. The exact position of the *Trilophosaurus* level in this section has not been determined, but it must be several hundred feet above the base.

¹ 840 feet N., 30° W. of Heusinger Well 3 of the Basin Oil Company, Howard Glasscock Oil Field, SE. $\frac{1}{4}$, sect. 67, block 29, Waco and Northwestern Railroad Company Survey, Howard County, Texas.

SYSTEMATIC SECTION

CLASS CHONDRICHTHYES SUBCLASS ELASMOBRANCHII

ORDER HYBODONTIFORMES

FAMILY HYBODONTIDAE

Genus and species undetermined

The presence of a hybodont shark in the Dockum Group has been verified by the distal portion of a dorsal fin spine (U.M.M.P. No. 15442) from San Creek Canyon, Crosby County, Texas. Its dimensions suggest that the entire spine was 70 to 80 mm. long. The surface of the crown is ornamented with parallel ridges. Some of these bifurcate proximally, and about half of them terminate before reaching the tip. The posterior surface has two vertical rows of tubercles, but these are badly worn and the total number cannot be determined. The posterior border of the spine is straight. In cross section the proximal portion of the fragment is triangular. A single enlarged ridge forms a keel on the anterior border.

According to Colin Patterson (personal communication), the Dockum specimen closely resembles the dorsal spines of *Palaeobates keuperinus* from the English Keuper and *Lissodus* (Brough, 1935) from the Lower Triassic of South Africa. The dorsal spines of the Newark *Carinacanthus* (Bryant, 1934) differ in having a curved posterior border and no posterior denticles. Their lateral surface ornamentation is poorly preserved (P.U. No. 13739), but proximally it appears to consist of short anastomosing ridges.

Because the specimen was brought to my attention too late for complete description and illustration, it will be the subject of a subsequent publication.

CLASS OSTEICHTHYES SUBCLASS ACTINOPTERYGII INFRAClass CHONDROSTEI

ORDER PALAEONISCIFORMES

SUBORDER PALAEONISCOIDEI

FAMILY PALAEONISCIDAE

TURSEODUS LEIDY, 1857

Turseodus LEIDY, 1857, p. 167.

Gwyneddichtis BOCK, 1959, p. 47.

Eurecana BOCK, 1959, p. 99.

TYPE SPECIES: *Turseodus acutus* Leidy.

DISTRIBUTION: Upper Triassic. North America: Newark Group and Chinle Formation.

REVISED DIAGNOSIS: Palaeonisciform closely resembling other genera in the family Palaeoniscidae as restricted and defined by Aldinger (1937) and Nielsen (1942), but differing from them in possessing ossified, compound ring centra.

Turseodus dolorensis,¹ new species

Plates 8, 9, plate 10, figures 2,
3, 5; text figures 3, 4D

TYPE: A.M.N.H. No. 5614, complete specimen, from upper part of Chinle Formation, near Bedrock, Locality A, Montrose County, Colorado.

HORIZON AND LOCALITY: Upper part of Chinle Formation: Dolores River Canyon, Locality A, near Bedrock, Montrose County, Colorado.

DIAGNOSIS: Differing from *T. acutus* in having relatively smaller scales (78 to 80 vertical scale rows) on all parts of the body, and in having marginal teeth of uniform size.

REFERRED SPECIMENS: A.M.N.H. No. 5602, impression of nearly complete specimen; A.M.N.H. No. 5603, posterior half of body; A.M.N.H. No. 5604, isolated skull; A.M.N.H. No. 5605, nearly complete specimen, preservation poor; A.M.N.H. No. 5606, nearly complete specimen, with squamation on posterior half; A.M.N.H. No. 5607, nearly complete specimen, showing indications of centra; A.M.N.H. No. 5608, partly dissociated specimen, showing indications of centra; A.M.N.H. No. 5609, partly dissociated specimen, with skull impression; A.M.N.H. No. 5610, partly dissociated specimen, with some skull elements; A.M.N.H. No. 5611, partial skull; A.M.N.H. No. 5612, posterior portion of body, with squamation; A.M.N.H. No. 5613, partial skull; A.M.N.H. No. 5633, incomplete specimen, with part of skull, squamation well preserved locally; A.M.N.H. No. 5634, skull and posterior half of body; A.M.N.H. No. 5635, dissociated skull and scale patches; A.M.N.H. No. 5648, nearly complete specimen, with indications of cen-

¹ For the Dolores River.

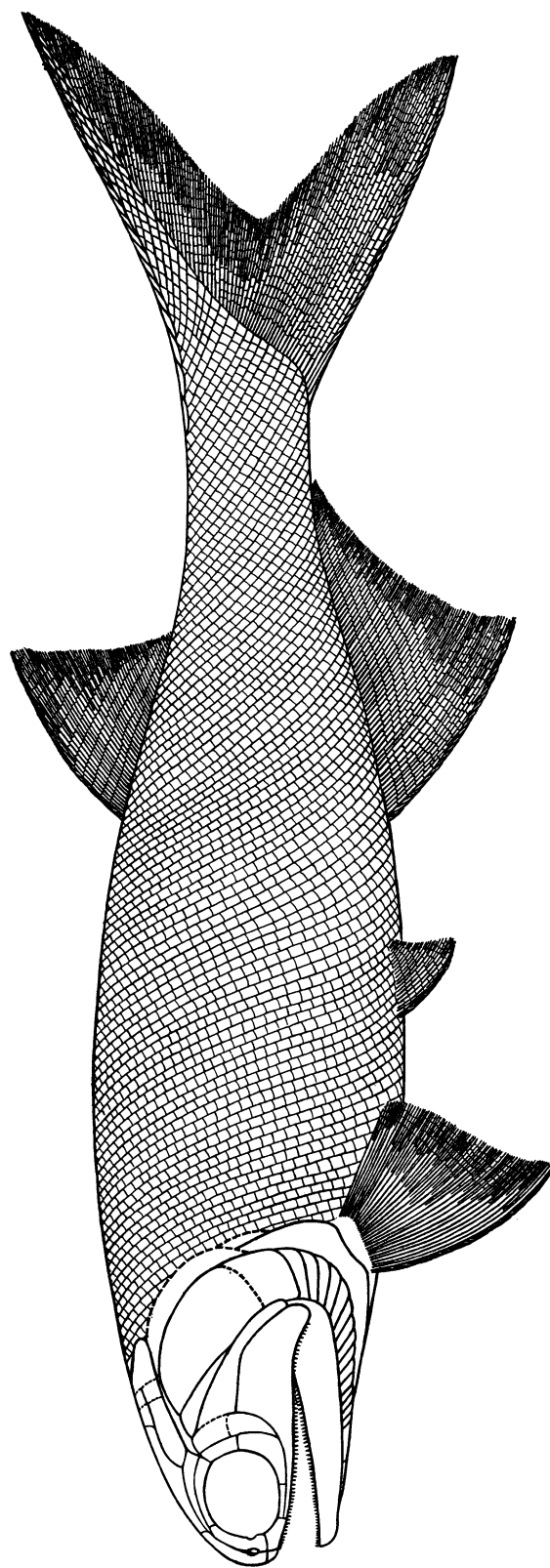


FIG. 3. *Turseodus dolorensis*, new species, restoration of body in lateral aspect.

tra; A.M.N.H. No. 5649, isolated parasphenoids; P. U. No. 19189, partial skull.

DESCRIPTION

BODY FORM AND MEASUREMENTS: The well-preserved specimens indicate that the body shape is similar to that of *T. acutus*. *Turseodus dolorensis* attained a known total length of 200 mm. According to Bock (1959), the Newark species reach 350 mm., although the individuals I have examined are less than half of that length.

SKULL: The dermal bones of the skull are ornamented with well-spaced tubercles except for the mandible which is covered with closely spaced, oblique ridges. Certain details of the cheek and roof pattern cannot be determined, but most of the diagnostic characters can be seen in A.M.N.H. Nos. 5602 and 5614.

A small rostral bone forms the anterior margin of the upper jaw below the postrostral which is typically constricted between the nares. The frontal has a slight projection midway along its lateral border, behind which there is a shallow embayment for the anterior portion of the dermopterotic. This relationship between the frontal and the dermopterotic appears to be characteristic of the Palaeoniscidae. The parietal, extrascapular, and suprascapular are vaguely defined in one specimen (A.M.N.H. No 5602) and seem to be typically palaeoniscid. The nasal forms the anterior border of the orbit and apparently meets a single supraorbital posteriorly. Unfortunately the upper orbital rim is poorly preserved in all specimens, but it is evident that the dermosphenotic extends forward as a narrow wedge between the supraorbital and the frontal almost as far as the anterior border of the frontal. In this respect the dermosphenotic resembles that of *T. acutus* (Schaeffer, 1952b), *T. minor* (Bock, 1959), and *Pteronisculus stensioi* (Nielsen, 1942). Several suborbitals are present in front of the preopercular. The postorbital and two infraorbitals are nearly identical with the same elements in *T. acutus* and *Pteronisculus* (Nielsen, 1942). The antorbital, which is well preserved in the type of *T. dolorensis*, is apparently distinctive for a palaeoniscid in having a narrow posterior elongation. Un-

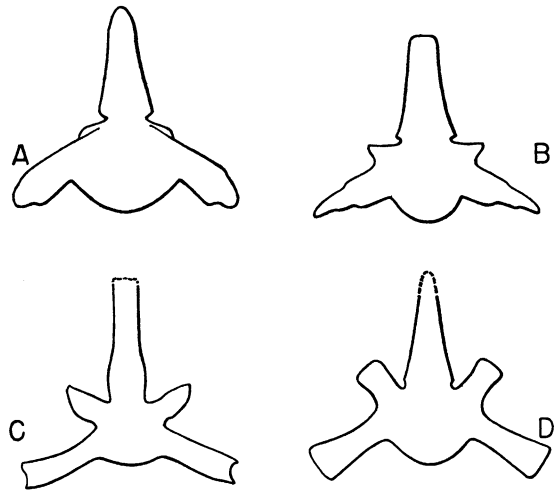


FIG. 4. Comparative series of palaeoniscid parasphenoids (depressed) in ventral aspect. A. *Palaeoniscus freieslebeni* (after Aldinger, 1937). B. *Pteronisculus magna* (after Nielsen, 1942). C. *Turseodus* cf. *acutus* (after Bock, 1959). D. *Turseodus dolorensis*, A.M.N.H. No. 5649.

fortunately, this element has not been described or figured for the Newark species.

The maxilla and mandible show no appreciable differences from those of the Newark species. In the vicinity of the symphysis, the fine diagonal ridges on the outer surface of the mandible are interrupted and nearly parallel. The dentigerous border of the *T. dolorensis* mandible appears to be more concave anteriorly than in the Lockatong forms, but this condition may be related to compression. Small acuminate teeth of about uniform length are present along the jaw margins. The pattern of the opercular complex agrees with that of the Newark species and with that of other palaeoniscids in that the opercular bone is larger than the subopercular and the branchiostegals number about 16.

An isolated parasphenoid found in association with other *T. dolorensis* remains compares closely with Bock's (1959, figs. 15 and 38) drawings of this element in the Lockatong species. The anterior and posterior processes have about the same proportions as in *Palaeoniscus* (Aldinger, 1937) and *Pteronisculus* (Nielsen, 1942; Lehman, 1952), except that the posterior one is narrower where it joins the central part. This difference may be

related to the greater separation of the two processes in *Turseodus*. As noted by Nielsen, the degree of separation cannot have the significance assigned to it by Aldinger. Rayner's (1951) observation that the size and configuration of the anterior process are tied to the dimensions and orientation of the basipterygoid process should also be mentioned in this regard (text fig. 4).

AXIAL SKELETON: The ossified, compound ring centra of *T. dolorensis* are identical with those of *T. acutus* (pl. 10, fig. 4) in consisting of delicate, separated, dorsal and ventral, wedge-shaped half-rings. Isolated centra from the upper bone bed in Dolores Canyon that apparently belong to *Turseodus* show that the neural arches are independent ossifications. Radiographs of the *T. dolorensis* type specimen indicate that centra are present along the entire length of the notochord.

PAIRED FINS: The pectoral fin has a nearly horizontal insertion and is composed of about 24 rays which are segmented distally. The origin of the much smaller pelvic fin is about midway between the origin of the pectoral and that of the anal. The total number of pelvic rays is estimated to be about 20.

MEDIAN FINS: The dorsal fin arises a short distance in front of the anal rather than opposite the pelvic fin, as in *Palaeoniscus* and *Pteronisculus*. It includes about 44 completely segmented rays, and is bordered by fringing fulcra. As in *T. acutus*, but in contrast with other palaeoniscids, the anal fin is elongated to include approximately 78 completely segmented rays. The scales covering the terminus of the body axis are attenuated and are difficult to separate from the fulcra and the fin rays. The caudal fin is bifurcate and externally homocercal.

SQUAMATION: The scales of *T. dolorensis* measure about 1 mm. on a side over all parts of the body. They are ornamented with low, nearly parallel ridges which are frequently interrupted, but rarely anastomose. The number of ridges per scale varies between four and five on most of the body, to seven on the scales of the peduncle; the flank scales of *T. acutus* (P.U. No. 16152b; pl. 10, fig. 1) have as many as 10 ridges. The number of vertical scale rows between the posterior border of the supracleithrum and the beginning of the caudal inversion is about 78. In

Bock's (1959) restoration of "*Gwyneddichtis*" there are about 70 vertical scale rows, and in *T. acutus* from the Princeton locality, approximately 55. In cross section the scales show only ganoine and bony layers. The bony layer is faintly laminated and cell spaces are not in evidence.

DISCUSSION

The genus *Turseodus* was erected by Leidy in 1857 on the basis of a single mandible (A.N.S.P. No. 14535) obtained from the Lockatong Formation of the Newark Group near Phoenixville, Pennsylvania. A few years later, C. M. Wheatley collected a number of isolated scales and skull elements (A.M.N.H. No. 8107) from the same area that were identified (?by him) as *Turseodus*. Additional specimens from the Lockatong at the Granton Quarry, North Bergen, New Jersey, and from the site of the Firestone Library at Princeton University were referred to *Turseodus* by Schaeffer (1952b).

Bock (1959) has also described palaeoniscid remains that he collected at a number of localities in the Lockatong Formation of the Newark Group in Bucks County, Pennsylvania. A single mandible was assigned by him to *Turseodus*, and other specimens were assigned to the new genera *Gwyneddichtis* and *Eurecana*. Bock distinguished these taxa from *Turseodus* mostly on the basis of differences in body size and scale ornamentation. In addition, he erected a new family, the Turseoidae.

The mandible described by Leidy in 1857, which is the type specimen of *Turseodus acutus* (A.N.S.P. No. 14535), is incomplete, but it must have been more than 4 cm. in length. The surface ornamentation, which is preserved only on a small area near the symphysis, consists of interrupted, nearly parallel ridges. The dentigerous border is gently curved, and the marginal dentition includes numerous small teeth situated between well-spaced, larger teeth. Mandibles in the Wheatley collection as well as those from Princeton and from the Granton Quarry are apparently identical except that they came from individuals of different sizes.

Bock (1959, pp. 47, 94) claimed that *Gwyneddichtis* could be distinguished from

Turseodus acutus "mainly by its lower jaw structure." Certainly the Princeton specimen figured by me in 1952, which Bock believed was close to his *G. gwyneddensis*, is virtually identical with *Turseodus*. The diagnostic characters of *Eurecana*, according to Bock (1959, pp. 99–101), are its greater size, deeper body, and squamation.

In my opinion, Bock has not presented satisfactory evidence for recognizing two additional genera. The mandible of *Gwyneddichtis* is certainly similar enough to the type of *Turseodus* to indicate, on this basis, that we are dealing with a single genus. *Eurecana* is based on two incomplete specimens, neither of which includes a lower jaw. The scales differ only in the number of ridges.

Although I believe that present evidence favors the recognition of only one palaeonisciform (*Turseodus*) in the Newark, Bock's data suggest that two or three species may be recognized. This conclusion is based on relative scale size (scale number and size are reasonably constant within an actinopterygian species) and on the number of scale ridges. Specific separation is indicated for individuals with about 55 transverse scale rows (e.g., Bock's *G. minor*) and for those with about 70 (Bock's *G. gwyneddichtis*). On the basis of scale size, *Eurecana* might fit into the *G. minor* category, but the presence of 20 ridges on the scales, as opposed to no more than 12 on the scales of other possible species, suggests that a third species may be present.

The genotypic species, *T. acutus*, is based on a specimen that is presently indeterminate, but it may be possible to relate it to more complete individuals when the Bock collection is reworked. The position of the dorsal fin in the restoration of the Princeton specimen (P.U. No. 16153) assigned to *T. acutus* (Schaeffer, 1952b) is now open to question. If its origin is actually behind that of the dorsal, which is not the case in other individuals of *Turseodus* showing the relative positions of the unpaired fins, there is further basis for specific separation.

Turseodus dolorensis differs from the several presumed Newark species in having the greatest number of transverse scale rows (78–80) and in having scales of uniform size except on the caudal axis. Also, the marginal

teeth are of the same size, which is apparently not the case in the Newark forms.

Bock's justification for erecting a separate family (the Turseoidae) to contain the *Turseodus* complex was based primarily on the presence of ossified ring centra. *Turseodus* is apparently unique among known palaeoniscoids in possessing these ossifications surrounding the notochord, but, as I pointed out in 1952 (before the discovery of the centra), this genus is otherwise difficult to distinguish from the other members of the Palaeoniscidae. Bock's figures of the skull roof (1959, p. 89) reinforce this opinion, particularly with respect to the shape of the frontal-dermopterotic contact.

Ossified centra evolved independently numerous times within the Osteichthyes. Although the morphogenetic mechanism has not been worked out, it is probable that the capacity to form serial ossifications around the notochord independently of the arch bases was present in nearly all the early osteichthyan groups. For reasons unknown, this capacity was rarely realized in the primitive actinopterygians and never in the coelacanth, but it was expressed in some Devonian dipnoans and in the rhipidistians. The development of ossified centra in relatively primitive actinopterygians such as *Turseodus* and the pholidophorids (Nielsen, 1942) suggests some adaptive advantage associated with locomotion. Such examples represent, in effect, experiments in vertebral design at the chondrostean level that anticipate the far greater experimentation at the holostean level. In several holostean families (e.g., the Semionotidae and the Amiidae) the earliest genera lack ossified centra, but the later ones possess them. Among the closely related *Acentrophorus*, *Semionotus*, and *Lepidotes*, which more or less follow one another in time, only the last has ossified centra. In view of this fact, I can see no reason to place the *Turseodus* complex in a separate family.

The allocation of *Turseodus* to the Palaeoniscidae as defined by Aldinger (1937) might be questioned on two other points. One pertains to the significance of certain non-vertebral characters. Aldinger's diagnosis of the Palaeoniscidae, by his own admission, was not completely restrictive, mainly because of modifications through time within the

family. But the four genera assigned by him to the Palaeoniscidae (*Palaeoniscus*, *Gyrolepis*, *Pteronisculus*, and *Cosmolepis*) possess eight characters (see Nielsen, 1942, pp. 276-277) that seem to set apart the palaeoniscids from presumably related families. Of these, seven are definitely present in *Turseodus*. The remaining one (two pairs of extrascapulars) cannot be determined with certainty in the available Lockatong or Chinle specimens. In addition, *Turseodus* shows many of the "progressive" features discussed by Nielsen which places it at about the *Glaucolepis-Gyrolepis* stage (see Schaeffer, 1952b, p. 22). It therefore appears entirely reasonable to assign *Turseodus* to the Palaeoniscidae as this family is presently understood.

Another problem is related to the fact that all the species in Aldinger's four genera are marine. Also, all are known only from Europe except the Early Triassic *Pteronisculus* which has a typical "*Bobasatrania* fauna" distribution, including Spitzbergen, Greenland, Madagascar, and British Columbia. Since *Turseodus* shows no particular affinity with the Middle or Upper Triassic *Gyrolepis* or, for that matter, with the Liassic *Cosmolepis*, it could represent a descendant of a North American *Pteronisculus* stock that subsequently entered fresh water. In this connection it is important to recall that Triassic palaeonisciforms are exceedingly rare in North America. It is therefore not reasonable to dismiss a palaeoniscid affinity for *Turseodus* because its presumed relatives are marine and apparently far removed in space or time. Further refinement of palaeonisciform classification plus additional finds on this continent will be required to provide a final solution to the *Turseodus* problem.

SUBORDER REDFIELDIOIDEI

FAMILY REDFELDIIDAE

CIONICHTHYS,¹ NEW GENUS

TYPE SPECIES: *Cionichthys dunklei*, new species.

DISTRIBUTION: Upper Triassic. North America: Chinle Formation and Dockum Group.

DIAGNOSIS: Similar to *Redfieldius* from the Newark Group in most dermal skull and

postcranial characters, but differing from that genus in having two rectangular parietals (rather than three or four), and in having much weaker ornamentation on dermal bones.

Cionichthys dunklei,² new species

Plates 11, 12; text figures 5, 6

TYPE: A.M.N.H. No. 5615, complete specimen, from upper part of Chinle Formation, Big Indian Wash, San Juan County, Utah.

HORIZON AND LOCALITIES: Upper part of Chinle Formation: Big Indian Wash and Little Valley, San Juan County, Utah; Dolores River Canyon, near Bedrock, Montrose County, Colorado; ?San Miguel, San Miguel County, Colorado.

DIAGNOSIS: Dermosphenotics and dermopterotics of nearly equal length and breadth; adnasal excluded from narial opening.

REFERRED SPECIMENS: Big Indian Wash, San Juan County, Utah: A.M.N.H. No. 5616, skull and anterior body; A.M.N.H. No. 5617, partial skull and body. Little Valley, San Juan County, Utah: A.M.N.H. No. 5618, specimen lacking tail; A.M.N.H. No. 5619, partial skull and anterior part of body; A.M.N.H. No. 5620, small, nearly complete specimen; A.M.N.H. No. 5621, skull roof; A.M.N.H. No. 5622, skull and anterior part of body; A.M.N.H. No. 5623, partial skull and body. Locality A, near Bedrock, Dolores River Canyon, Montrose County, Colorado: A.M.N.H. No. 5626, complete fish; A.M.N.H. No. 5627, nearly complete specimen, lacking tail; A.M.N.H. No. 5628, complete specimen; A.M.N.H. No. 5629, partial skull and body; A.M.N.H. No. 5650, fish lacking caudal fin; A.M.N.H. No. 5651, specimen lacking tail, skull in ventral aspect. Locality B, near Bedrock, Dolores River Canyon, Montrose County, Colorado: A.M.N.H. No. 5624, complete fish; A.M.N.H. No. 5625, nearly complete fish; A.M.N.H. No. 5630, skull and part of body; A.M.N.H. No. 5631, nearly complete dissociated fish; A.M.N.H. No. 5632, partial skull and anterior part of body. Vicinity of San Miguel, San Miguel County, Colorado: A.M.N.H. No. 5661, incomplete weathered specimen (collected by R. C. Hills, 1880, tentatively referred to *Cionichthys*).

¹ Greek *kion*, pillar, for Big Indian Rock, and *ichthys*, fish.

² For David H. Dunkle.

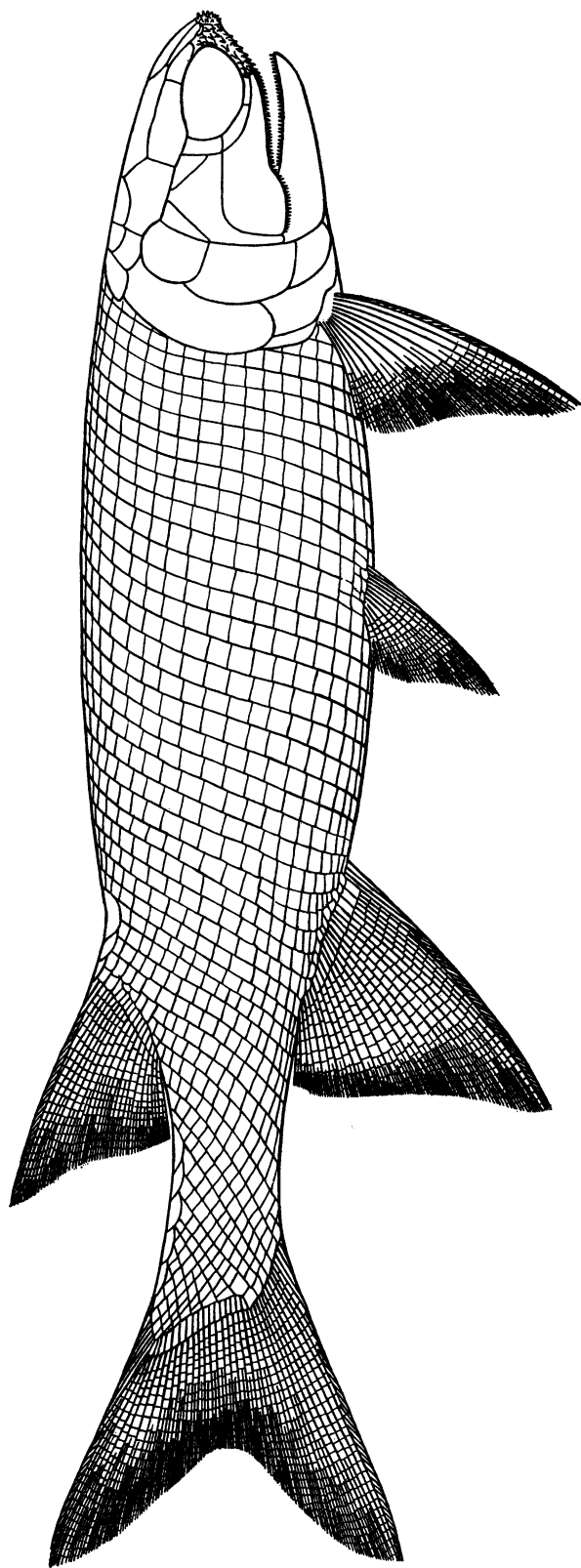


FIG. 5. *Cionichthys dunklei*, new genus and species, restoration of body in lateral aspect.

Cionichthys greeni,¹ new species

Plate 13, figures 1-3; text figures 5-7

TYPE: A.M.N.H. No. 5600, complete skull, from lower part of Dockum Group, near Otis Chalk, Howard County, Texas.

HORIZON AND LOCALITY: Dockum Group: near Otis Chalk, Howard County, Texas.

DIAGNOSIS: Differs from *C. dunklei* in having relatively longer and narrower dermosphenotics, smaller adnasals (which form posterior margin of narial opening but do not enter orbital rim), shorter posteroventral ramus on antorbital, posterior border of opercular bone and scales denticulated.

REFERRED SPECIMENS: A.M.N.H. No. 5596, numerous isolated skull bones and scale patches; A.M.N.H. No. 5597, partial skull and body; A.M.N.H. No. 5598, partial skull; A.M.N.H. No. 5599, partial skull.

DESCRIPTION

Although there is a close resemblance between *Cionichthys* and *Redfieldius*, certain consistent differences favor separate generic rank for the Chinle-Dockum form. The earlier account of the *Redfieldius* skull by Brough (1931) must be modified on the basis of specimens recently obtained from the Newark Group in Virginia. The following description includes both genera.

BODY FORM AND MEASUREMENTS: *Cionichthys* has a fusiform outline and characteristically remote dorsal and anal fins. The observed total body length is about 160 mm. The skull is somewhat less than one-fifth of the total length, and the maximum body depth is somewhat more than one-fifth of that length (text fig. 5). *Redfieldius* has similar proportions except for the greater body depth (about one-third greater than skull length) in *R. redfieldi*. The maximum length of *R. gracilis* and *R. redfieldi* is about 250 mm.

SKULL (TEXT FIGS. 6, 7): In *Cionichthys* the dermal bones of the skull, excepting the rostral and the antorbital, are ornamented with low, ovoid tubercles and ridges. In the two species of *Redfieldius* the tubercles are relatively higher and more crowded than in *Cionichthys*. These differences are evident in skulls of about the same size (text fig. 8).

The rostral bone in both genera is covered

externally with strong, toothlike denticles. Its posterior margin is gently rounded in *Cionichthys* and forms a broad V in *Redfieldius*. The canal for the rostral commissure, which is occasionally visible on the inner surface of the rostral bone, is situated fairly close to the dentigerous anterior border. The postrostral is nearly ovoid, with its more expanded posterior portion fitting into a wide notch between the frontals. The narrow nasal is notched anterolaterally for the narial opening. It is situated between the postrostral and the more lateral adnasal.

The element here named the adnasal (the prefrontal of Brough, 1931) is lateral to the nasal and the frontal. It articulates posteriorly with the dermosphenotic and anterolaterally with the antorbital. In *Cionichthys* and *Redfieldius* it enters the posterior border of the nares; in *C. dunklei* it also forms part of the orbital rim. The adnasal is present in all of the Chinle-Dockum redfieldiids, in *Redfieldius*, and in the South African *Helichthys* (Brough, 1931). It may represent an isolated anterior supraorbital or possibly a "subdivision" of the antorbital. A similarly situated bone occurs in the palaeoniscoid *Aeduellia* (Westoll, 1937), but its relationships with the other rostral elements are unknown.

The three-pronged antorbital bone forms the anterior margin of the orbit and the lateral margin of the nares. Anteriorly it is in contact with the rostral; medially it meets the adnasal, and in *C. greeni* also the frontal. The infraorbital canal runs through the orbital ramus to join the rostral commissure. Although the antorbital is rarely preserved in its natural position, there is ample evidence that the ventral border of its orbital ramus is in line with the maxillary margin (see also the "nasal+antorbital" in *Ptycholepis bollensis*; Gardiner, 1960). As is the rostral, the antorbital bone is covered with robust, toothlike denticles that are considerably larger than the maxillary or mandibular teeth.

As the mandibles are about the same length as the infraorbital ramus of the maxilla, the toothlike denticles along the ventral margin of the rostral and the antorbital could not have functioned in seizing prey. Furthermore, it has not been possible to reconstruct the well-preserved snout of *C.*

¹ For F. Earl Green.

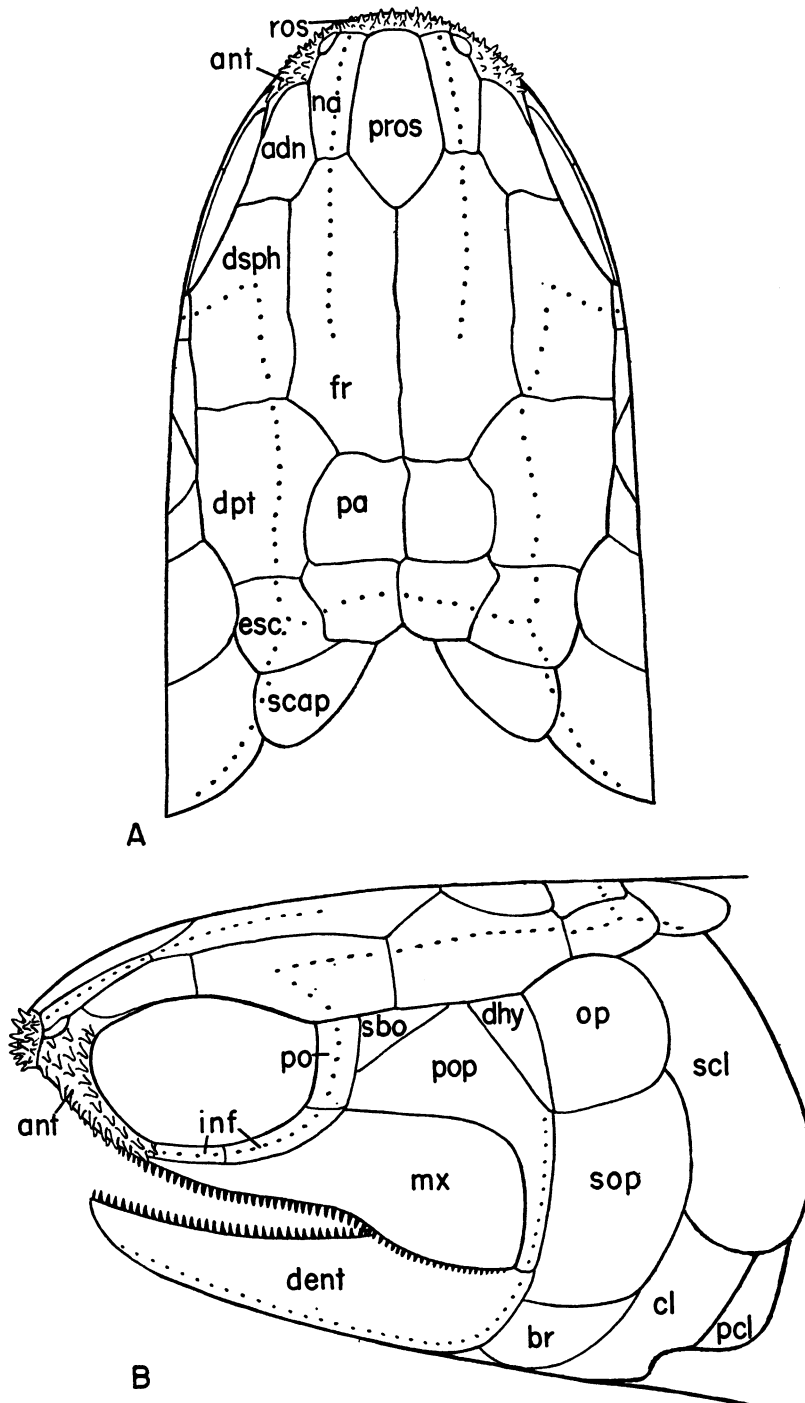


FIG. 6. *Cionichthys dunklei*, new genus and species, restoration of skull. A. Dorsal aspect. B. Lateral aspect. Both *ca.* $\times 3.35$.

Abbreviations: adh, adnasal; ant, antorbital; br, branchiostegal; cl, cleithrum; dent, dentary; dhy, dermohyal; dpt, dermopterygoid; dsph, dermosphenoid; esc, extrascapular; fr, frontal; inf, infraorbital; mx, maxilla; na, nasal; op, opercular; pa, parietal; pcl, postcleithrum; po, postorbital; pop, preopercular; pros, postrostral; ros, rostral; sbo, suborbital; scap, suprascapular; scl, supracleithrum; sop, subopercular.

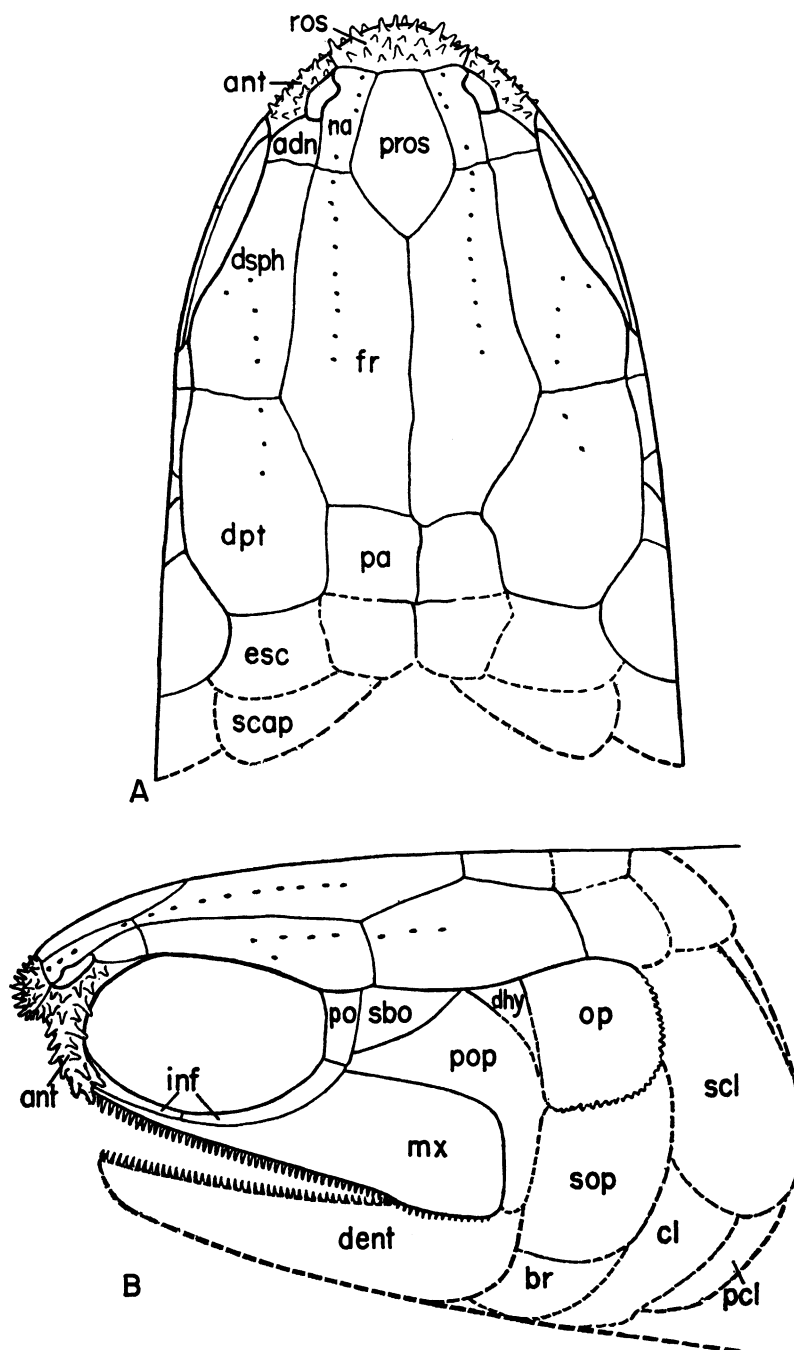


FIG. 7. *Cionichthys greeni*, new genus and species, restoration of skull. A. Dorsal aspect. B. Lateral aspect. Both *ca.* $\times 4$.

Abbreviations: adn, adnasal; ant, antorbital; br, branchiostegal; cl, cleithrum; dent, dentary; dhy, dermohyal; dpt, dermoterygoid; dsph, dermosphenoid; esc, extrascapular; fr, frontal; inf, infraorbital; mx, maxilla; na, nasal; op, opercular; pa, parietal; pcl, postcleithrum; po, postorbital; pop, preopercular; pros, postrostral; ros, rostral; sbo, suborbital; scap, suprascapular; scl, supracleithrum; sop, subopercular.

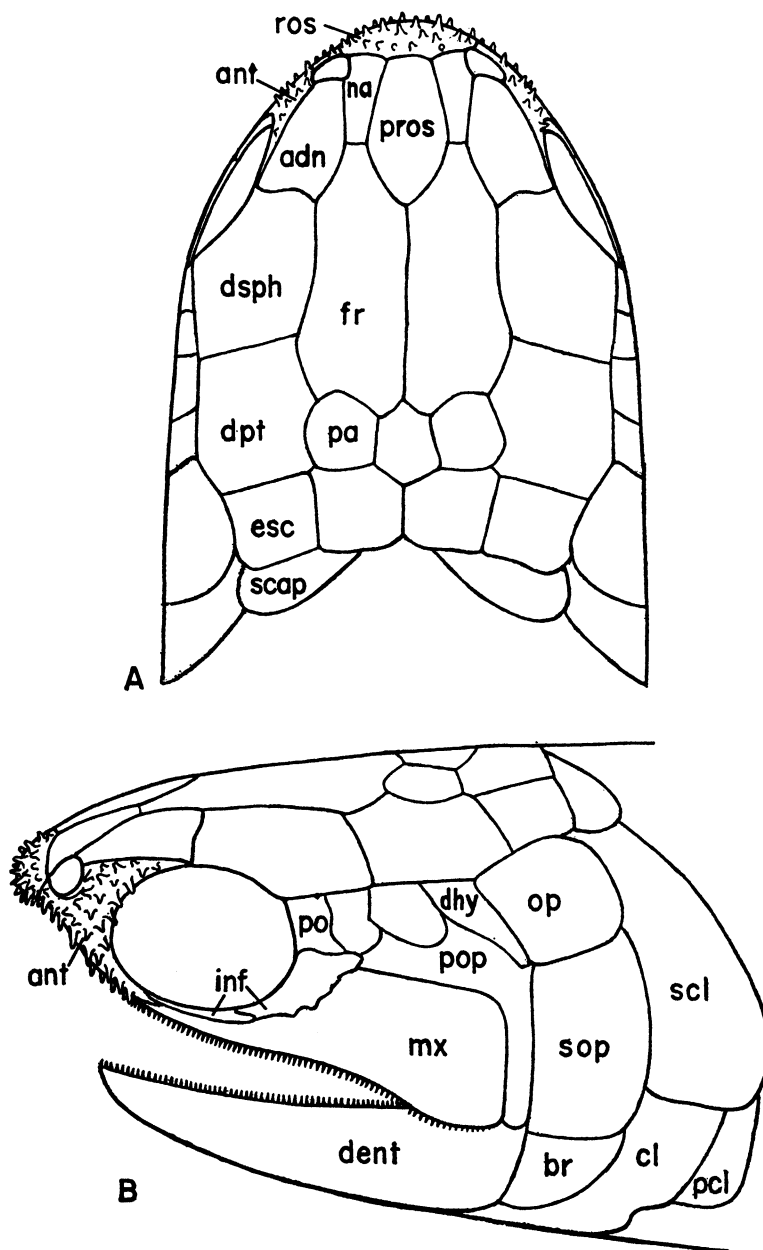


FIG. 8. *Redfieldius* sp., restoration of skull. A. Dorsal aspect. B. Lateral aspect. Both ca. $\times 2.76$.

Abbreviations: adn, adnasal; ant, antorbital; br, branchiostegal; cl, cleithrum; dent, dentary; dhy, dermohyal; dpt, dermopterygoid; dsph, dermosphenoid; esc, extrascapular; fr, frontal; inf, infraorbital; mx, maxilla; na, nasal; op, opercular; pa, parietal; pcl, postcleithrum; po, postorbital; pop, preopercular; pros, postrostral; ros, rostral; sbo, sub-orbital; scap, suprascapular; scl, supracleithrum; sop, subopercular.

greeni (A.M.N.H. No. 5600) in a way that would permit the rostral teeth to meet the mandibular ones even if the lower jaws were actually longer. Part of the space between opposite antorbitals must have been occupied by the mandibles when the mouth was completely closed, but we have been unable to eliminate the resulting space between the ventral margin of the rostral and the mandibular symphysis. The only apparent explanation for the overhanging rostrum and the gap is that *Cionichthys* (and other American redfieldiids) had a fleshly, sucker-like upper lip in which the rostral and antorbital denticles were embedded.

The narrow, nearly rectangular frontals are about three times the length of the parietals. The supraorbital canal, represented by a single row of pores in each frontal, terminates just behind the middle of the frontals. In *Cionichthys* there is always one pair of nearly square parietals. *Redfieldius* has three, or in some specimens four, parietals arranged in a transverse row.

The large dermosphenotic nearly equals the dermopterotic in length and area, and in *C. greeni* it reaches the antorbital. The infraorbital sensory canal makes a characteristic lateral swing within the dermosphenotic to enter the postorbital. The essentially rectangular dermopterotic requires no special comment. The extrascapular series consists of four elements carrying the posterior commissure. The bluntly rounded suprascapulars are separated at the midline.

Both genera have a barlike postorbital bone and two infraorbitals. The preopercular is expanded above the maxilla and has a narrow vertical ramus. A single suborbital borders the preopercular anteriorly, and a wedge-shaped dermohyal is situated above and behind the preopercular. The best available cheek of *Redfieldius* (A.M.N.H. No. 4803) shows an additional bone between the suborbital and the dermohyal (pl. 13, fig. 4) that can be equated with the "X²" bone in *Helichthys ctenipteryx* (Brough, 1931, fig. 9) and with the "supraspiraculars" in *Perleidus* (Lehman, 1952).

The postorbital expansion of the maxilla has a nearly horizontal dorsal border. The suborbital ramus is in contact with the antorbital. The opercular is about one-half the size of the narrow subopercular. A single

branchiostegal plate lies immediately below the subopercular. In *Redfieldius* and *Cionichthys* there is a median gular followed by at least one set of paired gulars (pl. 14).

APPENDICULAR SKELETON: The supra-cleithrum is ovoid in outline and ornamented with long ridges in both genera. One or two postcleithra, also ornamented, are situated along the posterior border of the cleithrum. The latter is heavily ossified and is covered with strong, longitudinal ridges.

The well-developed pectoral fin of *Cionichthys dunklei* is bordered anteriorly by delicate, fringing fulcra. It consists of 10 or 11 rays, apparently segmented only in their distal third. The pectoral of *Redfieldius* appears to be relatively shorter but with about the same number of rays. The pelvic fin, with about eight or 10 distally segmented rays, is situated midway between the pectorals and the anal. The dorsal fin arises behind the origin of the anal, is bordered anteriorly by basal and fringing fulcra, and is composed of about 15 completely segmented rays. The broad-based anal also has basal and fringing fulcra and includes about 24 completely segmented rays. The caudal fin is equilobate, is bordered above and below by fulcra, and is composed of about 33 completely segmented rays. The caudal axis is very short.

SQUAMATION: The scales of *Cionichthys dunklei* have a smooth posterior border; those of *C. greeni* are denticulated as in *Redfieldius*. In thin section, the scales show a lepidosteoid structure with lamellated enamel, no cosmine layer, and a thick, lamellated bony layer. Cell lacunae occur at the boundaries between the bone lamellae. Numerous canals extend from the base of the bony layer to the enamel but do not penetrate it. These presumably represent the lepidosteoid tubes of Kerr (1952), which in life probably contained bundles of collagen fibers that anchored the scales to the underlying connective tissues. Vascular canals are apparently absent.

DISCUSSION

Cionichthys is regarded as generically distinct from *Redfieldius* mainly because it has one pair of parietals. *Redfieldius* apparently invariably has three or four parietals (the median one may be subdivided) arranged in a transverse row. The difference in these two parietal patterns, in my opinion, favors ge-

neric separation (as in the case of *Sinamia* versus *Amia*), since each was apparently morphogenetically stabilized. In other forms at the chondrosteian level, such as *Australosomus merkei*, which lack such stabilization (Lehman, 1952, pp. 150–152), the number, disposition, and shape of the parietals may be different in each specimen. The same situation exists in a population sample of the holostean *Semionotus capensis* in the American Museum collection.

The bone between the subopercular and the dermohyal in *Redfieldius* must represent what Lehman (1952) has called a "supraspiracular" in *Perleidus*. The fact that this element is absent from *Cionichthys* raises the problem of its origin in *Redfieldius*. Lehman believes that the supraspiraculars were derived from a "fragmentation" of the dorsal part of the preoperculum, and that this phenomenon, as also exhibited in the parasemionotids, was responsible, in part, for the narrow, entirely vertical, holostean preoperculum. From the standpoint of morphogenesis, the fragmentation concept is hardly satisfactory. As Devillers (1965) has pointed out, a particular pattern of bone development must be dependent on osteogenic centers established in the mesenchyme before there is any visible ossification. Spiegelman (1945) has suggested that the independence or assimilation of these centers may be related to a competition-dominance interplay between them.

The difference in dermal bone ornamentation between *Cionichthys* and *Redfieldius* is clearly distinct. Tubercles in the former are low, frequently ovoid, and have a rounded surface except on the rostral and the antorbital where they are robust and toothlike. In *Redfieldius* the isolated tubercles tend to be relatively higher and more or less bluntly pointed, again particularly on the rostral and antorbital. On the cheek elements, they are relatively low and rounded; the parietals and extrascapulars are partly covered with large, irregular areas of enamel in addition to the tubercles.

LASALICHTHYS,¹ NEW GENUS

TYPE SPECIES: *Lasalichthys hillsi*, new species.

¹ For the La Sal Mountains, Utah, and *ichthys*, fish.

DISTRIBUTION: Upper Triassic. North America: Chinle Formation and Dockum Group.

DIAGNOSIS: Redfieldiid differing from the other members of family in following characters: Snout pattern distinctive in having relatively small, ovoid, postrostral bone enclosed anteriorly by expanded nasals. Parietals triangular; occasionally fused together. Mandible deep posteriorly, tapering rapidly to symphysis. Cranial sensory canals with double row of pores except on nasal and mandible. Supraorbital canals extending through parietals to join extrascapular commissure. Dermal skull elements covered with prominent ridges or tubercles. Anterior rays of pectoral fin robust, with numerous relatively large, fringing fulcra.

***Lasalichthys hillsi*,² new species**

Plates 15, 16; text figure 9

TYPE: A.M.N.H. No. 5636, impression of skull roof, from upper part of Chinle Formation, Little Valley, San Juan County, Utah.

HORIZONS AND LOCALITIES: Upper part of Chinle Formation: Big Indian Wash and Little Valley, San Juan County, Utah; ?Dolores River Canyon, near Bedrock, Montrose County, Colorado. Lower part of Dockum Group: Near Otis Chalk, Howard County, Texas.

DIAGNOSIS: Same as for genus.

REFERRED SPECIMENS: Upper part of Chinle Formation. Little Valley, San Juan County, Utah: A.M.N.H. No. 5637, skull; A.M.N.H. No. 5638, skull roof, including snout; A.M.N.H. No. 5639, skull impression; A.M.N.H. No. 5640, incomplete skull; A.M.N.H. No. 5641, incomplete skull; A.M.N.H. No. 5642, skull impression; A.M.N.H. No. 5644, skull and anterior part of body; A.M.N.H. No. 5645, skull; M.C.Z. No. 9029, skull; M.C.Z. No. 9030, several incomplete specimens; U.S.N.M. No. 2344, skull roof. Big Indian Wash, San Juan County, Utah: A.M.N.H. No. 5643, incomplete skull. Lower part of Dockum Group. Near Otis Chalk, Howard County, Texas: A.M.N.H. No. 5722.

DESCRIPTION

BODY FORM AND MEASUREMENTS: A complete individual that can be positively identified.

² For R. C. Hills, who discovered the first fishes in the Chinle Formation.

tified as *Lasalichthys* has not been found. Two specimens (A.M.N.H. Nos. 5644 and 5640) include the anterior part of the trunk, indicating a fusiform body with an estimated total length of 150 mm.

SKULL (TEXT FIG. 9): The snout pattern of *Lasalichthys* is basically similar to that of *Redfieldius*, *Cionichthys*, and *Helichthys*. The nasals are expanded anteriorly, however, and meet in front of the postrostral. The rostral and antorbital are poorly preserved but are apparently of the *Cionichthys* type. The dermosphenotic-dermopterotic suture has a more anterior contact with the frontal than in *Cionichthys*, and the posterior narrowing of the frontals is more gradual. The nearly triangular parietals are fused together in some specimens; in shape and orientation they resemble the posterior parietals (dermosupraoccipitals) of *Helichthys* (Brough, 1931). The paired, broadly triangular extrascapulars are usually in contact behind the parietals, but they may be separated or covered by a posterior extension of the parietals. The lobate suprascapulars apparently do not meet in the midline.

As in *Redfieldius*, the dermosphenotic has toothlike projections along its anterior orbital border. The dermopterotic is nearly as wide as it is long and has oblique contacts with the parietal and the extrascapular.

Lasalichthys has the usual barlike postorbital and probably two infraorbitals. The posterior border of the preopercular is gently curved throughout its length, thus lacking the nearly right-angle bend found in *Cionichthys*. Its dorsal border rises to an apex at the suture between the wedge-shaped dermohyal and the single, wide suborbital. The maxilla has a more rounded posterodorsal border than that of *Cionichthys*. The opercular is somewhat smaller than the subopercular, and the single branchiostegal plate is in the typical redfieldiid position.

The double row of sensory pores on all the canal-bearing bones except the nasal and dentary (which have a single row) contrasts with the uniformly single row in *Cionichthys* and *Redfieldius*. The posterior extension of the supraorbital sensory canals through the parietals to the extrascapular commissure also occurs in a related genus (described below), but it is otherwise unknown among the

redfieldiids. I can find no parallel to this condition in any other palaeonisciform except *Birgeria nielsenii* (Lehman, 1952).

The mandible is posteriorly deepened and tapers rapidly to the symphysis. The maxillary and mandibular teeth are more robust than those of *Cionichthys* or *Redfieldius* and are closely spaced.

Large, rounded tubercles are present on the snout elements and the frontals. The other dermal bones, including the cleithrum, are mostly covered with broad, closely set, parallel ridges. The ornamentation is in every case strongly developed, in contrast with its relatively weaker development in *Cionichthys*.

APPENDICULAR SKELETON: The shoulder girdle is similar to that of *Cionichthys* and requires no special comment. The pectoral fin consists of about nine rays, distally bifurcated and segmented. The first rays support a large number of well-developed, fringing fulcra. The anterior rays are particularly long and robust, forming a fin similar to the pectoral of *Cionichthys*.

SQUAMATION: The scales are without ornamentation and have a smooth posterior border. The belly scales in A.M.N.H. No. 5644 have about the same proportions as the flank scales.

DISCUSSION

Lasalichthys is more closely related to the genus next described than to *Cionichthys* or *Redfieldius*, as is evident from the pattern of the dermal skull, the sensory canals, and the form of the preopercular and maxilla.

The reduction in the relative size of the postrostral bone and its separation from the rostral by the nasals are unique among known redfieldiids. It is tempting to regard this condition as a stage in postrostral elimination, particularly as the next redfieldiid genus herein described lacks this bone entirely.

SYNORICHTHYS,¹ NEW GENUS

TYPE SPECIES: *Synorichthys stewarti*, new species.

DISTRIBUTION: Upper Triassic. North America: Chinle Formation and ?Dockum Group.

DIAGNOSIS: A redfieldiid closely resem-

¹ Greek *synoria*, borderland, in reference to the Colorado-Utah boundary, and *ichthys*, fish.

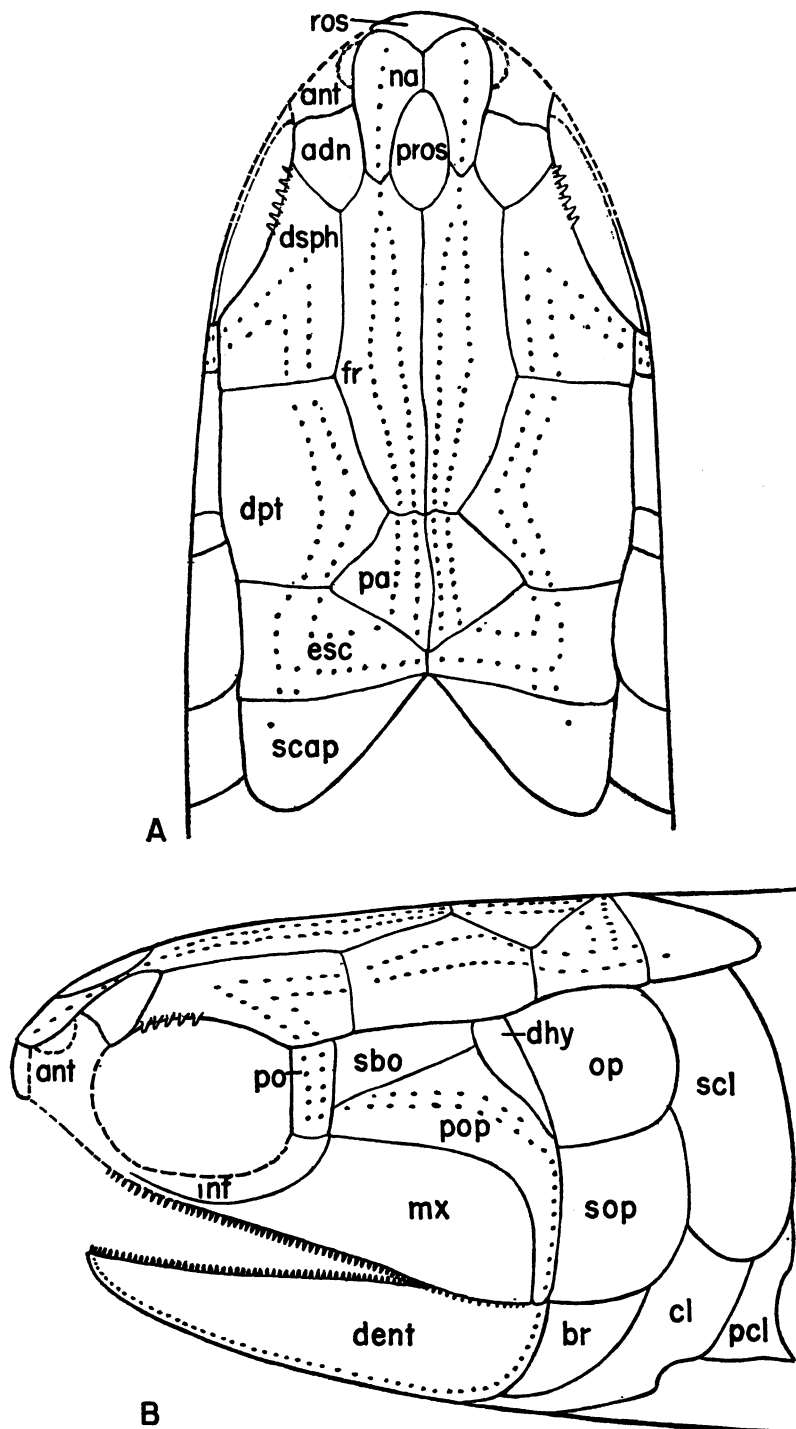


FIG. 9. *Lasalichthys hillsii*, new genus and species, restoration of skull. A. Dorsal aspect. B. Lateral aspect. Both ca. $\times 4$.

Abbreviations: adn, adnasal; ant, antorbital; br, branchiostegal; cl, cleithrum; dent, dentary; dhy, dermohyal; dpt, dermopterygoid; dsph, dermosphenoid; esc, extrascapular; fr, frontal; inf, infraorbital; mx, maxilla; na, nasal; op, opercular; pa, parietal; pcl, postcleithrum; po, postorbital; pop, preopercular; pros, postrostral; ros, rostral; sbo, suborbital; scap, suprascapular; scl, supracleithrum; sop, subopercular.

bling *Lasalichthys*, but with postrostral bone absent and nasals meeting in midline. Scales on belly and posterior part of body narrow, about one-half of depth of flank scales.

Synorichthys stewarti,¹ new species

Plates 17, 18; text figures 10, 11

TYPE: A.M.N.H. No. 5646, detailed impression of complete fish, from upper part of Chinle Formation, near Bedrock, Locality B, Montrose County, Colorado.

HORIZONS AND LOCALITIES: Upper part of Chinle Formation: Big Indian Wash and Little Valley, San Juan County, Utah; Dolores River Canyon, near Bedrock, Montrose County, Colorado. ?Lower part of Dockum Group: Near Otis Chalk, Howard County, Texas.

DIAGNOSIS: Same as for genus.

REFERRED SPECIMENS: Upper part of Chinle Formation. Locality A, Dolores River Canyon, near Bedrock, Montrose County, Colorado: A.M.N.H. No. 5669, weathered skull and body; A.M.N.H. No. 5675, partial skull; A.M.N.H. No. 5677, skull roof; P.U. No. 19321, skull. Locality B, Dolores River Canyon, near Bedrock, Montrose County, Colorado: A.M.N.H. No. 5663, complete specimen; A.M.N.H. No. 5664, complete specimen; A.M.N.H. No. 5668, partial specimen; A.M.N.H. No. 5671, partial skull; A.M.N.H. No. 5672, skull in dorsal aspect; A.M.N.H. No. 5676, partial skull and body; A.M.N.H. No. 5678, skull roof; U.S.N.M. No. 23416, complete specimen. Little Valley, San Juan County, Utah: A.M.N.H. No. 5665, partial skull and body; A.M.N.H. No. 5666, partial skull and body; A.M.N.H. No. 5667, skull roof; A.M.N.H. 5673, skull roof; A.M.N.H. No. 5674, partial skull roof; U.S.N.M. No. 23415, skull roof; M.C.Z. No. 9031, partial skull roof; M.C.Z. No. 9032, partial skull roof. ?Lower part of Dockum Group. Near Otis Chalk, Howard County, Texas: A.M.N.H. No. 5722.

DESCRIPTION

BODY FORM AND PROPORTIONS: The body shape of *Synorichthys* is very similar to that of *Cionichthys*. The maximum known length is approximately 160 mm. The skull is about

one-sixth of the total length, and the maximum body depth as reconstructed is a bit more than one-fifth of that length (text fig. 10).

SKULL (TEXT FIG. 11): The pattern of the snout, with the rectangular nasals meeting in the midline and the postrostral absent, represents a condition previously unknown in the Redfieldiidae and, indeed, in any "conservative" subholosteans, with the possible exception of the perleidids *Manlietta* and *Procheirichthys* (Wade, 1935). The parasemionotids (Lehman, 1952), which combine a palaeonisciform braincase and a dermal skull pattern of holostean level, also approach this pattern. The strongly tuberculated rostral of *Synorichthys* is thus in direct contact with the nasals, as in *Lasalichthys*, and the ant-orbital typically articulates medially with the rostral, nasal, and adnasal bones.

The remainder of the dermal skull differs only in minor proportions from that of *Lasalichthys*, and skulls lacking the snout region are consequently difficult to identify. In some individuals the extrascapulars meet behind the parietals, whereas in others posterior extensions of the parietals separate the extrascapulars rather widely. There is less postorbital expansion in the maxilla and perhaps a narrower mandible than in *Lasalichthys*. The sensory canal pattern is identical in these two genera, including the passage of the supraorbital canals through the parietals to join the extrascapular commissure.

APPENDICULAR SKELETON: Except to note the posterior embayment in the extrascapular, the shoulder girdle requires no special comment. The pectoral fin is more delicate than that of *Lasalichthys*; it consists of 12 or 13 rays, which are probably segmented only distally. The anterior ray is bordered by delicate fulcra. The origin of the pelvic fin is somewhat behind the midpoint between the origin of the pectoral and that of the anal. It includes about 13 partly segmented rays. The dorsal fin is made up of 20 completely segmented rays and has its origin well behind that of the anal fin. It is bordered anteriorly by four completely segmented rays and several basal and fringing fulcra. The caudal axis is somewhat longer than that of *Cionichthys*; the fin is equilobate and is composed of approximately 52 rays.

¹ For John H. Stewart.

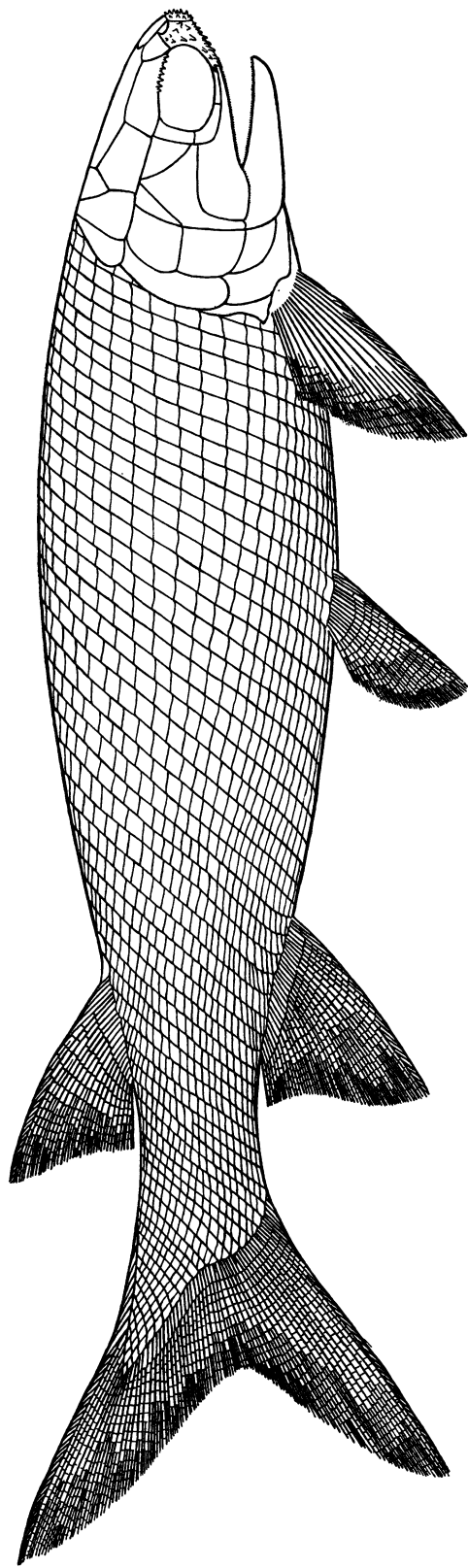


FIG. 10. *Synorichthys stewarti*, new genus and species, restoration of body in lateral aspect.

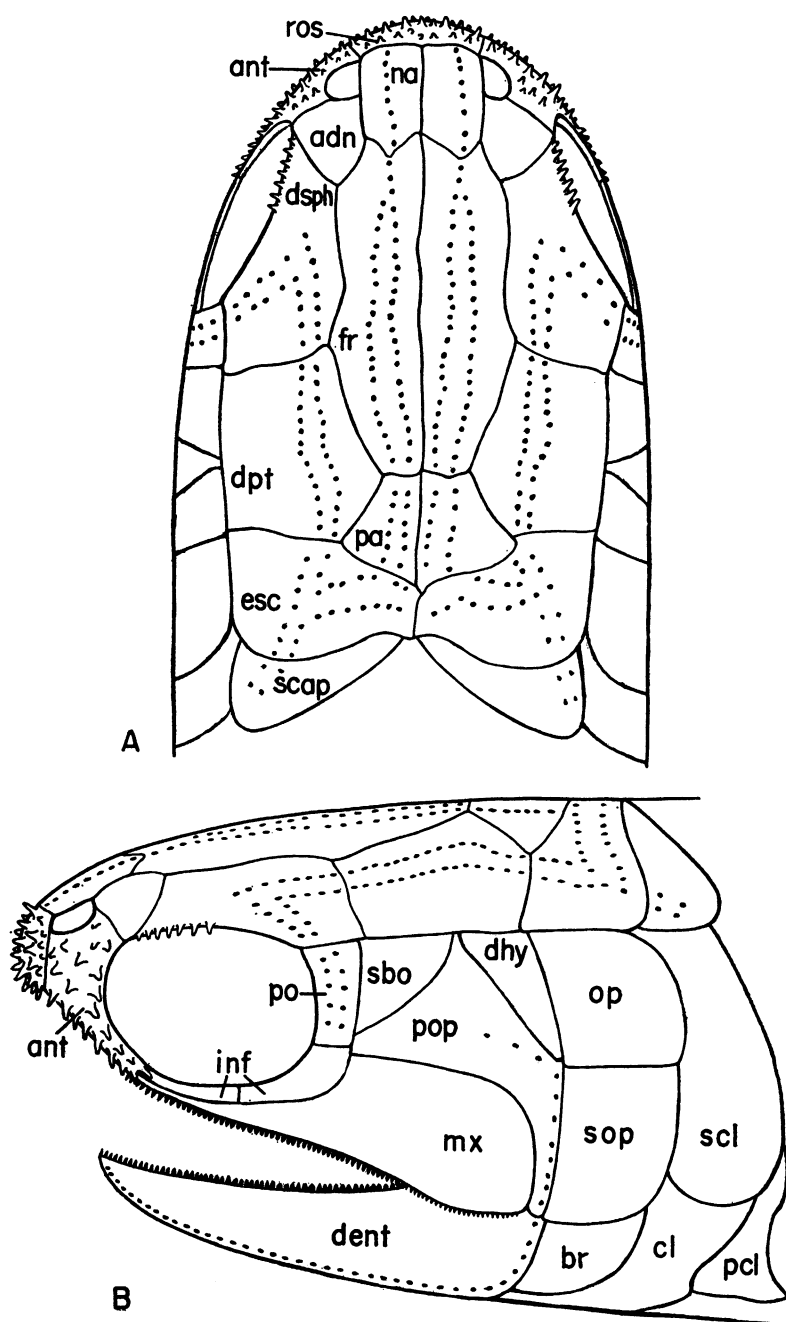


FIG. 11. *Synorichthys stewarti*, new genus and species, restoration of skull. A. Dorsal aspect. B. Lateral aspect. Both ca. $\times 3.35$.

Abbreviations: adn, adnasal; ant, antorbital; br, branchiostegal; cl, cleithrum; dent, dentary; dhy, dermohyal; dpt, dermopterygoid; dsph, dermosphenoid; esc, extrascapular; fr, frontal; inf, infraorbital; mx, maxilla; na, nasal; op, opercular; pa, parietal; pcl, postcleithrum; po, postorbital; pop, preopercular; pros, postrostral; ros, rostral; sbo, suborbital; scap, suprascapular; scl, supracleithrum; sop, subopercular.

SQUAMATION: The scales of *Synorichthys* (and *Lasalichthys*) are relatively smaller than those of *Cionichthys*. In the anterior flank region they are nearly square, but on the belly, and between the unpaired fins, the scales are curved and considerably narrowed dorsoventrally. In cross section they show a thin layer of laminated enamel and a thick bony layer without evidence of laminations or canals for collagen fibers.

DISCUSSION

The loss of the postrostral and the meeting of the enlarged nasals in *Synorichthys* seem to represent the culmination of a trend in snout pattern peculiar to the Chinle-Dockum redfieldiids. Competition between the postrostral and nasal ossification centers may have been involved, and the mesenchyme that usually formed the postrostral could have been taken over entirely by the nasal centers. *Synorichthys* and *Lasalichthys* are also distinctive among the redfieldiids in having a single pair of nearly triangular parietals and in having the paired supraorbital sensory canals extending through the parietals to join the commissure in the extrascapulars.

Although the dermal skull in these two genera is very similar, the snout pattern in each is distinctive and is not duplicated among other known redfieldiids. As in the case of *Cionichthys* versus *Redfieldius*, we are concerned here with the taxonomic significance of seemingly small but apparently constant differences in the dermal bone pattern. When intraspecific variability occurs in this pattern (for instance, in the parietal or cheek areas), it is usually obvious from a relatively small number of specimens and can be properly considered in the systematic evaluation. In the absence of such demonstrated variability, and in view of the usual constancy of the actinopterygian snout and parietal patterns at the generic level, the recognition of three new Chinle redfieldiid genera seems justified.

Dictyopyge from the Newark Group agrees with *Synorichthys* in skull ornamentation and in having narrow, curved, belly scales. It differs from this genus in having rectangular parietals and a characteristically lobate anal fin. All available specimens of *Dictyopyge*, including some 30 individuals recently collected

in the Newark Group in Virginia, have poorly preserved skulls. Until the dermal bone pattern can be worked out in detail, it will not be possible to determine the affinity of this form with either *Lasalichthys* or *Synorichthys*.

Partial skulls and bodies plus numerous isolated dermal bones (A.M.N.H. No. 5722) recovered from the Dockum locality near Otis chalk, Texas, undoubtedly belong to *Lasalichthys* or to *Synorichthys* (or to both). Unfortunately the snout is invariably missing. *Trilophosaurus* Quarry 3 also produced (among other indeterminate fish remains) a weathered but uncrushed braincase (U.T.B.E.G. No. 31098-44) that can be assigned to the *Lasalichthys-Synorichthys* group on the basis of the dermal roof. The dermopterotics are relatively longer than those of the Chinle forms, but otherwise resemblance to these genera is very close. The specimen, therefore, represents the first known redfieldiid braincase, and it is unfortunate that poor preservation prevents a detailed description. Although some features can be identified, they indicate little more than that the neurocranium is, as expected, of the palaeonisciform type. Comparison, for instance, with the braincase of *Boreosomus* (Nielsen, 1942) and that of *Perleidus* (Lehman, 1952) shows that the occipital surface has the typical bipartite opening for the foramen magnum and the notochord. There is a prominent craniospinal protuberance that extends anteroventrally as a ridge below the lateral occipital fissure. The wall in the area of the vestibular fontanelle is thin, and it is probable that a fontanelle was present. The hyomandibular facet, preserved on the left side, is somewhat more vertical than that of *Perleidus*. There is apparently an unpaired posterior myodome above the remnant of the ventral orbitotemporal bar. Canals and foramina are not clearly in evidence.

ORDER PALAEONISCIFORMES

INCERTAE SEDIS

TANAOCROSSUS,¹ NEW GENUS

TYPE SPECIES: *Tanaocrossus kalliokoskii*, new species.

¹ Greek, *tanao*, outstretched, and Greek *krossos*, fringe.

DISTRIBUTION: Upper Triassic. North America: Chinle Formation.

DIAGNOSIS: A fusiform palaeonisciform fish of unknown affinity, with dorsal fin apparently composed of unbifurcated rays and extending from near posterior skull margin to caudal peduncle. Preopercular broadly ovoid. Maxilla probably fixed and expanded posteriorly. Opercular somewhat larger than subopercular; interopercular absent. Branchiostegals numerous. Dermal bones ornamented with low, rounded, anastomosing striae. Flank scales rhombic, unornamented; decreasing in size toward dorsal fin, at base of anal fin, and on caudal peduncle. Single row of minute scales at base of dorsal fin ornamented with striae. Segmented rays of dorsal, pelvic, anal, and caudal fins also ornamented with striae. Caudal fin hemiheterocercal, probably equilobate.

Tanaocrossus kalliokoskii,¹ new species

Plate 20

TYPE: A.M.N.H. No. 5700, only known specimen, represented by detailed impression of the body, lacking anterior half of skull and pectoral fins.

HORIZON AND LOCALITY: Upper portion of Chinle Formation: Dolores River Canyon, Locality A, near Bedrock, Montrose County, Colorado.

SPECIFIC DIAGNOSIS: Same as for genus.

DESCRIPTION

BODY FORM AND PROPORTIONS: *Tanaocrossus* is a compactly fusiform "subholostean" distinguished mainly by its elongated dorsal fin. The approximate total length (allowing for the missing part of the skull) is 150 mm. In life, the maximum depth of the body was not more than 30 mm.

SKULL: The posterior portion of the skull has a definite palaeonisciform aspect. The roofing elements present some identification problems, but impressions of the suprascapular, probably two extra scapulars on one side of the midline, the dermopterotic, part of the parietal, and a large anterior bone that must be the frontal can be made out. Several small, displaced bones are present in the area of the dermosphenotic and the suborbitals,

but their shape and disposition cannot be determined. An ovoid element in the position of the posterior infraorbital has a groove in line with the sensory grooves and pores traversing the middle of the preopercular. The broad preopercular has a slight anterior embayment for the maxilla. The opercular is somewhat deeper than the subopercular, which is followed ventrally by at least 10 branchiostegals. There is no indication of an interopercular. All the dermal bones, including the branchiostegals, are ornamented with delicate, anastomosing striae.

POSTCRANIAL SKELETON: No details of the pectoral girdle are visible; the pectoral fin, with the possible exception of a single ray, is missing. The pelvic fin is situated about halfway between the presumed position of the pectoral and the origin of the anal. It consists of about 13 completely segmented rays ornamented with longitudinal striae.

As preserved, the dorsal fin begins at the level of the sixth vertical scale row and extends without interruption to the caudal peduncle. The total number of rays is 74, but there may have been a few more anteriorly. They are completely segmented and apparently increase in length anteroposteriorly, with the longest ones opposite the anal. The segments comprising at least the proximal half of each ray are ornamented with longitudinal and oblique striae. Similar ornamentation is present on a single row of very small, rectangular scales at the base of the dorsal fin.

The anal fin includes about 24 rays, completely segmented and covered with longitudinal striae as far as they can be followed distally. There is a marked change in the size, shape, and orientation of the scales in the vicinity of this fin which gives it a lobed appearance. Although compression makes the interpretation of this area difficult, it is possible that the fin base was covered with several transverse rows of small, unornamented, elliptical scales.

The hemiheterocercal caudal is composed of 15 or more segmented rays, again longitudinally striated. The dorsal rays of this fin are fairly complete, and their nearly equal length suggests that the posterior fin margin was truncated or only slightly notched.

SQUAMATION: In the anterior flank region

¹ For J. O. Kalliokoski.

the scales are about twice as deep as wide; otherwise they are essentially equilateral. They are reduced in size below the dorsal fin, on the caudal peduncle, and, as noted, at the base of the anal fin. There is no evidence of scale ornamentation except on the row immediately beneath the dorsal fin.

DISCUSSION

The relationships of *Tanaocrossus* present a real problem, since nothing like it has been found in the Late Paleozoic or the Triassic of North America. Dr. Brian Gardiner (personal communication) has suggested that it may be related to his scanilepid-atherstonid-sphaerolepid complex, mainly because the included genera also have unbifurcated fin rays. Although both *Scanilepis* (Aldinger, 1937) and *Evenkia* (Berg, 1941) have elongated dorsal fins, it is evident that this character arose a number of times in the early actinopterygians and that it does not necessarily indicate close relationship. Gardiner is of the opinion, however, that the palaeonisciforms with unbifurcated fin rays may form a related complex. If this can be substantiated on other grounds, then perhaps *Tanaocrossus* has Old World affinities. Little can be said about the presumed habits of *Tanaocrossus* except that undulation of the elongated dorsal would bring about slow locomotion in quiet water.

INFRAClass HOLOSTEI

ORDER SEMIONOTIFORMES

SUBORDER SEMIONOTOIDEI

FAMILY SEMIONOTIDAE

SEMIONOTUS AGASSIZ, 1832

Semionotus AGASSIZ, 1832, p. 144.

Palaeoniscus REDFIELD, 1837, p. 38 (in part).

Ischypterus EGERTON, 1847, p. 277.

TYPE SPECIES: *Semionotus bergeri* Agassiz.

DISTRIBUTION: Lower to Upper Triassic: Europe. ?Lower Triassic: South America. Upper Triassic: Australia; South Africa; North America.

DIAGNOSIS: See Woodward (1895, p. 55).

Semionotus sp.

Plates 21-23

HORIZON AND LOCALITIES: Upper part of Chinle Formation: Big Indian Wash and

Little Valley, San Juan County, Utah; Dolores River Canyon, near Bedrock, Montrose County, Colorado.

REFERRED SPECIMENS: Little Valley, San Juan County, Utah: A.M.N.H. No. 5679, skull and anterior part of body; A.M.N.H. No. 5680, complete specimen; A.M.N.H. No. 5682, complete specimen; A.M.N.H. No. 5685, complete specimen; A.M.N.H. No. 5686, specimen lacking posterior half of body; A.M.N.H. No. 5687, specimen with incomplete skull; A.M.N.H. No. 5688, complete specimen; A.M.N.H. No. 5689, several incomplete specimens; A.M.N.H. No. 5690, specimen with incomplete skull lacking caudal fin; A.M.N.H. No. 5692, nearly complete impression; A.M.N.H. No. 5693, complete specimen; A.M.N.H. No. 5694, distorted anterior part of body; A.M.N.H. No. 5695, trunk; A.M.N.H. No. 5698, posterior half of body; A.M.N.H. No. 5702, partial specimen; A.M.N.H. No. 5703, two partial specimens; A.M.N.H. No. 5705, anterior half of body; U.S.N.M. No. 23418, specimen lacking caudal fin, skull incomplete; U.S.N.M. No. 23419, specimen lacking posterior half; U.S.N.M. No. 23420, complete specimen; U.S.N.M. No. 23421, partial specimen; M.C.Z. No. 9033, two partial specimens. Big Indian Wash, San Juan County, Utah: A.M.N.H. No. 5683, specimen lacking posterior half. Locality A, near Bedrock, Dolores River Canyon, Montrose County, Colorado: A.M.N.H. No. 5696, trunk. Locality B, near Bedrock, Dolores River Canyon, Montrose County, Colorado: A.M.N.H. No. 5681, specimen lacking skull; A.M.N.H. No. 5684, complete specimen; A.M.N.H. No. 5691, weathered specimen lacking skull; A.M.N.H. No. 5706, poorly preserved specimen.

DISCUSSION

Because of the confused state of *Semionotus* taxonomy, no attempt has been made to recognize species from the Chinle Formation. The range in body form illustrated in plate 21 is nearly duplicated in the Newark *Semionotus* complex, but the number of described Newark species (Eastman, 1905, 1911) is clearly too large. A survey of the American Museum specimens from various localities in the Connecticut Valley, New Jersey, and

Virginia by Harold Roellig and the writer has emphasized the difficulties involved in providing a realistic basis for distinguishing the Newark species. In addition to the generally poor preservation, which makes character analysis in a large number of specimens nearly impossible, several of the apparently distinctive Newark forms show a considerable degree of overlap in a few obtainable body measurements and meristic characters. Nevertheless, some basis must be found for defining the Newark species before the Chinle ones can be meaningfully described.

The European species of *Semionotus* are also in need of critical revision. Available descriptions (mostly by Woodward, 1895) suggest that the body form is more conservative than in the American representatives which vary from fusiform to cycloidal. The gibbose condition is variously expressed in both the Newark and the Chinle *Semionotus* and is apparently present in the European *S. bergeri* (Woodward, 1895, pl. 2). Its taxonomic significance is also presently obscure.

The size range of the Chinle sample is generally smaller (60 to 100 mm.) than that for the Newark (75 to 255 mm.), but a few incomplete specimens suggest a total length of about 200 mm. The number of vertical scale rows along the lateral line is between 32 and 34 as in most of the Newark "species." The number of fulcra and rays in the dorsal and anal fins is also well within the range of the Newark forms. One exceptional Chinle specimen (A.M.N.H. No. 5680) shows prominent tubercles on the anterior dorsal ridge scales and adjacent flank scales (pl. 22).

Restoration drawings of the *Semionotus* skull have been provided for *S. kanabensis* (Schaeffer and Dunkle, 1950), for *S. capensis* (Gardiner, 1960), and for *S. normanniae* (Larsonneur, 1964). According to Gardiner, the snout of *S. capensis* is similar to that of *Acentrophorus* in having a median, enlarged rostral (the postrostral of Gardiner) that covers the ascending processes of the premaxillae and separates the nasals. A separate rostral bone is presumably absent from *S. normanniae*, but Larsonneur believes the canal for the ethmoidal commissure is present in the "rostromaxillae."

A concerted effort to clarify the snout pattern in relatively well-preserved *Semionotus*

specimens from the Newark series has failed to reveal either a rostral or nasals. Nasals may be represented in the Chinle specimen referred to above (A.M.N.H. No. 5680) by thin ossifications lying on each side of the ridge formed by the posterior extensions of the premaxillae. Less certain is the presence of a rostral bone situated over the dentigerous portion of the premaxillae. The apparent absence of these elements from the Newark *Semionotus*, from *S. kanabensis*, and from the type specimen of *S. nilsonni* (M.C.Z. No. 5067) from the Rhaetic of Sweden may mean that they were reduced or lost in some of the Late Triassic species. It is possible, however, that they were loosely connected to the snout and were usually separated from it prior to burial.

The few Chinle and nearly all of the Newark specimens exhibiting the skull roof have a single pair of square parietals. One specimen from Sunderland, Massachusetts (M.C.Z. No. 8592), and several from Virginia in the United States National Museum collection have two pairs of rectangular elements. The type of *S. nilsonni* also has two pairs, the posterior ones being smaller and of irregular shape. Among seven specimens of *S. capensis* (A.M.N.H. Nos. 8828-8834) originally associated on a single slab, three individuals have one pair of parietals, and four have two pairs, but in three of the latter the anterior parietals are irregular and do not meet in midline. The frequency of such variation in the parietal region is unknown for any "species" of *Semionotus*, but the geographic and temporal distribution of this phenomenon suggests that it occurred in widely separated populations.

The Chinle and Newark specimens of *Semionotus* differ from the Moenave *S. kanabensis* in having four or more suborbital bones. In the Moenave species, and in *S. nilsonni*, there is a single enlarged suborbital situated below the dermopterotic. As *Acentrophorus* (the probable ancestor of *Semionotus*), *S. bergeri*, and *S. capensis* have a multiple suborbital series, the possession of such a series is presumably the primitive condition. The occurrence of two suborbitals in *S. normanniae* suggests that a reduction in the number of these elements occurred independently in different species lineages. It is

therefore probable that *S. kanabensis* was derived from one of the Chinle forms and that it is not closely related to *S. nilsonni*. The extreme variation in both the suborbital and circumorbital series in English species of *Lepidotes* (Jain and Robinson, 1963) also supports such a conclusion.

The genus *Semionotus* includes species that show considerable difference in the snout pattern, reduction in the number of suborbitals, modifications in the shape of the maxilla (*S. capensis*), and at least intraspecific variation in the number and arrangement of the parietals. More information is needed on these variations in dermal skull pattern, however, before it is possible to assess their taxonomic significance. Although the meristic characters, along with the differences in body form, still pose problems in regard to specific separation, it is apparent that such characters will prove useful when the preservation is adequate. For instance, Larsonneur's (1964) restoration of *S. normanniae* has more than 40 vertical scale rows, whereas the American forms consistently have 32 to 34.

HEMICALYPTERUS,¹ NEW GENUS

TYPE SPECIES: *Hemicalypterus weiri*, new species.

DISTRIBUTION: Upper Triassic. North America: Chinle Formation.

DIAGNOSIS: Nearly cycloid, compressed semionotid differing from other deep-bodied genera in this family by the following combination of characters: squamation consistently absent from posterior half of body; body depth above and below notochord about equal; postrostral probably present, separating nasals; premaxillae with long, delicate, posterior processes; maxillary not extending beyond middle of orbit; dentition styliform; preopercular expanded ventrally and exposed dorsally; interopercular anterior to subopercular in typical semionotid position; branchiostegals and cleithrum of normal shape, not modified as in *Tetragonolepis*; no central ossification around notochord; paired fins small and delicate; origin of pectorals at level of branchiostegals; dorsal fin somewhat longer than anal; caudal symmetrical, slightly

forked; scales rectangular, smooth, on flank about three times deeper than wide; dorsal and ventral ridge scales with strongly denticulated outer borders.

Hemicalypterus weiri,² new species

Plates 24, 25; text figure 12

TYPE: U.S.N.M. No. 23425, nearly complete specimen, part and counterpart, from upper part of Chinle Formation, Little Valley, San Juan County, Utah.

HORIZON AND LOCALITY: Upper part of Chinle Formation: Little Valley, San Juan County, Utah.

SPECIFIC DIAGNOSIS: Same as for genus.

REFERRED SPECIMENS: Little Valley, San Juan County, Utah: A.M.N.H. No. 5709, nearly complete specimen; A.M.N.H. No. 5710, three partial specimens; A.M.N.H. No. 5711, anterior half of specimen; A.M.N.H. No. 5712, anterior half of specimen; A.M.N.H. No. 5713, partial specimen; A.M.N.H. No. 5714, partial trunk; A.M.N.H. No. 5715, partly dissociated trunk; A.M.N.H. No. 5716, trunk and partly dissociated skull; A.M.N.H. No. 5717, trunk and dissociated skull; A.M.N.H. No. 5718, specimen lacking caudal fin; U.S.N.M. No. 23422, specimen lacking posterior portion; U.S.N.M. No. 23423, skull and dorsal region of trunk; U.S.N.M. No. 23424, partial trunk; U.S.N.M. No. 23426, partly dissociated specimen; U.S.N.M. No. 23427, nearly complete specimen; U.S.N.M. No. 23428, specimen lacking caudal fin; U.S.N.M. No. 23429, specimen lacking caudal fin; M.C.Z. No. 9034, partial specimen.

DESCRIPTION

BODY FORM AND PROPORTIONS: *Hemicalypterus* is represented by some 20 specimens ranging in total length from about 45 mm. to 100 mm. The squamation is restricted to the anterior half of the trunk, terminating posteriorly in a somewhat oblique line extending from the highest point on the dorsal profile to the lowest point on the ventral margin. Both the body form and the absence of scales from the posterior trunk area represent a convergence to certain pycnodont holosteans (text fig. 12). However, *Hemicalypterus* is clearly a semionotiform and, on the basis of

¹ Greek *hemi*, half, and Greek *kalyptos*, covered.

² For Gordon W. Weir.

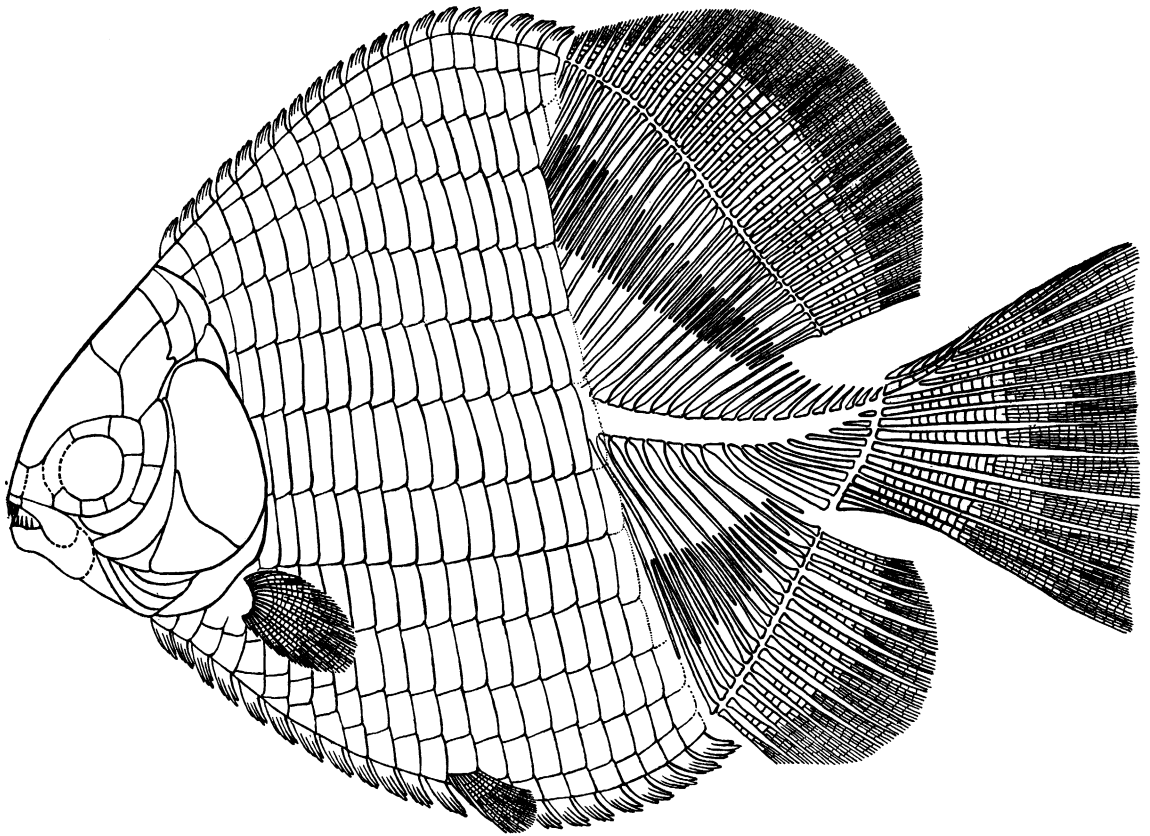


FIG. 12. *Hemicalypterus weiri*, new genus and species, restoration of body in lateral aspect.

dermal skull characters, can be assigned to the Semionotidae. It differs from other deep-bodied semionotids such as *Dapedius* (Lehman, 1966, fig. 158A) in having a relatively smaller skull, in various details of the dermal skull pattern, including the shape and position of the interopercular, in body shape, and in squamation. It also can be distinguished from *Tetragonolepis* (Gardiner, 1962, fig. 42) in the pattern of the opercular series, including the branchiostegals, in the absence of ossification around the notochord (alternating wedge-shaped pleurocentra and hypocentra are present in *Tetragonolepis*), in the nearly equal expansion of the body above and below the notochord, and finally in the squamation.

SKULL: The dermal bones of *Hemicalypterus* are thin and delicate. The roofing elements plus the opercular and subopercular are ornamented with low tubercles and radiating ridges.

The snout pattern is poorly defined, but

there are indications of narrow nasals separated by a rostral. The tiny premaxillae (pl. 25, fig. 4) have long, narrow, dorsal processes. Each bears four styliform teeth. The frontals are narrow anteriorly but increase markedly in width over the orbits. The parietals are rectangular and are bordered laterally by dermopterotics of nearly the same size. Two or three extrascapulars are present on each side of the midline.

The orbit is completely surrounded by circumorbital bones, and the suborbital series includes at least three elements. The maxilla is broad posteriorly and does not extend beyond the middle of the orbit. The opercular bone is about twice as deep as wide, obliquely overlapping the subopercular. The interopercular is partly covered by the preopercular as in *Semionotus*; it extends directly forward from the subopercular. The preopercular is expanded ventrally; its dorsal ramus is completely exposed.

The exact shape of the mandible is not in-

licated in any of the specimens, but it appears to be less robust than that of *Tetragonolepis* or that of *Dapedius*. There are four crescentic branchiostegals and an expanded gular.

AXIAL SKELETON: The bases of the neural and haemal arches are moderately expanded and well separated. There is no indication of ossification associated with the notochordal sheath. The notochord occupied a nearly central position as in *Dapedius* rather than being relatively closer to the dorsal border as in *Tetragonolepis*.

APPENDICULAR SKELETON: The suprascapulars meet at the middorsal line. Most of the supracleithrum and the upper part of the cleithrum are concealed by the opercular. The small pectoral fin (U.S.N.M. No. 23428), consisting of about 16 segmented rays, is inserted at the level of the branchiostegals and below the opercular complex (pl. 25, fig. 5). The smaller pelvic fin is situated midway between the pectoral and the origin of the anal. It consists of about seven or eight segmented rays. The dorsal fin is composed of 24 to 26 segmented and distally bifurcated rays, and the anal fin, of about 17 rays. Because the dorsal and anal rays, along with their basipterygia, are twice as numerous as the related neural and haemal spines, two basipterygia are inserted between successive spines, as in *Tetragonolepis*.

The caudal fin (composed of about 14 segmented, bifurcated rays) is hemiheterocercal, symmetrical, and slightly forked. It is bordered dorsally by fringing and basal fulcra and by fringing on the ventral border. The haemal spines associated with the caudal are moderately expanded, resembling those in *Tetragonolepis*.

The apparently abrupt termination of the squamation along a vertical line between the origin of the dorsal and that of the anal fin represents a modification previously unknown in the Semionotidae. There is no indication of thinner or smaller scales behind this line, and it is evident that the posterior part of the body was naked as in some pycnodonts. The individual scales are rhomboidal, and in the vicinity of the lateral line are about three times deeper than wide. The outer edges of the dorsal and ventral ridge scales have three or four pointed, toothlike projections. The bony layer of the scales is

clearly laminated and is covered externally with a thin layer of enamel.

DISCUSSION

The semionotids are mostly fusiform to deeply fusiform fishes with small mouths. The jaw mechanism suggests that they fed on relatively small food by nibbling and sucking.

The three hypsisomatic semionotid genera are (including *Hemicalypterus*) clearly derivable from the fusiform *Acentrophorus-Semionotus* type, but each shows distinctive specializations suggesting independent origin. *Hemicalypterus* is the most conservative in its dermal skull pattern, but is nevertheless unique in the absence of posterior squamation. The Lower Jurassic (Lower Liassic), marine *Dapedius* has lost the postrostral bone, and the nasals meet in the midline behind the rostral. The preopercular is narrow, and the interopercular is entirely exposed. The mandible is robust and deep; the teeth are styliiform. Both the vomer and the palatine are dentigerous. The squamation is complete, and the scales are not much deepened.

Tetragonolepis is an Upper Liassic marine genus with a large postrostral separating the nasals (Gardiner, 1960). As in *Dapedius*, the mandible is deepened, the preopercular is narrow, and the interopercular is exposed. The marginal teeth are styliiform, and there is no indication of heavier teeth within the mouth. The branchiostegals, in contrast with the "normal" ones of *Hemicalypterus* and *Dapedius*, are widened and projected ventrally. The ventral end of the cleithrum is recurved posteriorly. In association with these modifications, the body is greatly deepened below the notochord. The latter is surrounded by crescent-shaped pleurocentra and hypocentra. The elongated scales cover the entire body and, as Woodward (1895) noted, are thinner in the posterior part of the caudal region.

Although *Hemicalypterus* is the oldest of the three hypsisomatic semionotid genera, there is no reason to believe that it is ancestral to the other two. The hypsisomatic body form, with the dorsal and anal fins situated on the posterior angles, has evolved a number of times independently throughout the history of the actinopterygians. The common factors may be increased maneuverability re-

lated to the shorter, more compact body and the reduction of body mass. Hypsisomatic fishes usually inhabit quiet water and are capable only of short bursts of speed. The deepening of the body may represent a compensation for lateral compression, not only to increase stability but also to provide an adequate body musculature. Most fishes of this type are either suction feeders or nibblers or both. They can approach small prey with minimum exposure, and they present a minimum surface area to predators approaching from above or below. Because the lateral surface area is increased, the living forms almost invariably have disruptive color patterns related to their particular habitat.

Breder (1926) has pointed out that elevation (lift) of the posterior part of the body is minimized in short-bodied hypsisomatic forms when the pectorals are used to brake forward locomotion. The pectorals are closer to the center of the body in many of the deep-bodied teleosts, and the pelvics, which also cause tipping, may be greatly reduced in size. Although the pectorals are frequently low in primitive hypsisomatic actinopterygians (e.g., *Platysomus*, *Paramesolepis*), there is a tendency toward higher insertion in forms such as *Cheirodopsis*, *Cleithrolepis*, in the semionotid examples, and particularly in the pycnodonts. There seems to be a rough correlation in the earlier deep-bodied forms between dorsal migration of the pectorals, reduction in the size of the pelvic fins, and reduction of the caudal fin axis.

Except for *Hemicalypterus*, the known deep-bodied fishes of chondrosteian level are completely covered with rhomboidal scales. Compared with their teleostean counterparts, they must have been slow swimmers, with relatively poor maneuverability. The loss of squamation on the posterior part of the body in *Hemicalypterus*, as in some pycnodonts, indicates increased flexibility in that region and a more powerful forward thrust. A similar trend is suggested by the deep-bodied pholidophoroid *Aetheolepis* (Woodward, 1895), in which the heavy, quadrate scales of the abdominal region are replaced in the caudal area by thin, cycloid ones.

As noted above, a hypsisomatic species of *Semionotus* occurs in both the Newark and

the Chinle faunas. The shape of the body, and particularly of the dorsal and anal fin, is quite unlike that of *Hemicalypterus*. No trend toward a hypsisomatic body form is evident in the Old World species of *Semionotus*.

Present evidence suggests that *Hemicalypterus*, *Dapedius*, and *Tetragonolepis* were derived independently from a more fusiform *Semionotus* stock. The hypsisomatic trends in the North American fresh-water semionotids involved one or more species of *Semionotus* and *Hemicalypterus*. They probably assumed ecological roles similar to certain species of *Cyprinodon*, the centrarchids, and the deep-bodied characins. Lehman's (1966) implication of common origin in assigning *Dapedius* and *Tetragonolepis*, along with *Heterostrophus* and *Dandya*, to the family Dapediidae is, in my opinion, not supported by the known facts.

SUBCLASS SARCOPTERYGII
INFRAClass CROSSOPTERYGII
SUPERORDER COELACANTHINI
ORDER COELACANTHIFORMES
FAMILY COELACANTHIDAE
CHINLEA,¹ NEW GENUS

TYPE SPECIES: *Chinlea sorenseni*, new species.

DISTRIBUTION: Upper Triassic. North America: Chinle Formation and ?Dockum Group.

DIAGNOSIS: Coelacanth resembling *Diplurus* in form of basisphenoid, in length of ossified pleural ribs, in shape of pelvic plates and unpaired basal plates, and in length of supplementary caudal lobe, but differing from that genus in following characters: greater posterior extension of supratemporal (dermopterotic); more complete ossification of extrascapulars; robust anteroventral process on lateral rostral; postorbital relatively larger and triangular; relatively longer dentary, with notched posterior border; angular narrower anteriorly; teeth on dentary numerous, small, closely spaced; teeth on premaxilla, dermopalatine, ?ectopterygoid and precoracoid large and tusklike; denticles absent

¹ After the Chinle Formation.

from anterior borders of dorsal and caudal fins.

Chinlea sorenseni,¹ new species

Plates 26–28; text figures 13A, 14

TYPE: A.M.N.H. No. 5652, nearly complete specimen, from upper part of Chinle Formation, Little Valley, San Juan County, Utah.

HORIZONS AND LOCALITIES: Upper part of Chinle Formation: Little Valley, San Juan County, Utah; Dolores River Canyon near Bedrock, Montrose County, Colorado. ?Upper part of Petrified Forest Member, Chinle Formation: Ghost Ranch, New Mexico. ?Upper part of Tecovas Formation, Dockum Group: Palo Duro Canyon, Randall County, Texas.

SPECIFIC DIAGNOSIS: Same as for genus.

REFERRED SPECIMENS: Chinle Formation. Upper bone bed, near Bedrock, Dolores River Canyon, Montrose County, Colorado: A.M.N.H. No. 3201, pterygoid. Locality A, near Bedrock, Dolores River Canyon, Montrose County, Colorado: A.M.N.H. No. 5653, nearly complete skull. Locality B, near Bedrock, Dolores River Canyon, Montrose County, Colorado: A.M.N.H. No. 5654, skull and partial body impression; A.M.N.H. No. 5655, isolated scale; A.M.N.H. No. 5658, incomplete specimen; A.M.N.H. No. 5659, skull with exposed basisphenoid. Little Valley, San Juan County, Utah: A.M.N.H. No. 5656, isolated basisphenoid; A.M.N.H. No. 5660, partial specimen, with cleithrum exposed; A.M.N.H. No. 5704, pterygoid. Petrified Forest Member, Ghost Ranch, New Mexico: A.M.N.H. No. 5657, fragmentary skull and cleithrum. Dockum Group. Crosby County, Texas: M.P.U.M. No. 9630, isolated quadrate; T.T.C.M. No. 527, isolated quadrate; U.M.M.P. No. 38320, fragment of cleithrum. Palo Duro Canyon, Randall County, Texas: Y.P.M. No. 3928, nearly complete weathered skull.

DESCRIPTION

BODY FORM AND PROPORTIONS: Aside from the differences in the dermal skull and dentition, the skeleton of *Chinlea* must have been very similar to that of *Diplurus*

¹ For Walter Sorensen.

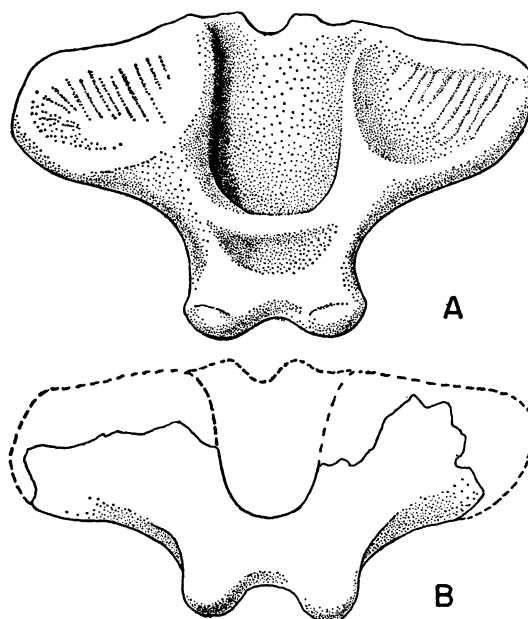


FIG. 13. Basisphenoid in dorsal aspect. A. *Chinlea sorenseni*. Ca. $\times 2.7$. B. *Diplurus newarki*. Ca. $\times 9.4$.

(Schaeffer, 1952a, fig. 9). Specimens collected in the Chinle Formation range in length from 160 mm. to an estimated 500 mm. A skull from the Tecovas Formation described by Schaeffer and Gregory (1961), which I am here referring to *Chinlea*, belonged to an individual with an approximate length of 800 mm. The type of *Diplurus longicaudatus* (Schaeffer, 1948) from the Newark Group is about 690 mm. long.

NEUROCRANIUM: The exposed dorsal aspect of the basisphenoid in A.M.N.H. No. 5659 is identical with that of a complete, isolated element (A.M.N.H. No. 5656) from the fish horizon in Little Valley. Both specimens show that this ossification is closer to that of *Diplurus* than to that of any other genus in which it has been described.²

The basisphenoid of *Chinlea* has broad, nearly triangular antotic processes, with well-defined articular areas for the pleurosphenoids.

² Previous illustrations of the *Diplurus* basisphenoid (Schaeffer, 1952a, fig. 3; Schaeffer and Gregory, 1961, fig. 3F) must be revised, particularly in regard to the shape and relationships of the antotic processes. A new restoration is included in the present paper as text figure 13.

In dorsal aspect, the connection between these processes and the main body of the element is sharply constricted. Although the isolated specimen is somewhat compressed dorsoventrally, it is evident that the pituitary notch is wider and deeper than in any other genus except *Diplurus* and perhaps *Latimeria*. The distance from the anterior border of the dorsum sellae to the dorsal border of the notochordal face is shorter in comparison with the other genera, again excepting *Diplurus*. The sphenoid condyles are well defined and are separated by a small depression for the intracranial ligament. Shallow fossae for the attachment of the adductor palatoquadrate muscles are situated on the ventral surface of the antotic processes where they join the lateral laminae. The form and extent of the laminae cannot be determined, and foramina are not evident. Lateral longitudinal grooves that articulate with corresponding flanges on the parasphenoid are preserved on the ventral surface.

VISCERAL SKELETON: Portions of the palatoquadrate are visible in several of the *Chinlea* skulls, but the entire complex could not be exposed without removing most of the dermal cheek elements. An isolated pterygoid impression (A.M.N.H. No. 3201) from the Dolores River Canyon bone bed probably belongs to *Chinlea*. Except for the gentle curvature of the dorsal border, it is close to the *Diplurus* type (see Schaeffer and Gregory, 1961, fig. 6). The right metapterygoid exposed in A.M.N.H. No. 5653 is a well-ossified, nearly rectangular element with a thickened anterior border that continues ventrally as the vertical ridge of the pterygoid. The articular facet for the antotic process is expanded transversely as in *Diplurus*, but is less pronounced. The quadrate is typically constricted above the condyles as in the isolated element from the Dockum Group figured by Warthin (1928).

DERMAL SKULL: The dermal bone nomenclature employed here is a combination of that used by Schaeffer (1952a), that of Lehman (1952), and that of Gardiner (1960). In my opinion, no current system for naming the dermal elements in the coelacanth skull is satisfactory mainly because many of the homologies with the rhipidistian dermal skull have not been, and perhaps cannot be, firmly established (text fig. 14).

The snout of *Chinlea* is composed of numerous small rostral elements as it is in *Whitea* (Lehman, 1952), *Diplurus* (Schaeffer, 1952a), the unnamed form of Nielsen (1936), and *Latimeria*. This subdivided area is apparently bordered anteriorly by small premaxillaries that support small, styliform teeth. In A.M.N.H. No. 5652 the roof of the anterior moiety is covered by two pairs of elongated elements representing the anterior and posterior frontals and probably two pairs of nearly square nasals. In another specimen (A.M.N.H. No. 5654) it appears that the posterior nasals and the anterior frontals have fused.

In two specimens six supraorbital elements border the orbit; five occupy an apparently equivalent distance in a third skull. The most posterior element in this series fits into a recess on the anterolateral border of the parietal (intertemporal). The supraorbitals (or antorbitals) diminish in size where they border the nasals and are associated anteriorly with the rostral complex. There is no indication of an enlarged antorbital or tectal element as in *Whitea* (Lehman, 1952) and *Holophagus* (Gardiner, 1960). The parietals are nearly as broad as they are long. Separate dermopterotics (supratemporals) fit into wide embayments in the parietals and extend posterolaterally into distinct processes that enclose five rectangular extrascapulars.

The lateral rostral (rostral) has a characteristically elongated marginal portion with two large sensory pores. Anteriorly it has a ventrally directed process similar to that in *Undina* and *Macropoma*. This process is present, but weakly developed, in *Diplurus*. A distinct anterodorsal process on the lateral rostral is not evident in *Chinlea*, and therefore the anterior and posterior external nares cannot be located with certainty (see discussion in Schaeffer, 1952a, p. 37; also in Millot and Anthony, 1954). The infraorbital (lacrymo-jugal) articulates anteriorly with the lateral rostral and with two supraorbitals; posteriorly it is in contact with the postorbital and the preopercular.

The postorbital is triangular, as in *Whitea* or *Macropoma*, and it differs considerably from the distinctively shaped element in *Diplurus*. The preopercular (or squamosal of the earlier literature) and the preoperculoquadratojugal (or preopercular) are shaped

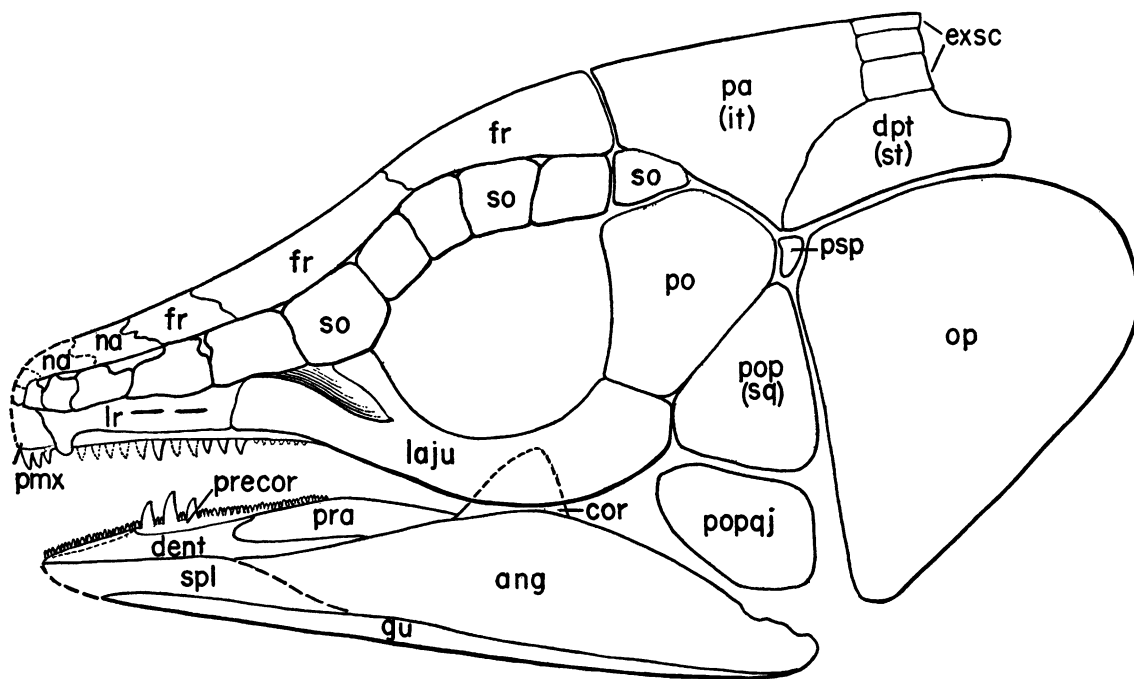


FIG. 14. *Chinlea sorenseni*, new genus and species, restoration of skull in lateral aspect. Ca. $\times 2.53$.

Abbreviations: ang, angular; cor, coracoid; dent, dentary; dpt, dermopterotic (supratemporal); exsc, extrascapular; fr, frontal; gu, gular; laju, lacrimo-jugal (infraorbital); lr, lateral rostral; na, nasal; op, opercular; pa, parietal (intertemporal); pmx, premaxilla; po, postorbital; pop, preopercular (squamosal); popqj, preoperculoquadratojugal (preopercular); pra, prearticular; precor, precoracoid; psp, prespiracular; so, supraorbital; spl, splenial.

much as in the above genera. A small bony mass superimposed on the ventral angle of the opercular in the type specimen may represent the subopercular or possibly an ossification in Meckel's cartilage.

The relatively large dentary is forked posteriorly, much as in *Macropoma*. Its dorsomedian surface is covered with small, closely spaced teeth that are presumably attached to thin, superficial plates. As in *Latimeria*, the precoracoid supports a cluster of robust, tusklike teeth. The coracoid is triangular, with a thickened anterior border.

The rugose ornamentation of the dermal skull elements becomes more pronounced with increase in size (compare fig. 1 with fig. 2 of pl. 28). The opercular is apparently the only element to remain relatively smooth.

AXIAL SKELETON: The neural arches are typical for the family and require no comment. The long, delicate, ossified, pleural ribs must have been attached to the notochordal sheath; they are longest in the mid-abdominal region and decrease in length in

the vicinity of the anal basal plate. The haemal spines, which are in series with the ribs, typically attain their maximum length as supports for the lower lobe of the caudal fin.

GIRDLES AND PAIRED FINS: The cleithrum (the only element in the pectoral skeleton preserved well enough for description) resembles that of *Diplurus* in all observable respects. The pelvic plates are likewise similar to the *Diplurus* type in having a short and broad median process, two anterior apophyses, and a posterior triangular expansion. The pelvic fins are composed of about 18 rays.

UNPAIRED FINS: The basal plate of the anterior dorsal fin is typically triangular; the fin is made up of about nine relatively heavy rays that articulate directly with the plate. The bifurcated basal plate of the posterior dorsal fin has a slightly expanded posterior portion. The fin includes about 15 rays. The anal basal plate is typically like that of the posterior dorsal; the fin includes about 15 rays. The caudal fin has about 13 partly seg-

mented lepidotrichia in each lobe and a long, supplementary, caudal lobe.

SQUAMATION: Scale impressions are preserved in A.M.N.H. No. 5654 (pl. 26, fig. 1), and a number of isolated scales have been found in the Dolores Canyon bone bed. The exposed portion of the scale is covered with as many as 40 more or less parallel ridges of varying length, closely spaced as in *Diplurus longicaudatus*. Fine corrugations on the surface of the isopedine layer are evident between them. Typical circuli are also present.

DISCUSSION

Chinlea and *Diplurus*¹ are the only coelacanth known to have long, ossified, pleural ribs. *Coelacanthus* (Moy-Thomas and Westoll, 1935), and perhaps *Laugia* (Stensiö, 1932), have short ribs, apparently also pleural. Other coelacanth genera, including *Latimeria*, show no evidence of rib ossification. Both the ossification and the elongation of the ribs probably had some biomechanical significance related to the contraction of the myomeres and to increased swimming efficiency. If so, the pleural ribs of *Diplurus* and *Chinlea* are an example of "improvement" that for some reason did not persist in the coelacanthiforms. The anteriorly situated pelvic fins in *Laugia* and several other genera represent another example of this phenomenon.

Chinlea resembles *Diplurus* in the general configuration of the basisphenoid, in the shape of the fin supports, in possessing long, ossified, pleural ribs, and in having an elongated, supplementary caudal lobe. The most

obvious differences between them are found in the dermal skull. The roof of the anterior moiety may be more subdivided in the frontal-nasal (postrostral) portion in *Chinlea*, but the variation in the ossification pattern in *Diplurus* makes such a possible subdivision difficult to determine. The supratemporals (dermopterotics) are relatively large in both, but their posterior extension is broader in *Chinlea*. The extrascapulars are also larger and better ossified in *Chinlea*. The anteroventral process of the lateral rostral is more pronounced. The rectangular supraorbital elements of *Chinlea* do not have large pores between them for the supraorbital canal as is the case in *Diplurus newarki*, but the arrangement of these bones is nearly identical in both genera. The *Chinlea* postorbital is relatively larger and more triangular than the corresponding element in *Diplurus*. The angular is much deeper anteriorly in *Diplurus* than in *Chinlea*, and the dentary of the latter, with its posterior notch and elongated dentigerous portion, is more suggestive of this bone in *Undina* or *Macropoma*. The tusklike teeth on the precoracoid and presumably on the dermopalatines and the ectopterygoid are not present in *Diplurus*, although both have smaller teeth on the premaxillary and the dentary.

The weathered coelacanth skull from the Tecovas Formation of the Dockum Group (Schaeffer and Gregory, 1961) and the isolated quadrate discussed by Warthin (1928), also from the Dockum, can be tentatively assigned to *Chinlea*. Certainly the form of the mandible and the observable aspects of the roof in the Tecovas skull agree with these features in the *Chinle* form.

In spite of the obvious differences between *Chinlea* and *Diplurus*, it is reasonable to conclude that they are more closely related to each other than to any other coelacanth genus thus far described. *Moenkopia* (Schaeffer and Gregory, 1961), which lived in the same general area as *Chinlea* during the Early Triassic, has a very different basisphenoid, and there is no evidence that it is ancestral to these Late Triassic forms.

INDETERMINATE REMAINS

In addition to the genera described in the preceding parts of this section, there is evi-

¹ The validity of the name *Diplurus* for the coelacanth from the Newark Series has been discussed in a previous paper (Schaeffer, 1952a). *Rhabdiolepis* (Emmons, 1857) is undoubtedly the oldest name available in the literature for a Newark coelacanth, but Emmons' specimens have been lost, and his inadequate description and illustrations (some of which are understandably misidentified) do not include the really diagnostic characters. Also, *Rhabdiolepis* could qualify as a *nomen oblitum*. For these reasons I have preferred to regard *Rhabdiolepis* as taxonomically indeterminate and have continued to use *Diplurus* for the Newark form. This nomenclatural problem has been further complicated by Bock (1959) who has synonymized *Diplurus* in part with *Rhabdiolepis* and in part with *Osteopleurus* (Schaeffer, 1941). In 1952 (1952a) I presented evidence for regarding *Osteopleurus* as a synonym of *Diplurus*. Until circumstances permit a critical systematic review, I prefer to use *Diplurus* in an inclusive sense for the Newark coelacanth complex.

dence for other kinds of fishes in the Moenave, Chinle, and Dockum that are presently too incomplete for meaningful taxonomic treatment. Certain of these elusive forms are discussed below in the hope that more complete examples will, in time, be discovered.

The *Semionotus* or *Lepidotus* remains in the bone beds around Kanab, Utah (which have not been critically studied), must represent only a part of the Moenave fish fauna. The undescribed remains from the Dinosaur Canyon Sandstone (Harshberger, Repenning, and Irwin, 1957) should increase our knowledge of this assemblage.

A partial skull (A.M.N.H. No. 5719) found with the *Coelophysis* skeletons in the upper part of the Petrified Forest Member of the Chinle at Ghost Ranch, New Mexico, shows some resemblance to *Synorichthys* in the cheek and opercular pattern and in the ornamentation of the dermal elements (text fig. 15). The maxilla is quite narrow under the orbit, and it apparently fits posteriorly

into an embayment in the preopercular. The teeth are fairly robust and styliform. Several rows of scales behind the shoulder girdle demonstrate that at least the anterior flank scales are about twice the size of similarly situated ones in *Synorichthys*. The fins are not preserved.

In addition to the redfieldiid remains described above, the Dockum fish locality near Otis Chalk, Texas, has yielded parts of at least two or three other kinds of fishes that have not been found in the Chinle. Two of these are represented by small patches of scales on the same matrix block (A.M.N.H. No. 5720). One scale type has strongly developed, nearly parallel ridges that apparently project beyond the scale border. The other has more widely spaced bifurcating ridges (pl. 29). It is possible that both come from different areas of the same squamation, but it is more probable that two different palaeonisciforms are represented.

Another distinctive palaeonisciform (pl.

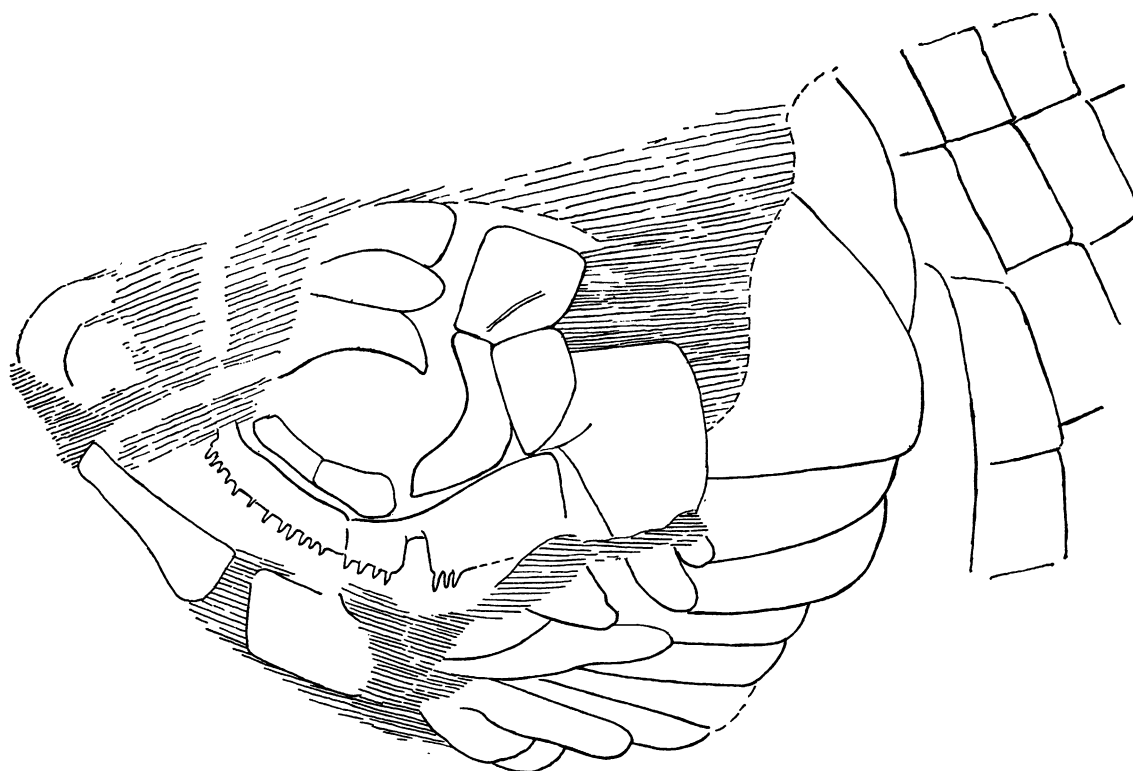


FIG. 15. Indeterminate chondrosteian, A.M.N.H. No. 5719, from the Petrified Forest Member of the Chinle Formation, Ghost Ranch, New Mexico. Ca. $\times 3.14$.

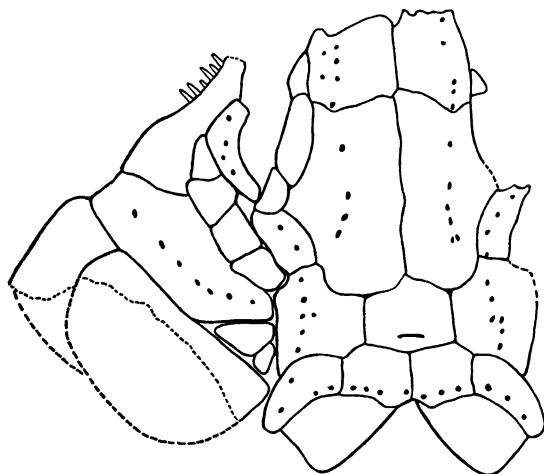


FIG. 16. Indeterminate palaeonisciform from the Dockum Group, Otis Chalk, Howard County, Texas, partial restoration of skull based on A.M.N.H. No. 5662. *Ca.* $\times 3.4$.

30; text fig. 16) from the same Texas locality is represented by several partial skulls and bodies plus isolated jaw and opercular elements (collectively catalogued as A.M.N.H. No. 5662). The dermal bones are ornamented with low, rounded, almost scalelike tubercles. The roof is composed of four

extrascapulars, a single parietal, uniformly broad frontals, and equally broad nasals that meet in the midline. The dermosphenotics are about the same size as the supraorbitals and are much smaller than the dermopterotics. One isolated roof (pl. 30, fig. 1) differs from the others in that the median parietal is fused with the right dermopterotic. Another smaller roof exhibits no sutures, although the pores of the supraorbital canals are clearly evident. The cheek area has an ovoid preopercular with an embayment for the posterior border of the maxilla. Between the preopercular and the elements forming the posterior border of the orbit there is a vertical series of four small suborbitals. One or two wedge-shaped dermohyals are present behind the preopercular. The dorsal border of the maxilla is gently concave from its posterior margin to suborbital ramus, much as in certain perleidids (e.g., *Meidiichthys*). The mandible is fairly deep and, as does the maxilla, supports well-spaced, styliform teeth. Snout elements have not been recovered, and the opercular is represented only by isolated elements. The associated scales are rhombic and devoid of ornamentation. Fins are unknown.

REMARKS ON THE REDFIELDIIDAE

THE FAMILY CATOPTERIDAE was established by Woodward (1890, p. 16) for *Catopterus* Redfield, 1837, and *Dictyopyge* Egerton, 1847. In 1899 Hay pointed out that *Catopterus* Redfield was preoccupied by *Catopterus* Agassiz, 1833, which, in turn, proved to be a synonym for *Dipterus*. Hay, therefore, synonymized *Catopterus* with the new name *Redfieldius*. In the same publication, Hay also changed the name of the family to Dictyopygidae. Most later students of the group, however (Eastman, 1905, 1911; Stensiö, 1921; Brough, 1931, 1934, 1936; Wade, 1935; Lehman *et al.*, 1959), have used the name Catopteridae, although Romer in his 1945 classification followed Hay. In 1940 Berg introduced the family name Redfieldiidae as a substitute for Catopteridae and Dictyopygidae (see also Berg, 1958). Although the names Dictyopygidae and Redfieldiidae have been employed with about equal frequency since Hay's publication, the latest version of the International Code (Article 39) favors Redfieldiidae as the proper name for this family.

Woodward's (1890) original diagnosis of the Redfieldiidae is hardly restrictive; he mentioned only the remote dorsal fin, the anterior orbits, the prominent snout, and the somewhat oblique suspensorium. His reasons for removing *Catopterus* and *Dictyopyge* from the "Lepidosteoidei" included the excess of fin rays over basals in the anal fin of *Dictyopyge macrura* and certain other "vaguely discernible features" in the Australian *D. illustrans* (indeterminate, according to Wade, 1940, but possibly a species of *Brookvalia*) that suggest the palaeonisciforms. Woodward, in his 1895 diagnosis of the family, added the hemiheterocercal tail and a series of branchiostegal rays (without citing the evidence). Eastman's 1905 and 1911 diagnoses are identical and add little beyond a mention of dermal bone ornamentation and some details of the unpaired fins.

De Alessandri (1910) included *Perleidus* from the Middle Triassic of Lombardy in the Catopteridae. Although this assignment was questioned by Stolley (1920), Stensiö, in 1921, expressed the opinion that *Perleidus*,

along with all the genera then assigned to the Colobodontidae, should be placed in the Catopteridae. His summary description of the enlarged family (*op. cit.*, pp. 269–270) thus includes characters that were later used, in part, to distinguish the Catopteridae from the Perleidiidae. Brough (1931, pp. 279–288) finally separated these two families¹ on the basis of numerous dermal skull and fin characters.

Berg (1940, 1955, 1958) assigned the Lower Triassic redfieldiid *Brookvalia* (Wade, 1935) to a separate family, the Brookvaliidae, and included the latter, along with the Redfieldiidae, in the order Redfieldiiformes. In Berg's opinion, *Brookvalia* should be separated from the other redfieldiids mainly because the supraorbital sensory canal joins the infraorbital canal in the dermopterotic bone. Lehman (1958, 1966), however, included *Brookvalia* in the Catopteridae and placed this family, along with the Perleidiidae, in the order Perleidiformes. He believed that these families are closely related (Lehman, 1952, p. 145) and that they differ mainly in the dentition and in fin characters. The important differences in the branchiostegals and other characters discussed by Schaeffer (1955) are not considered. In my opinion, the Redfieldiidae and the Perleidiidae show no close affinity, and it is difficult to justify their inclusion in the same order.

The term "subholostean" was first used by Brough in 1936 "merely as one of convenience" in a discussion of certain palaeonisciform families that, in one way or another, independently approached the holostean level. He noted that the redfieldiids are subholosteans in several characters. Although I do not agree with him that these fishes are the "least modified of the subholostean groups," it is evident that they retained a number of primitive characters. It is also clear that their

¹ Uncertain about the taxonomic position of *Colobodus*, Brough rejected the name Colobodontidae in favor of Perleidiidae. In a review of the Perleidiidae, Schaeffer (1955) placed the *Colobodus* of Stensiö in this family and further distinguished it from the Redfieldiidae. The fact remains, however, that the type of *Colobodus* Agassiz is a jaw fragment of uncertain affinity.

specialized characters preclude the possibility of their being ancestral to other subholostean groups or to any of the holostean lines.

Brough's conclusion (1936, pp. 403-404) that the redfieldiids arose from the dicelopygids is possible but difficult to substantiate. Most of the points of agreement, including the general proportions of the skull, the angle of the suspensorium and the cheek-opercular pattern, can be more or less duplicated in other palaeonisciform groups. For instance, *Aeduellia* (Westoll, 1937) is similar to the redfieldiids in having enlarged dermosphenotics and "adnasals," but the cheek design is quite different. Several genera with a nearly vertical suspensorium have a similarly shaped maxilla and preopercular. Even reduction of the branchiostegal series has occurred a number of times independently among the actinopterygians. In my opinion, the origin and the affinities of the redfieldiids are still open to question.

The genera currently included in the Redfieldiidae exhibit some rather striking differences in the dermal skull (text figs. 17 and 18) and the fins that represent degrees of approach to the holostean level. Although a number of these genera are still poorly known, an attempt is made below to summarize our present knowledge of the group in order to assess the meaning of this apparent diversity.

SNOUT: The bones of the redfieldiid snout are frequently missing or crushed beyond recognition. Even the nasal bone, which is a key element in the deciphering of the snout pattern, often cannot be positively identified because the pertinent portion of the supraorbital canal is not in evidence. The shape of the entire snout and its orientation in relation to the jaw margin are also difficult to determine, as the various restorations indicate. Detailed evidence on this part of the skull is provided mostly by the American genera, supplemented with observations and diagrams of the South African and Australian forms supplied by Dr. Brian Gardiner.

The American genera demonstrate that the snout consists of a rostral and postrostral plus paired nasals, adnasals, and antorbital, except in *Synorichthys* from which the postrostral is absent. The single nostril is situated between the nasal and the antorbital, or, in other words, below, or posterior to,

the supraorbital sensory canals. The rostral bone is considerably smaller than the postrostral except in *Lasalichthys*. The antorbital enters, but may not be functionally part of, the upper jaw margin, with the anterior process of the maxilla overlapping only its posterior extension. The infraorbital sensory canal typically extends forward through the antorbital to join the rostral commissure below the supraorbital canal. The only deviation from this pattern involves the reduction (in *Lasalichthys*) or the elimination (in *Synorichthys*) of the postrostral. In relation to the stability of the snout pattern in other families at the chondrosteian level, this is a radical modification that apparently can be duplicated only in certain perleidids (Schaeffer, 1955). It is possible but not probable that this change is related to some unknown alteration in the anterior part of the conservative, palaeonisciform type of neurocranium.

Specimens in the American Museum collection show that the snout of the South African *Helichthys* (Brough, 1931) is nearly identical with that of *Redfieldius* and *Cionichthys*, indicating that this pattern persisted from the Lower Triassic (Lower *Cynognathus* Zone) to the Upper Triassic, when the redfieldiids apparently became extinct. In two other genera from the Lower *Cynognathus* Zone, *Daedalichthys* and *Atopocephala*, Brough (1931) identified a bone lying below and behind the nostril as the nasal. Although the course of the supraorbital sensory canal was not determined, the topographic relationships of this bone indicate that it should be the antorbital, and that this part of the snout should include the adnasal. Otherwise, the snout pattern in these genera cannot be reconciled with the *Redfieldius* one. Brough also found a single element capping the snout between the nostrils that he considered to be the postrostrals. There is apparently no indication of separate nasal bones related to the supraorbital sensory canals. Gardiner (personal communication) has confirmed some of the details described by Brough, but it is hoped that specimens will be found that will reveal additional information.

The snout pattern of the Australian forms described by Wade (1935) from the Middle Triassic (probably Anisian or Ladinian, or

both) Hawkesbury Formation in New South Wales is somewhat clearer. *Brookvalia* definitely has the *Redfieldius* pattern. The only problem here is the relationship between the maxilla and the antorbital bone which, incidentally, has a decided anteroventral notch as in *Cionichthys*. According to the sketches supplied by Gardiner, the poorly preserved specimens of *Beaconia* and *Geitonichthys* have a rostral element anterior to the antorbitals that exclude it from the snout margin. In Wade's (1935) figure of the latter, however, the postrostral, nasal, and adnasal are again like those in *Redfieldius*. The same is true for *Molybdichthys*, but the rostral and antorbital have not been identified. There is thus evidence in all but three of these genera that the snout agrees with the *Redfieldius* type. Certainly the pattern should be basically the same in all of them, even if we allow for the reduction or loss of the postrostral in two.

The shape of the snout is related to the association of the rostral, antorbital, and maxillary. It is possible that the suborbital portion of the maxillary excludes the antorbital from the jaw margin in some genera and that the maxillary may therefore be in contact with the rostral, but such is definitely not the case in the Chinle-Dockum redfieldiids.

The peculiar form of the snout in most of the genera suggests that a well-developed, fleshy upper lip was present and that the mouth was subterminal. The robust, tooth-like tubercles on the rostral and antorbitals in *Helichthys* and the American forms were presumably entirely embedded in this lip, and, in fact, they may have developed to support the lip tissues. This specialization points to bottom feeding but not necessarily in a sucker-like manner. The presence of teeth along the entire ventral border of the maxilla indicates that the mouth could be opened widely. As the snout was fixed and not prehensile, it seems more probable that the redfieldiids scooped detritus from the bottom rather than sucked it into the mouth cavity.

Neither the American nor the Australian redfieldiids show evidence of premaxillae, although Brough (1931, 1934) has claimed their presence in the South African genera. Gardiner (1963) and others have suggested that these elements arose within the palaeo-

nisciforms by a "fragmentation" of the rostral which they would call the rostro-premaxilla. A possible morphogenetic interpretation of this phenomenon is that the mesenchyme available for the rostral bone was subdivided into three rudiments through the development of separate premaxillary and rostral osteogenic centers. The appearance of the premaxillae was thus dependent on changes that occurred early in ontogeny before ossification occurred. I would therefore regard the premaxillae as new structures that arose several times independently.

Roof: The redfieldiid dermosphenotics are nearly equal in size to the dermopterotics and are invariably entirely anterior to them. As noted above, enlarged dermosphenotics, either overlapping the dermopterotics laterally or situated anterior to them, occur in a number of chondrosteian-level forms (e.g., *Cheirolepis*, *Nematoptychius*, *Aeduella*, and *Boreosomus*) but not in the parasemio-niids or in the groups at the holostean level. The relative size of the dermosphenotic is probably related to the growth rate, arrangement, and number of surrounding elements. In some genera, such as the redfieldiids *Atopocephala* and *Daedalichthys* (Brough, 1934), the width of the dermosphenotic was perhaps also influenced by the relatively large orbits, but in *Brookvalia*, which has relatively small orbits, the narrowness of the dermosphenotics may have resulted from the posterior expansion of the frontals.

The differences in the redfieldiid parietal pattern are referred to in the description of the American genera. *Helichthys*, *Brookvalia*, and probably *Beaconia* have two pairs of triangular parietals, one pair situated behind the other. *Lasalichthys* and *Synorichthys* have a single pair of triangular elements. All the other genera in which the roof is known have one pair of rectangular parietals except *Redfieldius*, which has three or four bones in a single transverse row. A single pair of parietals undoubtedly represents the ancestral condition, but some palaeoniscoids and subholosteans show variation in the number of parietal elements at the infraspecific (e.g., *Australosomus merlei*; Lehman, 1952), at the specific (e.g., *Birgeria mougeoti*), or at the generic (e.g., *Redfieldius*) level. An explanation for the relative susceptibility of the

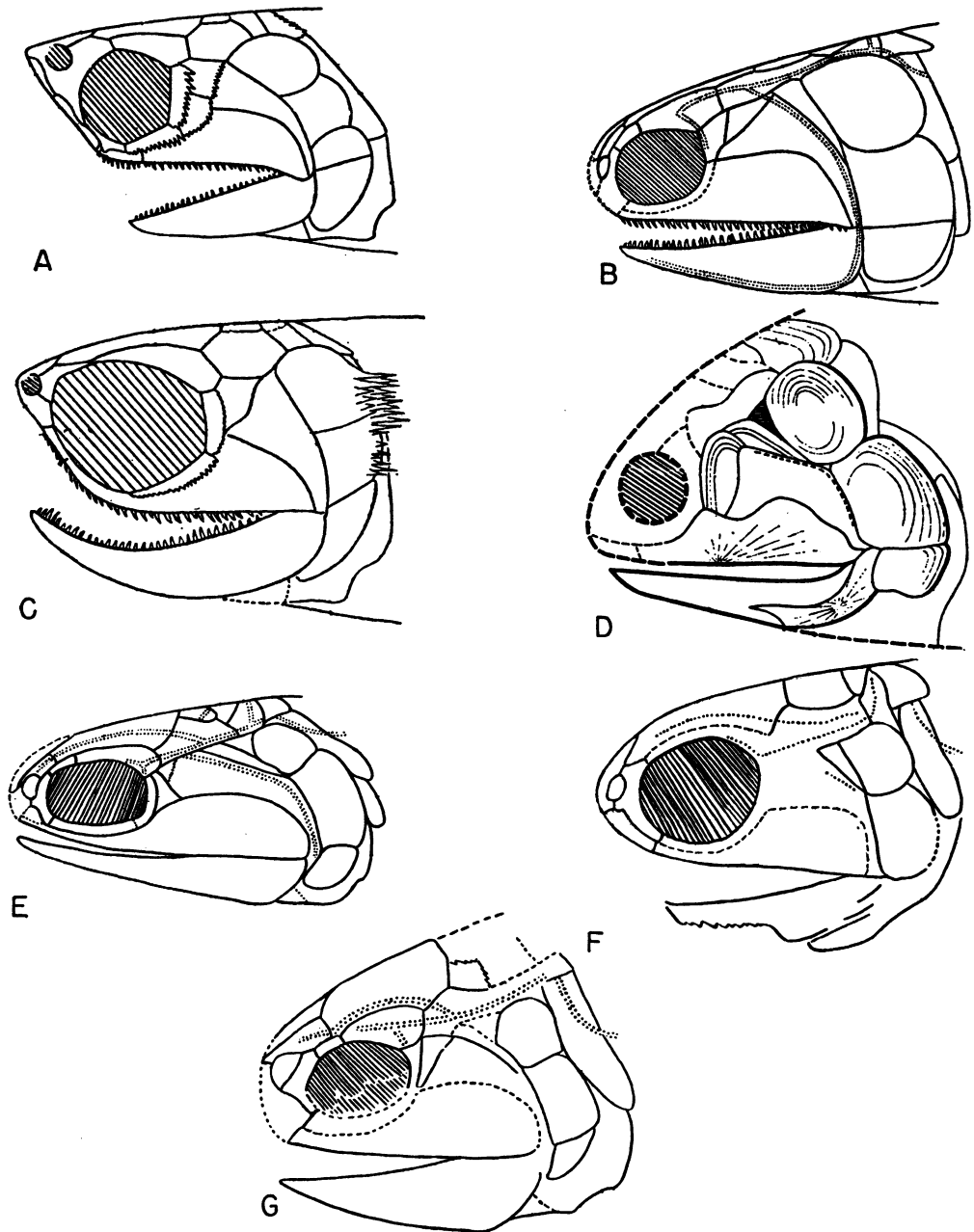


FIG. 17. Restorations of redfieldiid skulls. A. *Daedalichthys*. B. *Helichthys*. C. *Atopocephala*. D. *Sakamenichthys*. E. *Brookvalia*. F. *Beaconia*. G. *Geitonichthys*. A-C, modified after Brough (1931, 1934); D, after Lehman *et al.* (1959); E-G, modified after Wade (1935).

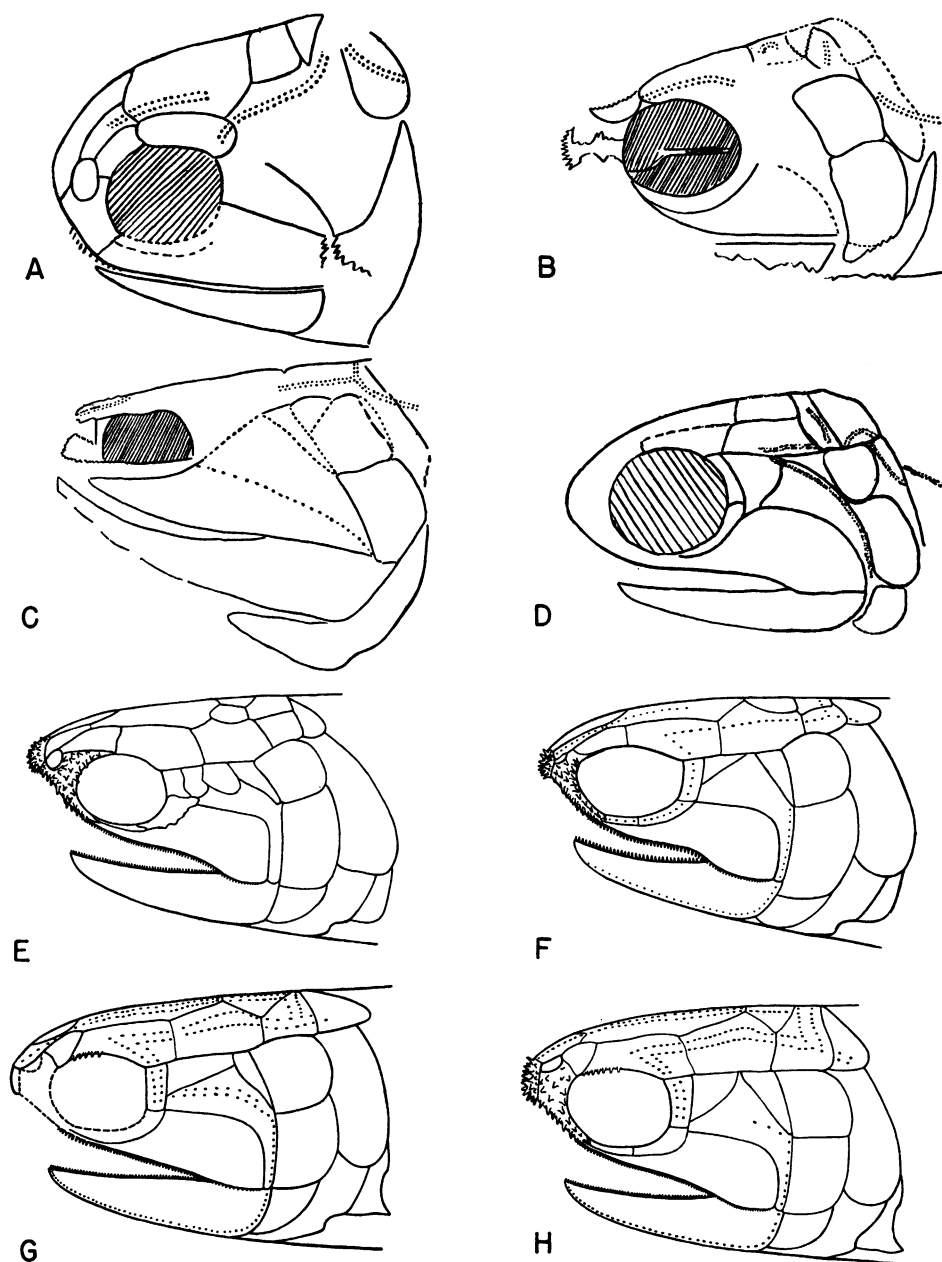


FIG. 18. Restorations of redfieldiid skulls. A. *Molybdichthys*. B. *Phlyctaenichthys*. C. *Schizurichthys*. D. *Ischnolepis*. E. *Redfieldius*. F. *Cionichthys*. G. *Lasalichthys*. H. *Synorichthys*. A-C, modified after Wade (1935); D, modified after Haughton (1934).

parietal area to increase in number of elements in contrast to the stability of the other dermal roofing elements is difficult to provide. It may be related to delayed ossification of the parietals or to the presence of more than one parietal rudiment on each side, as Pehrson (1940) has noted in *Amia*. Although no extensive study of dermal bone variation in the actinopterygians is available, it seems that the parietal pattern is more constant at the holostean (*Semionotus africanus* represents a notable exception) and teleostean levels than at the chondrosteian.

CHEEK: Aside from differences in proportion related to minor changes in the angle of the suspensorium, the redfieldiid cheek pattern is fairly constant. The r-shaped preopercular is characteristic of nearly all palaeonisciforms and subholosteans with an oblique to moderately oblique suspensorium, and its shape in the redfieldiids must represent derivation from some palaeoniscoid stock. The other cheek elements are also found in more primitive chondrosteans and present no particular derivation problem. *Brookvalia* has the most oblique suspensorium within the family, but, with this exception, the angle is fairly constant. It is therefore difficult to substantiate Brough's (1936) conclusion that the redfieldiid suspensorium became more vertical during the course of the Triassic.

OPERCULAR-BRANCHIOSTEGAL SERIES: The redfieldiid opercular bone may equal the size of the subopercular or be considerably smaller. One or two ovoid, platelike elements situated immediately below the subopercular seemingly represent the remains of the branchiostegal series. Haughton (1934) described structures in the throat region of *Ischnolepis* that he regarded as branchiostegals, but re-examination of his specimen (S.A.M. No. 9338-5) suggests that they are fragments of the gill arches. The single branchiostegal of *Redfieldius* and *Cionichthys* was presumably in direct contact with the posterior gulars.

Reduction of the branchiostegal series has occurred independently in a wide variety of actinopterygian families (e.g., the Haplolepididae, Aduellidae, Acipenseridae, Saurichthyidae, Pycnodontidae, and Syngnathidae). Usually the branchiostegals provide expansible but rigid support for the opercular

fold in the throat region, particularly during the suction phase in gill respiration when the fold presses tightly against the shoulder girdle. The reduction of the branchiostegal series in such groups as the haplolepidids and the redfieldiids indicates that the opercular opening was essentially restricted to the side of the head. Although this modification must have reduced the expansibility of the orobranchial chamber, there is no evidence that the feeding and gill ventilation mechanisms (see Schaeffer and Rosen, 1961) were otherwise altered.

Westoll (1944) has suggested that reduction of the branchiostegals in certain paleonisciforms and in the redfieldiids was associated with decreasing obliquity of the suspensorium. This decrease may have been a correlated modification, but it must be recalled that most chondrosteian-level forms with a vertical suspensorium retained more than two typical branchiostegals (e.g., *Cano-bius*). There is the possibility, also discussed by Westoll, that reduction of these elements was coupled with the development of accessory respiratory organs for breathing in oxygen-deficient water.

POSTCRANIAL SKELETON: The ossified ribs of the American forms are moderately long; there is no indication of centra. Aside from the unusually long and broad supracleithrum, the shoulder girdle presents no unusual features. The rays of the paired fins, as Brough (1936) has noted, show considerable variation in number and in amount of segmentation. In *Helichthys obesus*, for example, the rays in the posterior half of the pectoral fins are completely divided, whereas those in the anterior half are unjointed. Both the pectoral and pelvic fins of *Daedalichthys* have a relatively small number of unsegmented rays. Some decrease in segmentation is also evident in the Australian and American genera, particularly in the anterior rays, but there is no significant reduction in ray number. As in the palaeonisciforms, the rays of the remote dorsal and anal fins are completely segmented and greater in number than their endoskeletal supports.

Brough (1936) has noted various degrees of reduction in the body axis of the caudal fin. *Daedalichthys* has the longest axis, which terminates near the tip of the dorsal lobe. In the other genera, the axis is considerably

shorter, and it apparently attained maximum reduction in the Upper Triassic forms. The mode of reduction, according to Brough (1936, p. 390), was "by the loss of transverse rows of scales from the tip of the tail forward." In the semionotids, on the other hand, reduction of the axis was accomplished "by the removal of longitudinal scale rows from below upwards" (Brough, 1936; see also Gill, 1923). The assumption for the semionotids is based on the fact that *Acentrophorus* retained a single row of scales extending to the tip of the tail. I find it difficult, however, to make a sharp distinction between these two "methods." The disappearance of scales from the posterior border of the body axis means that they were lost simultaneously from the intersecting transverse and longitudinal scale rows. Reduction thus seems to involve only a somewhat variable emphasis on the persistence (or loss) of the last remnant of the body axis.

Brough's (1936) attempt to recognize evolutionary trends in the Redfieldiidae is for the most part equivocal. Aside from the oblique suspensorium of *Brookvalia*, there is little difference in this angle from the Early to the Late Triassic. Unless we interpret the reduction and loss of the postrostral in the Late Triassic as a trend, the skull roof shows no long-range change. Also, Brough's conclusion that there was a successive reduction in orbital size, in the number of infraorbital elements, and in the number of suborbital elements is difficult to substantiate. The loss of segmentation in the pectoral and pelvic rays seems to follow no definable temporal sequence. There is, however, some evidence of progressive decrease in the caudal-fin axis.

A few genera that do not contribute significantly to our understanding of the family have been omitted from the above discussion. *Sakamenichthys* (Lehman *et al.*, 1959) from the Lower Triassic of Madagascar shows no clear affinity with the South African forms or, for that matter, with any later genera. The skull roof and the snout are unknown. *Ischnolepis* (Haughton, 1934) from the Upper Triassic (?Upper Beaufort or Lower Stormberg) of Rhodesia is likewise too poorly preserved for adequate comparison with other genera. Examination of Haughton's specimens indicates a single pair of rectangular parietals and a cheek pattern resembling the

Redfieldius-Cionichthys type.

The description of *Pseudobeaconia* (Bordas, 1944) is not adequate to demonstrate that this form from the Triassic of Argentina is a redfieldiid. The "operculares suplementarios" are considered to be absent, but no other really diagnostic characters are discussed. *Sinkiangichthys* (Liu, 1958) from the Lower Triassic of Sinkiang, China, gives better evidence of belonging to the group. Branchiostegals are not in evidence, the dorsal and anal are in a remote position, and their rays are more numerous than the radials. Unfortunately the description is based on a single specimen that has a poorly preserved skull.

Dictyopyge from the Newark Group has received only cursory treatment, because the generally inadequate preservation has long rendered interpretation difficult. Recently acquired specimens from Virginia confirm the opinion of Brough (1931) that this genus possesses a typical redfieldiid opercular series, enlarged dermosphenotics, and rectangular parietals. The large, lobate anal fin remains its most distinguishing character. The characters cited on page 315 that show resemblance to *Lasalichthys* and *Synorichthys* are by themselves insufficient to indicate close affinity. Specimens assigned to *Dictyopyge* from Australia and Europe in the British Museum (Natural History) collection are also poorly preserved, and their affinities are problematical. The Australian forms may be young individuals of *Brookvalia* (Wade, 1933).

Although the redfieldiids have a greater time range than any other known subholostean family, their occurrence, with a few exceptions, is restricted to a different continent for each major subdivision of the Triassic. The Lower Triassic forms are found mainly in South Africa; the Middle Triassic, in Australia; and the Upper Triassic, in North America. The record is thus a discontinuous one, both temporally and geographically. The observable diversity among the known genera is difficult to evaluate, and little can be said about their interrelationships. In view of these limitations, it is perhaps more meaningful to consider the ways in which the redfieldiids experimented with the "subholostean" combination of primitive (palaeonisciform), specialized, and holostean-like characters.

The form of the braincase, the fixed maxillary, and the position and structure of the dorsal and anal fins represent retained palaeoniscoid features. The scale histology, including the absence of the dentine layer, is not significantly different from that of an advanced palaeoniscid or a holostean. Several aspects of the snout and roof pattern are also duplicated in other palaeonisciforms. These include the presence of both adnasals and nasals, the inclusion of the antorbital in the upper jaw margin, the absence of premaxillaries, the enlarged dermosphenotics, the reduction of the branchiostegal series, and the restriction of the gill opening. But the particular combination of these characters, along with a single nostril between the nasal and the antorbital (not certainly, but probably a constant feature), is distinctive for the family. Modifications representing experiments in a holostean direction include the reduction and loss of the postrostral, a decrease in segmentation of the pectoral and pelvic fin rays, and a reduction of the caudal fin axis.

Turning to redfieldiid systematics, I can find no valid reason for assigning *Brookvalia* to a separate family on the basis of the sensory canal modifications. Although unique within the family, this deviation hardly seems more significant than the differences in the parietal area or the absence of the postrostral. The redfieldiids, like most other subholostean groups, are still phylogenetically isolated, and their taxonomic rank remains problematical. They are clearly distinct enough from the Perleidiidae to invalidate Lehman's (1958, 1966) incorporation of both families into the order Perleidiformes. Elevation of the redfieldiids to the ordinal level (Berg, 1955) or, better, to subordinal rank within the order Palaeonisciformes is a reasonable conclusion. Attempting to recognize more than one family within the suborder raises the almost unanswerable problem of which differences, or degrees of differences, deserve family status. I therefore favor grouping the presently known genera in a single family. It is obviously one of considerable diversity, but hardly more so than a teleost family such as the Poeciliidae (Rosen and Bailey, 1963).

Redfieldiid remains are often locally abundant, and it is reasonable to assume that they were common fresh-water fishes in certain

parts of the world during the Triassic Period. Unfortunately the negative aspects of the redfieldiid record make a discussion of their distribution or their persistence in a particular region nearly impossible. Although the earliest known occurrences are in Africa, Madagascar, and possibly Australia, it is probable that these fishes will be found elsewhere in the Lower Triassic, for instance, in the Moenkopi Formation. According to Liu (1958), *Sinkiangichthys* is also of this age. If the redfieldiids were entirely restricted to fresh water, they must have reached Australia and Madagascar before these land masses were isolated. In summary, the redfieldiids were a fairly conservative group (in spite of the differences discussed above) of fresh-water palaeonisciforms that were probably specialized for detritus feeding. They invaded most or all of the continents, where they frequently evolved distinctive dermal bone patterns. There is no evidence, however, of significant adaptive radiation in either the feeding or the locomotor mechanisms.

The evidence presented in this paper necessitates a new diagnosis for the family Redfieldiidae, as follows:

Lower to Upper Triassic fresh-water subholostean palaeonisciforms. Braincase of palaeoniscoid type. Snout usually composed of rostral, postrostral, paired nasals and adnasals (postrostral absent from one genus, with nasals meeting in midline); presumably specialized for support of fleshy upper lip. Single narial opening surrounded by adnasal, nasal, and antorbital. Antorbital usually (perhaps consistently) forming part of snout margin. No separate premaxillae. Maxilla expanded posteriorly and attached to cheek. Suspensorium moderately oblique. Two to four parietals, either exclusively triangular or rectangular. Dermosphenotic equal to size of dermopterotic. Branchiostegals reduced to one or two platelike elements situated below subopercular. Gill opening mostly restricted to side of head. Gular plates present. Rays of paired fins either partly segmented or unsegmented. Rays of remote dorsal and anal fins completely segmented and more numerous than endoskeletal supports. Fulcra on paired and unpaired fins well developed, reduced, or absent. Caudal fin axis variably reduced. Scales rhomboidal, frequently with denticulated posterior border; dentine layer absent.

CONCLUSIONS

CORRELATION

THE CORRELATION of the various stratigraphic units within the Chinle Formation and the Dockum Group as determined by the phytosaur evidence (text fig. 2) cannot be corroborated by the distribution of the fish taxa, owing partly to the spotty occurrence of the fishes. However, the limited evidence also suggests that most of the genera, if not all of them, persisted for a much longer time interval than any single phytosaur genus. There is, in fact, reason to believe that they were distributed throughout the Chinle-Dockum-Moenave flood-plain during most of its history. The redfieldiid genera in the lower part of the Dockum are the same as those in the upper part of the Chinle. The coelacanth *Chinlea* occurs in the upper part of the Chinle and probably also in the Tecovas. *Turseodus* and *Semionotus* must have been present in the area of Dockum sedimentation, and surely such forms as *Hemicalypterus* and *Synorichthys* had a wider dispersal than current evidence indicates. The Moenave forms are too poorly known for the degree of resemblance to the Chinle-Dockum fauna to be determined.

A comparison of the fish assemblage of the Newark Group with that of the Chinle-Dockum shows some obvious similarities and some interesting differences. *Turseodus* with its ossified centra occurs in both sequences. Although the common presence of *Semionotus* is perhaps not surprising, it is important to note that the Chinle representatives show the same range of body form as the Newark ones—a range that is apparently not duplicated elsewhere. *Cionichthys* is closely related to *Redfieldius*, and the coelacanth *Chinlea* shows affinity with *Diplurus*.

The differences between the two assemblages probably reflect the considerable geographic separation (roughly 1700 miles) of these two Triassic lowland areas, and perhaps the introduction into each of faunal elements from different source areas. The well-collected Newark Group has not yielded a redfieldiid of the *Lasalichthys-Synorichthys* type (unless it is *Dictyopyge*), or a specialized semionotid resembling *Hemicalypterus*, or the

lungfish *Ceratodus*. On the other hand, it alone contains the hybodont shark *Carinacanthus* (Bryant, 1934) and the subholostean *Ptycholepis*. The latter is otherwise known only from the marine Liassic of Europe.

Turseodus and *Semionotus* were widely distributed over North America in the Late Triassic. The redfieldiids were also apparently well dispersed, but some of the western forms presumably never reached the Newark basin. *Ceratodus* was present in western North America throughout the Mesozoic, but various geographic factors apparently prevented its spread eastward. The presence of *Carinacanthus* and *Ptycholepis* in the Newark can be most readily explained if it be assumed that they entered the Newark lowlands from the sea.¹

Upper Triassic continental formations in other parts of the world cannot be meaningfully correlated with the Chinle-Dockum-Newark deposits on the basis of their fish assemblages. *Semionotus* and *Ceratodus* range throughout the Triassic and will be of little use in correlation unless some evolutionary trends can be worked out. The occurrence of *Dictyopyge* in Europe is very dubious, and the undoubted redfieldiids from elsewhere indicate only a Triassic age. A current study of *Ptycholepis* by Dunkle, Applegate, and Schaeffer indicates that the cheek region of the Newark species is similar to that of both the Triassic and Liassic European species in having a covered preopercular (see Brough, 1939). The phytosaurs therefore provide the best basis (Gregory, 1957, 1962a, 1962b) for a correlation of the Dockum, Chinle, and Newark with one another and with the type Triassic section of southwestern Germany.

FEEDING AND FOOD CHAINS

With the exception of the semionotids, all the actinopterygians in the Chinle-Dockum fauna have fixed maxillae and a palaeonisciform jaw structure. As noted above, the redfieldiid snout and subterminal mouth indicate that these fishes were mainly bottom feeders. Because they were unable to protrude the

¹ The indeterminate hybodont in the Dockum Group presumably represents an independent introduction.

mouth, food was probably obtained by grubbing and "scooping." *Turseodus* and several of the indeterminate forms (text figs. 15, 16) with relatively wide gapes and well-developed marginal teeth presumably fed on planktonic invertebrates and young fishes. Although the jaws of *Tanaocrossus* are unknown, its elongated dorsal fin suggests *Amia*-like behavior—stalking in quiet water by undulations of the dorsal, followed by rapid movement of the body when chasing prey. The small mouth and mobile maxillae of *Semionotus* and *Hemicalypterus* indicate that these fishes could engulf prey by suction; the jaw structure also suggests browsing and nibbling. Their diet may have included sessile organisms and a wide variety of plankton. *Chinlea* was undoubtedly a fish feeder and the only member of the fauna that grew large enough to subsist on adults of the other members. Although *Ceratodus* has not been found at the Big Indian or Bedrock localities, it was widespread throughout the lowlands. Like *Neoceratodus*, it presumably ingested vegetation along with mollusks and a variety of soft-bodied invertebrates.

Because so little is known about the non-piscine organisms in the aquatic environments of the Chinle-Dockum lowlands, attempts to work out a hypothetical food chain,

or pyramid, related primarily to the fishes have not been very enlightening. As many modern plants, invertebrates, and the teleosts had not yet evolved, the Triassic chain would be different from the chain for a modern semi-tropical lowland. The Chinle-Dockum osteichthyans undoubtedly changed or amplified their diet as they grew in size (Keast, 1965), and they also may have moved to different subenvironments. The fact that most of the redfieldiids are nearly the same size (between 160 and 200 mm.) suggests that the samples are composed of individuals on the flattened part of the growth curve, but we cannot rule out the possibility that they grew larger in other habitats. Both *Semionotus* and *Hemicalypterus* show a greater range in size than the redfieldiids.

It is evident that most of the fishes in the Chinle-Dockum fauna were browsers, grubbers, and consumers of small prey—the Triassic counterparts of the minnows, sunfishes, perches, and catfishes. *Chinlea* was near the top of the pyramid. Its food may have been diversified during its younger stages, but with increasing size the diet presumably became more piscivorous. The apex of the pyramid was occupied by the ubiquitous phytosaurs and possibly by the metoposaurs.

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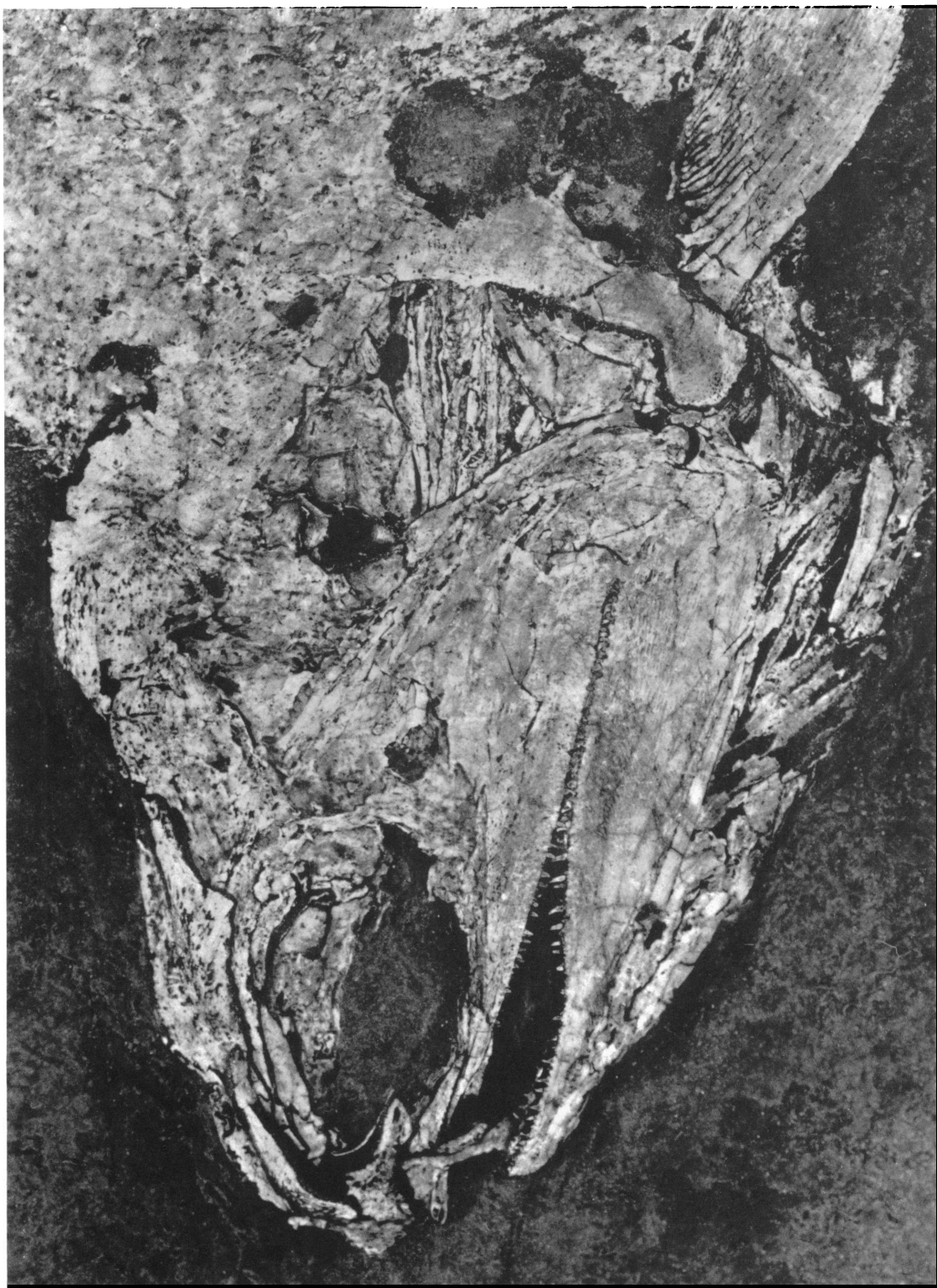
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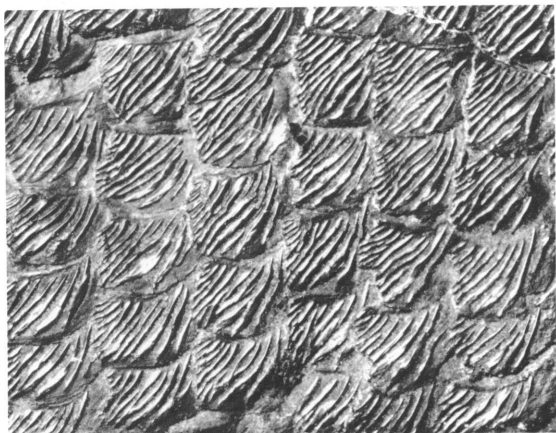
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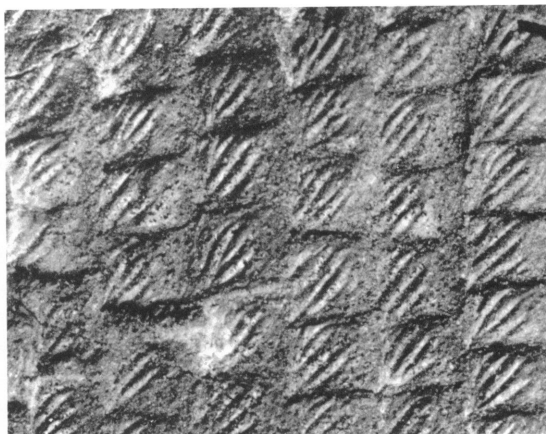
Turseodus dolorenensis, new species, A.M.N.H. No. 5614, fluorescence photograph of type specimen. *Ca.* $\times 1.1$



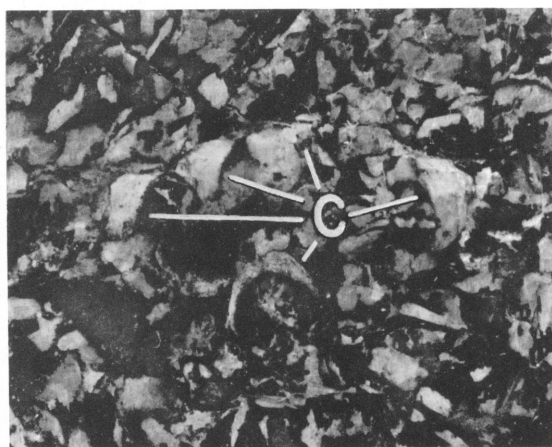
Turseodus dolorenensis, new species, A.M.N.H. No. 5614, fluorescence photograph of skull of type specimen. Ca. $\times 3.7$



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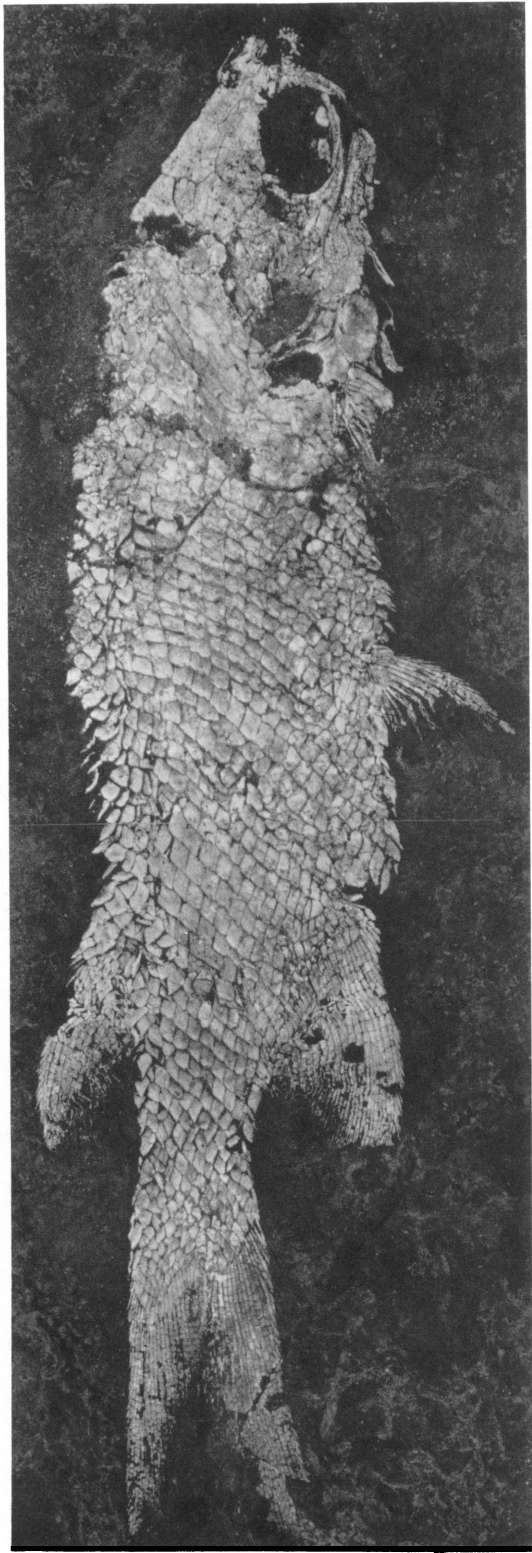
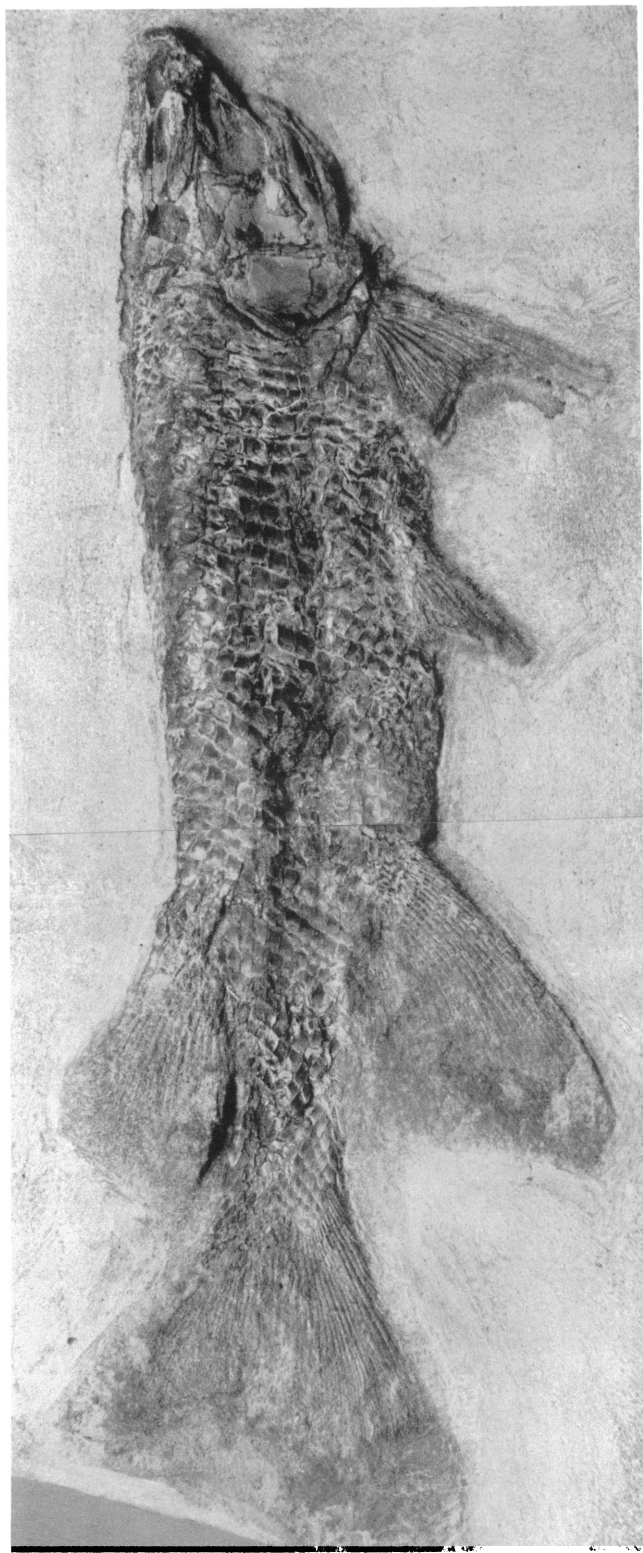
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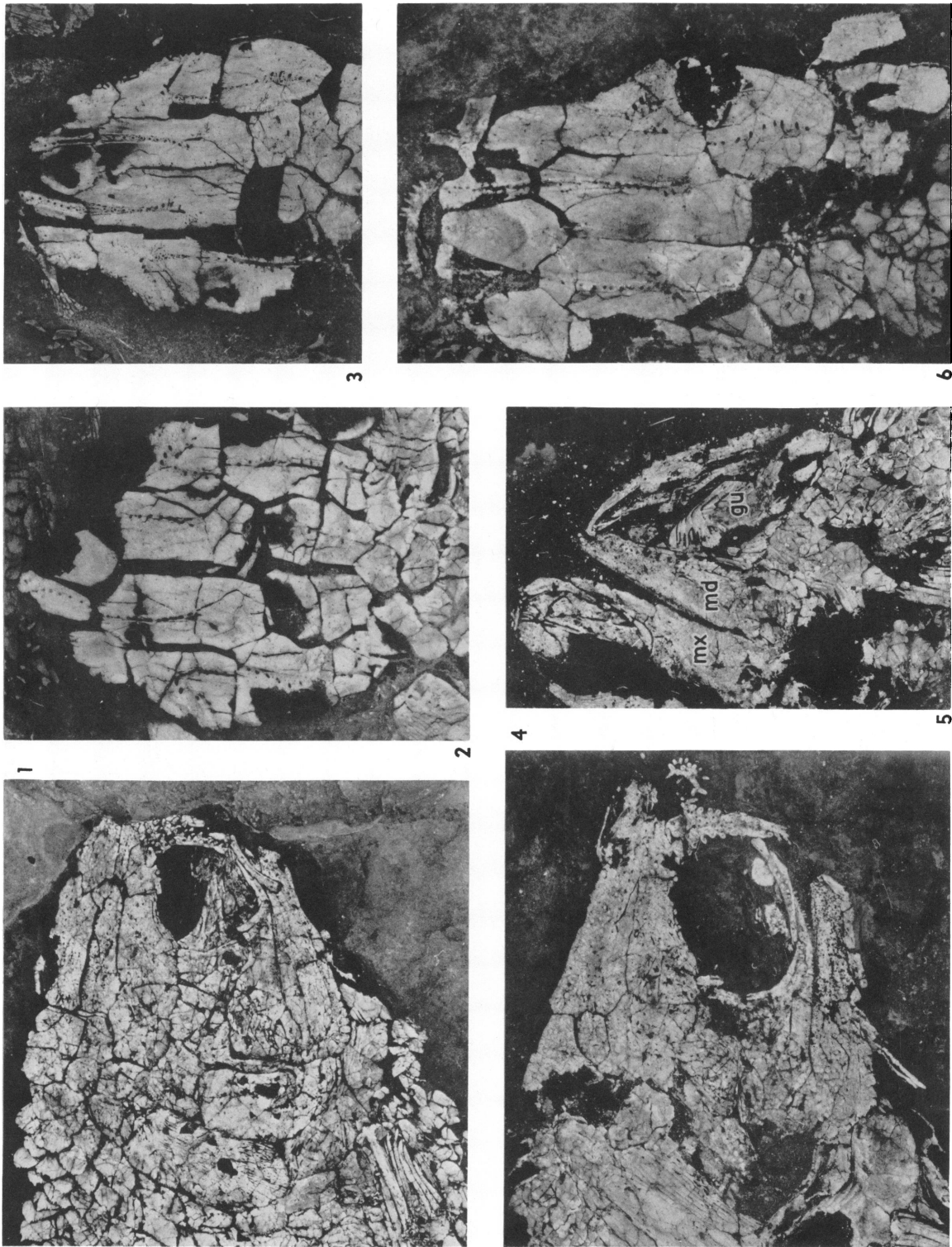
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1. *Turseodus acutus*, P.U. No. 16152b, flank scales. Ca. $\times 10.5$. 2. *Turseodus dolorensis*, new species, A.M.N.H. No. 5603B, flank scales. Ca. $\times 13.5$. 3. *Turseodus dolorensis*, new species, A.M.N.H. No. 5603, dorsal and ventral ossifications of centrum. Ca. $\times 5.1$. 4. *Turseodus* cf. *acutus*, A.M.N.H. No. 4792, central ossifications. Ca. $\times 3.2$. 5. *Turseodus dolorensis*, new species, A.M.N.H. No. 5723, impression of mandible, showing ornamentation. Ca. $\times 8$?

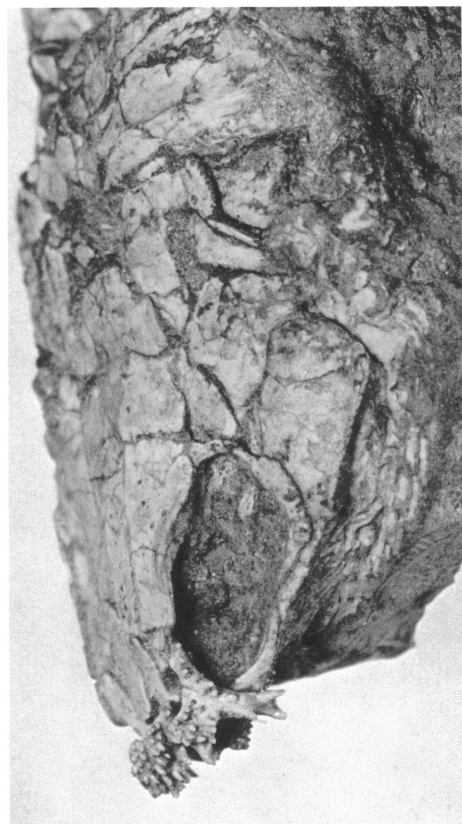
Abbreviation: c, central ossification.



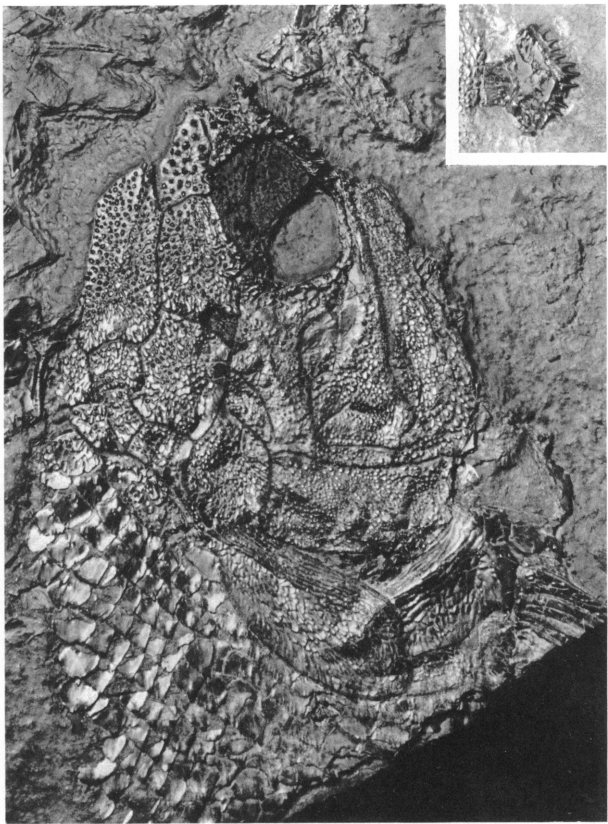
Cionichthys dunklei, new genus and species. 1. Type specimen, A.M.N.H. No. 5615. Ca. $\times 1.3$. 2. Fluorescence photograph of A.M.N.H. No. 5628. Ca. $\times 1.4$



Cionichthys dunklei, new genus and species, fluorescence photographs of dermal skull. 1. A.M.N.H. No. 5650. Ca. $\times 1.6$. 2. M.C.Z. No. 9028. Ca. $\times 2.3$. 3. A.M.N.H. No. 5645a. Ca. $\times 2.4$. 4. A.M.N.H. No. 5628. Ca. $\times 2.4$. 5. A.M.N.H. No. 5651. Ca. $\times 2$. 6. A.M.N.H. No. 5621. Ca. $\times 3.2$.
Abbreviations: gu, gular; md, mandible; mx, maxilla



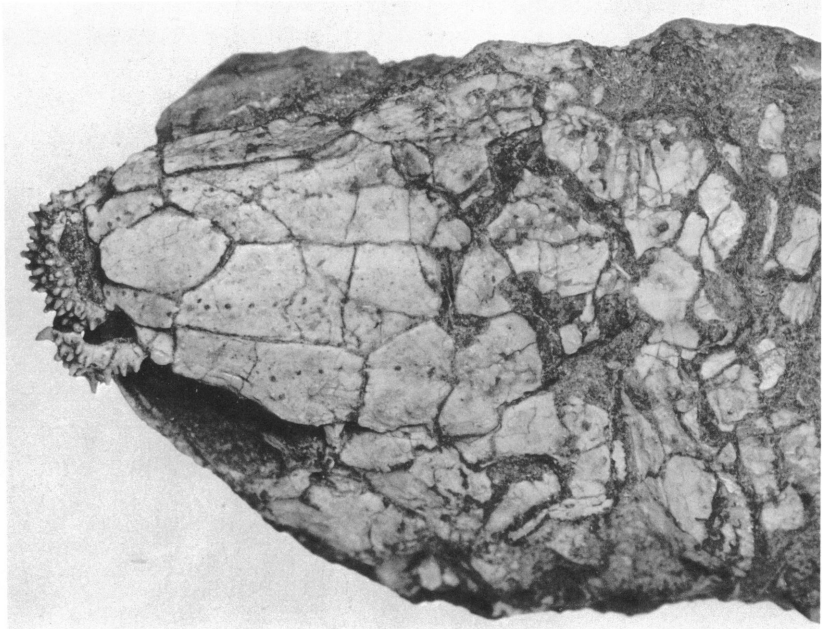
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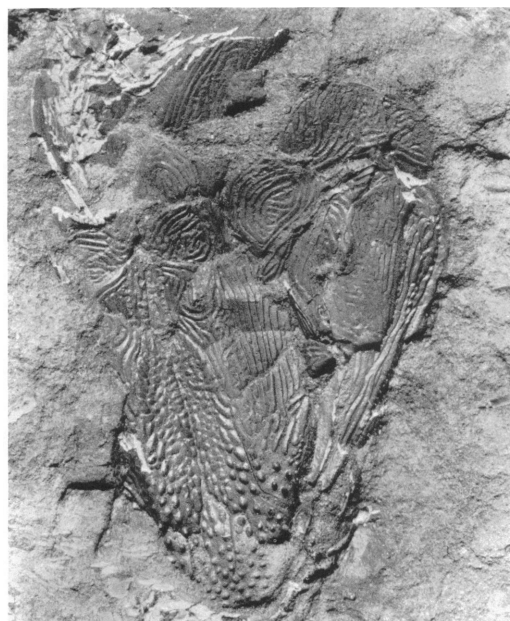


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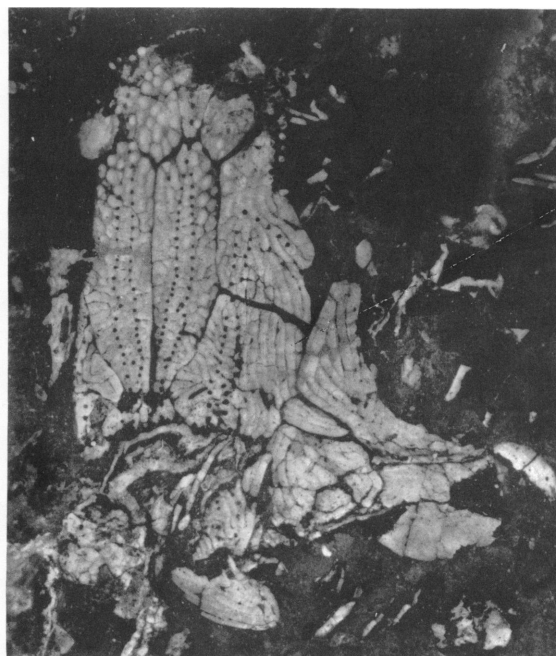
1-3. *Cionichthys greeni*, new genus and species, A.M.N.H. No. 5600, type specimen. 1. Snout in dorsal aspect. 2. Skull in lateral aspect. 3. Skull in dorsal aspect. All ca. $\times 3.8$
4. *Redfieldius* sp., A.M.N.H. No. 4803, partly dissociated skull from Midland, Virginia, with isolated rostral bone inset in lower right from same specimen. sutures emphasized. Ca. $\times 1.9$



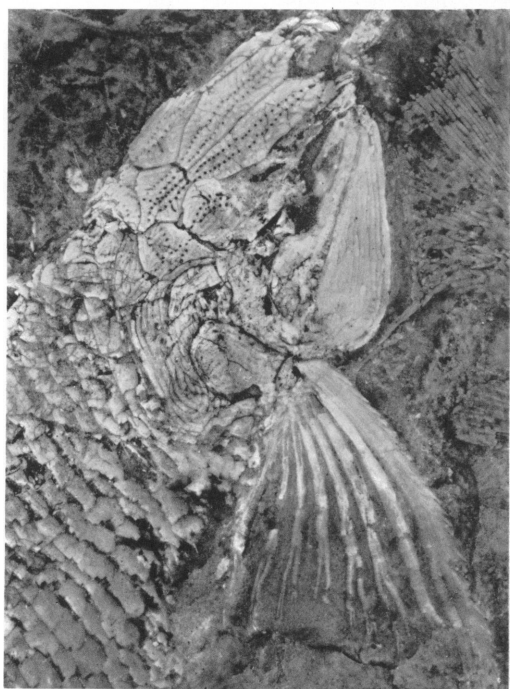
Redfieldius sp., A.M.N.H. No. 5721, skull from Midland, Virginia, preserved in ventral aspect. *Ca.* 5.3
Abbreviations: adn, adnasal; ant, antorbital; dent, dentary; dsph, dermosphenoid; gu, gular; mx, maxilla; ros, rostral



2



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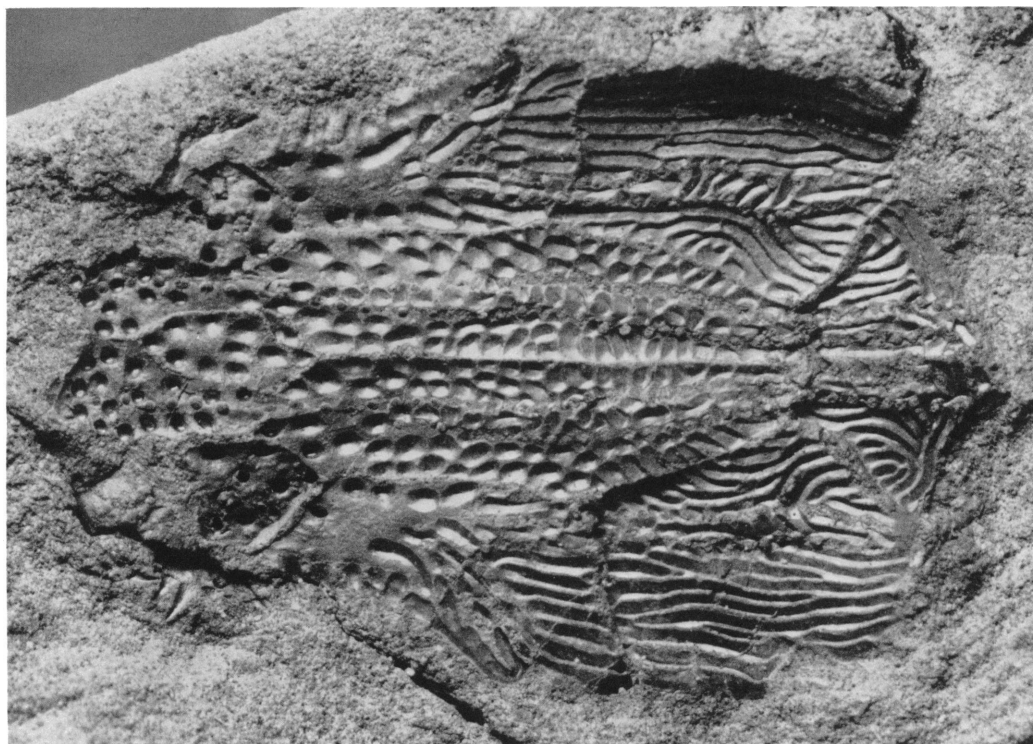


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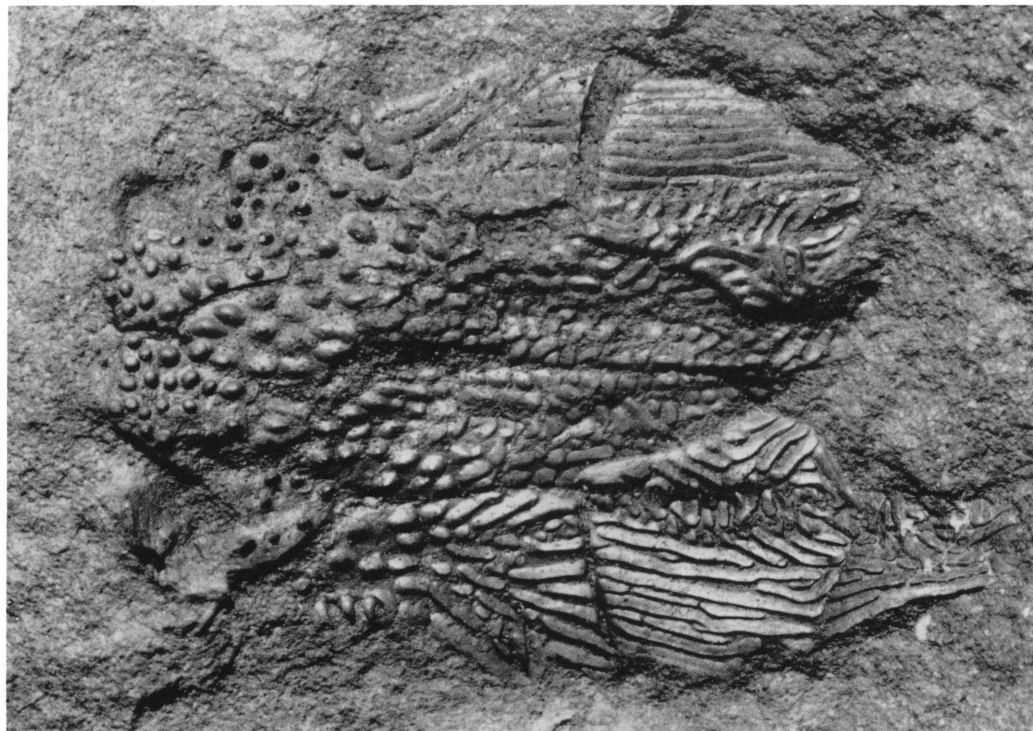
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Lasalichthys hillsi, new genus and species, fluorescence photographs (except 2) of dermal skull. 1. A.M.N.H. No. 5644. Ca. $\times 2.2$. 2. U.S.N.M. No. 23414. Ca. $\times 2.8$. 3. A.M.N.H. No. 5640. Ca. $\times 3.1$. 4. A.M.N.H. No. 5641. Ca. $\times 3.5$



2

Lasalichthys hillsi, new genus and species, impressions of skull roof, showing nasals meeting in front of postrostral. 1. A.M.N.H. No. 5638. Ca. $\times 5.6$.

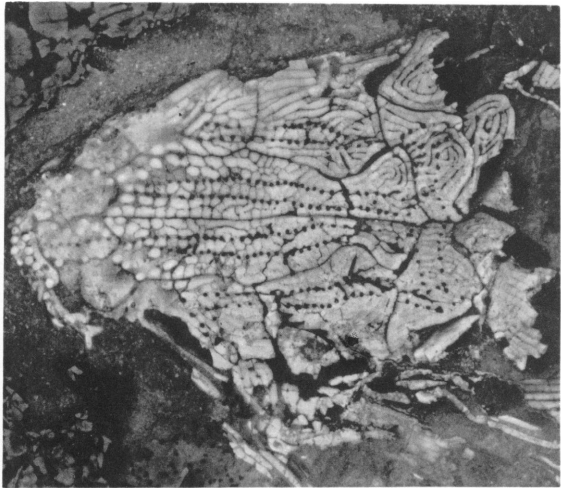


1

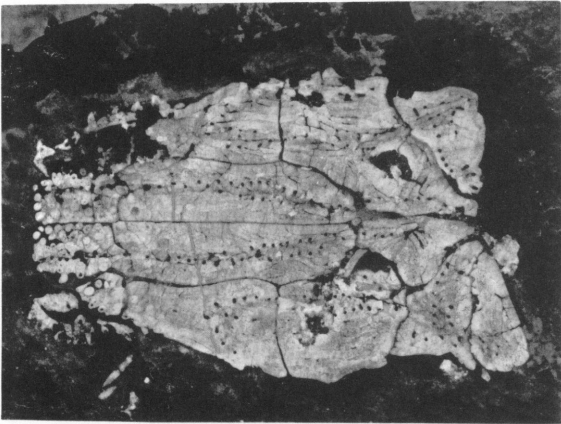
2. A.M.N.H. No. 5636, type specimen, showing pores of sensory canals on nasal bones. Ca. $\times 7$.



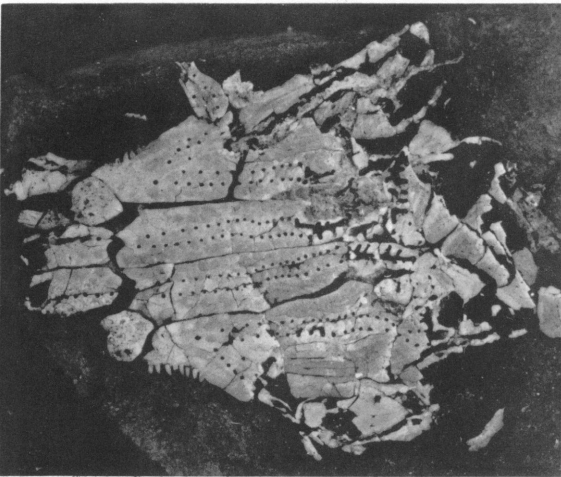
Synorichthys stewarti, new genus and species, A.M.N.H. No. 5646, type specimen; matrix area somewhat lightened. Ca. $\times 1.4$



3



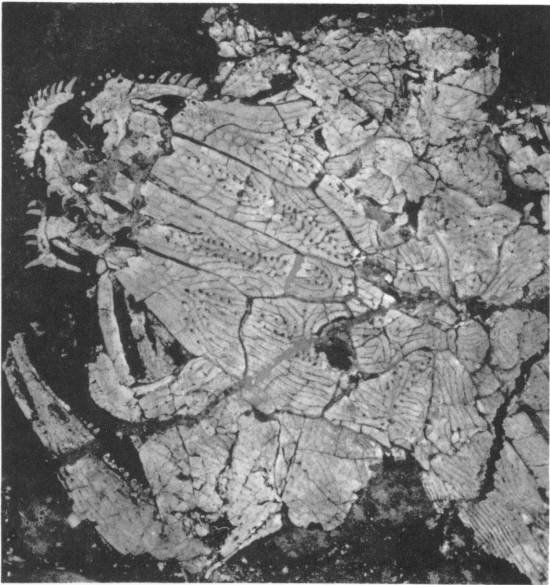
2



1

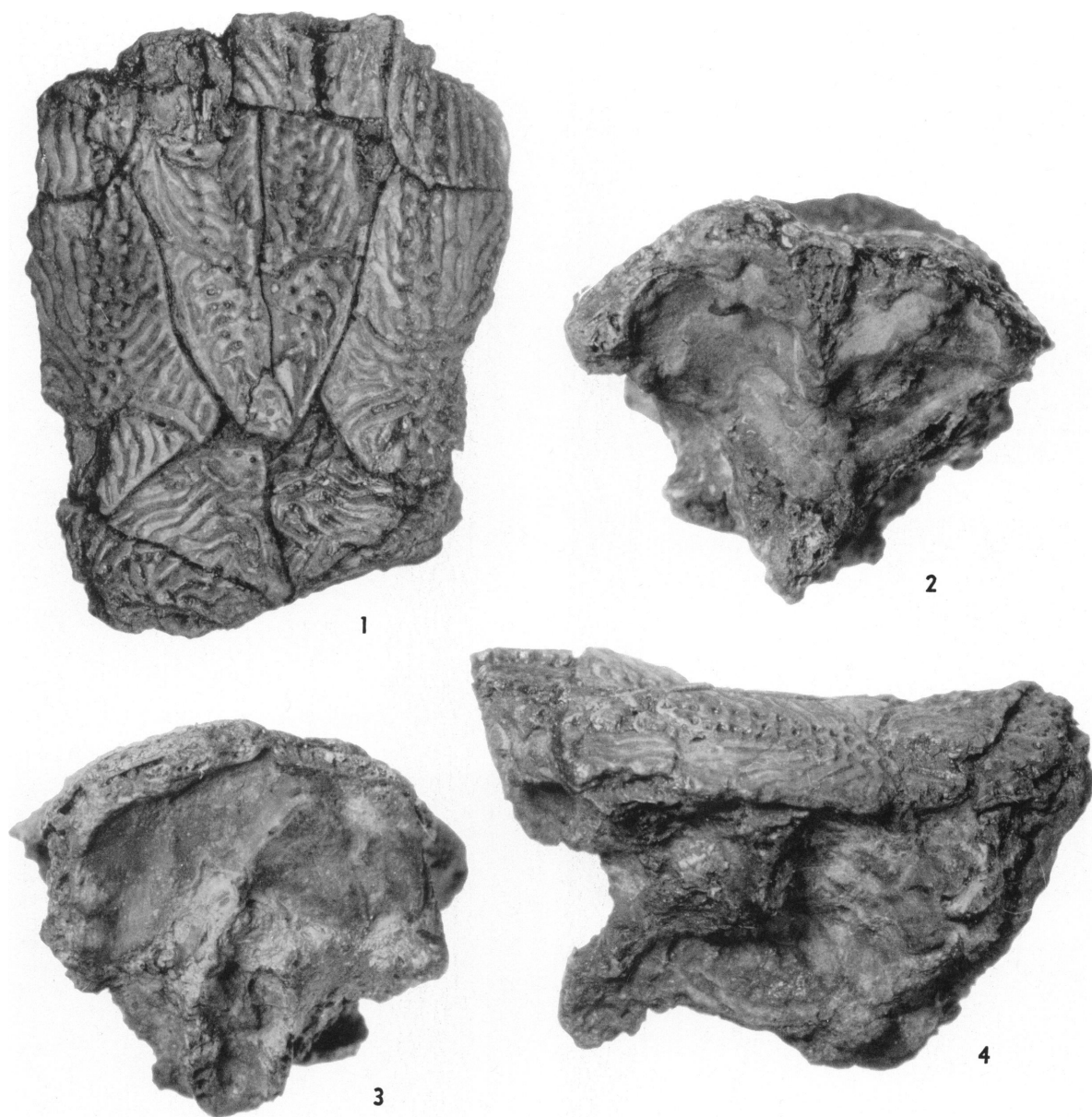


5



4

Synorichthys stewarti, new genus and species, fluorescence photographs (except 5) of dermal skull. 1. A.M.N.H. No. 5673. Ca. $\times 3.1$. 2. A.M.N.H. No. 5677. Ca. $\times 2.3$. 3. A.M.N.H. No. 5667. Ca. $\times 3.1$. 4. A.M.N.H. No. 5672. Ca. $\times 2.4$. 5. A.M.N.H. No. 5646, type specimen. Ca. $\times 2.3$



Redfieldiid braincase, U.T.B.E.G. No. 31098-44, from the Dockum Group, Otis Chalk, Howard County, Texas. 1. Dorsal aspect. 2. Anterior aspect. 3. Posterior aspect. 4. Lateral aspect. All *ca.* $\times 5.2$



1

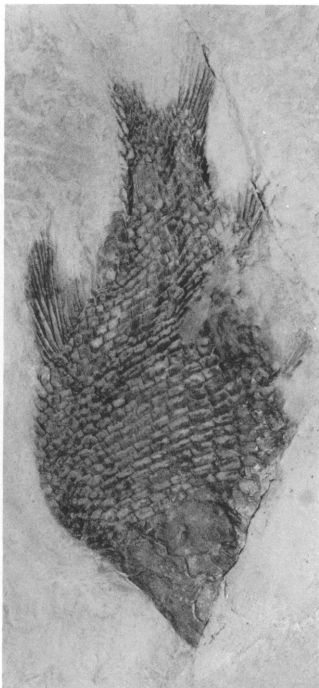


2

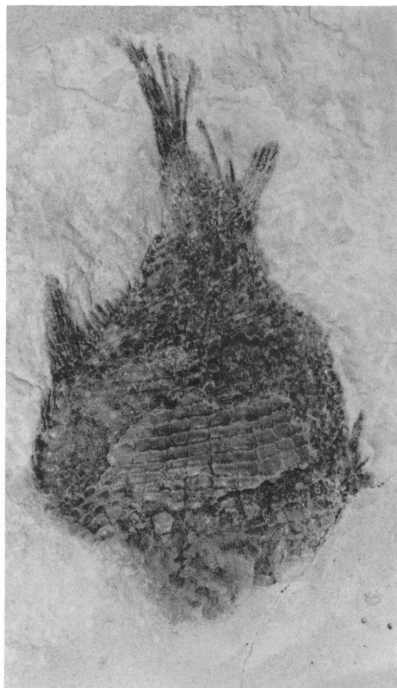
Tanaocrossus kalliokoskii, new genus and species. 1. A.M.N.H. No. 5700, smooth-on peel of type specimen; matrix area painted out. 2. A.M.N.H. No. 5700, type specimen. Both *ca.* $\times 1.4$



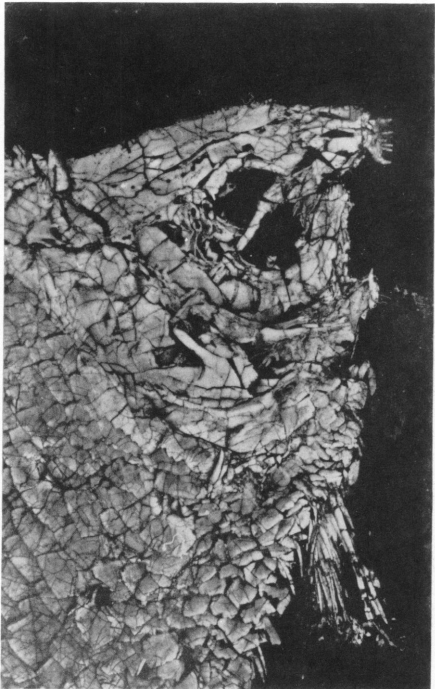
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4



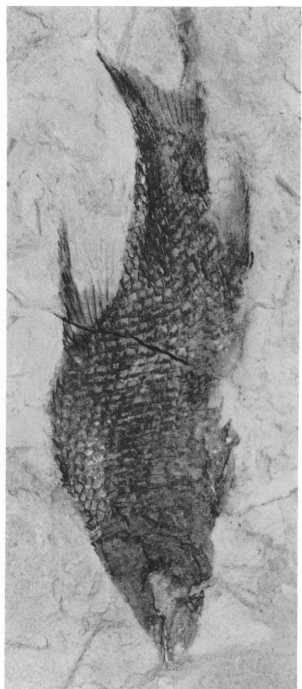
6



1



3

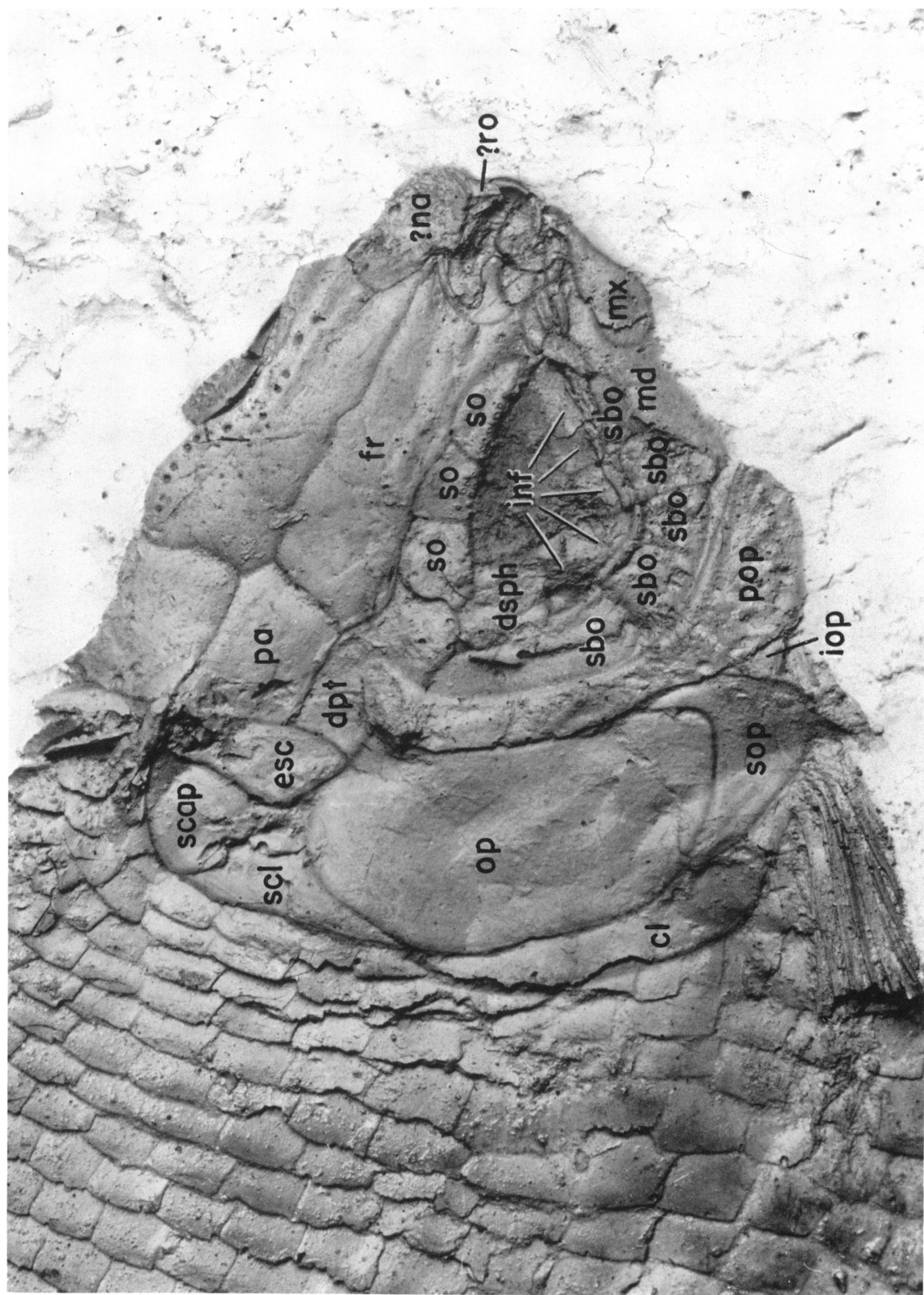


5

Semionotus sp. 1. A.M.N.H. No. 5679, fluorescence photograph of skull, showing characteristic form of premaxillae. *Ca.* $\times 1.4$. Specimens selected to indicate range in body form in the Chinle representatives: 2. A.M.N.H. No. 5680. *Ca.* $\times 0.8$. 3. A.M.N.H. No. 5684. *Ca.* $\times 1$. 4. U.S.N.M. No. 23417. *Ca.* $\times 0.9$. 5. A.M.N.H. No. 5682. *Ca.* $\times 1.2$. 6. A.M.N.H. No. 5681, reversed. *Ca.* $\times 0.9$

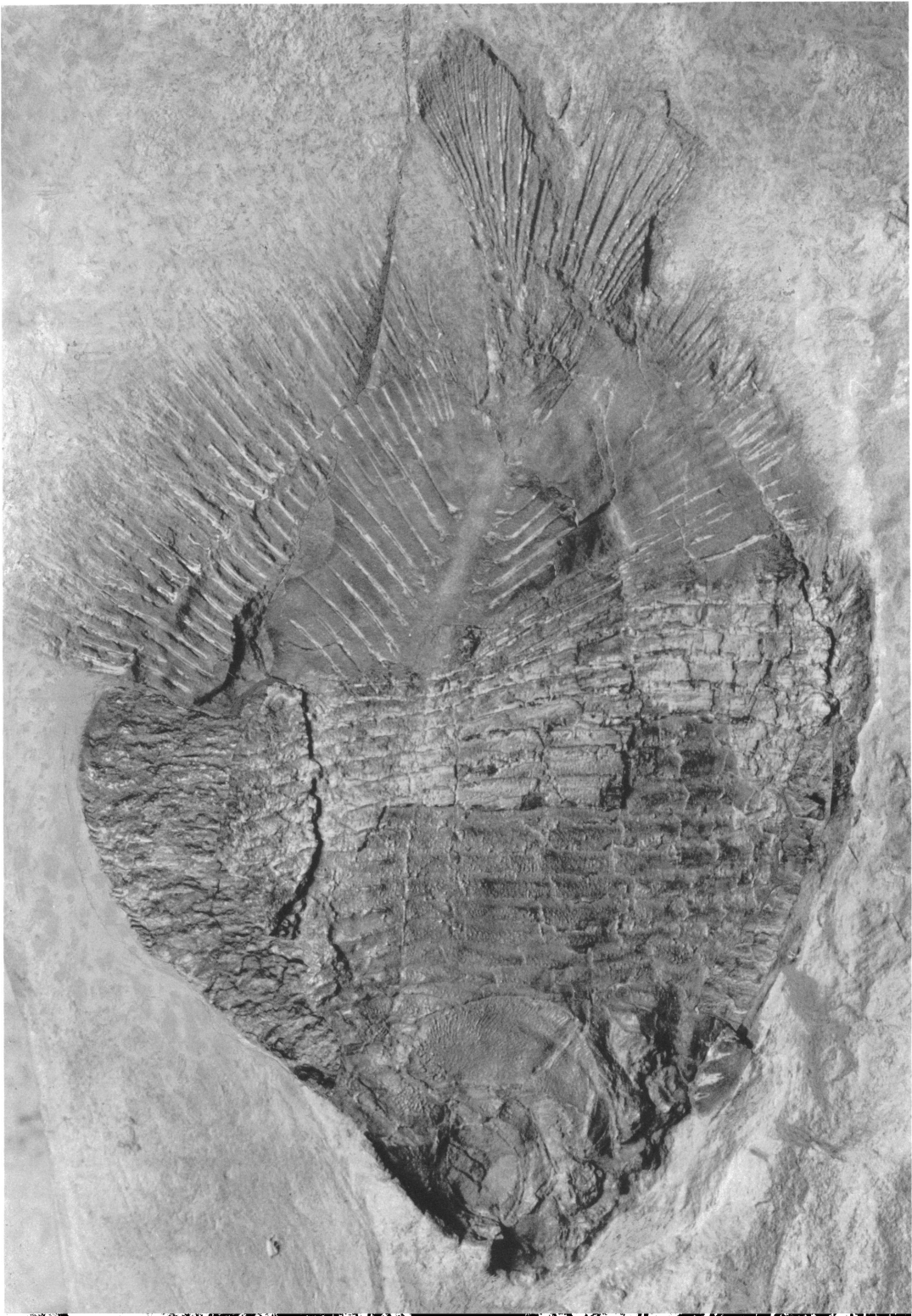


Semionotus sp., smooth-on peel of A.M.N.H. No. 5680, showing details of squamation, including tubercles on anterior ridge scales; matrix area painted out. Ca. $\times 1.8$

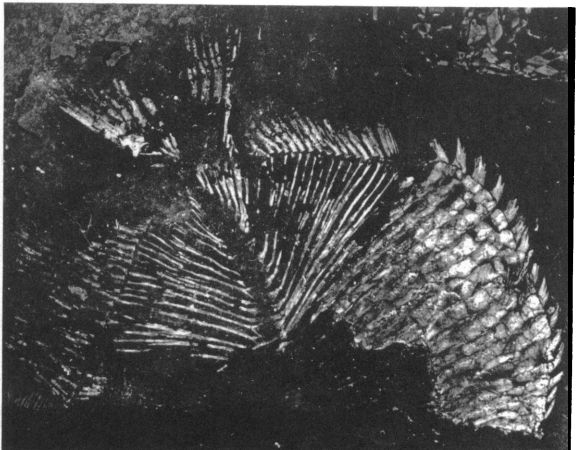
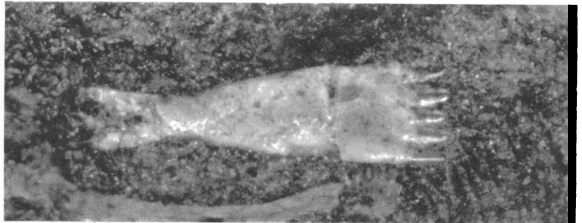
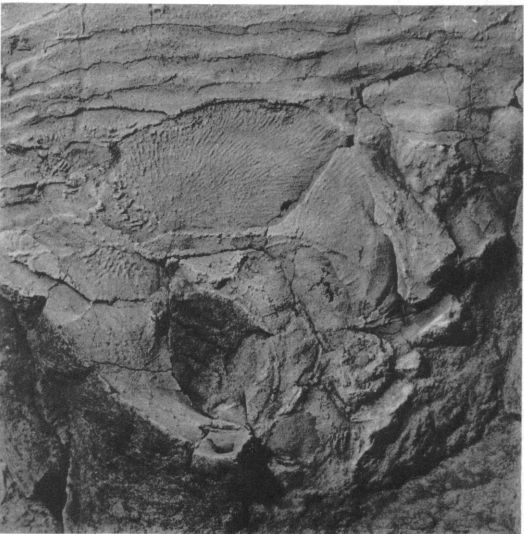
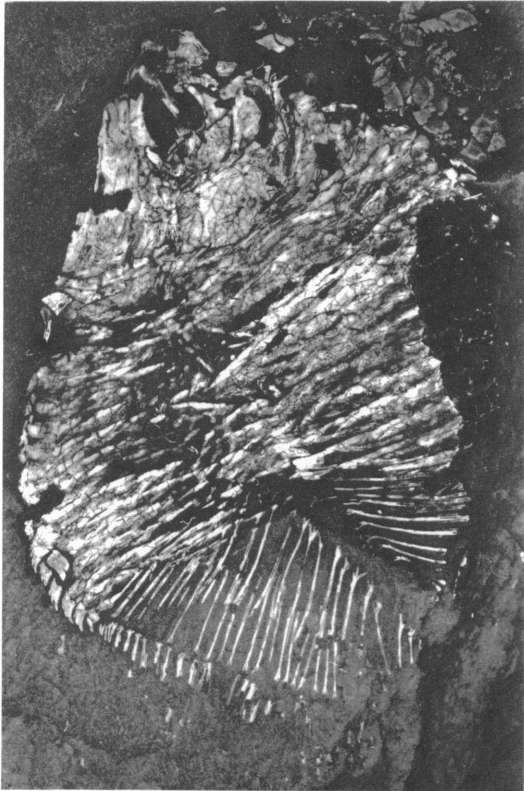


Semionotus sp., A.M.N.H. No. 5680, skull detail from smooth-on peel; sutures emphasized. Ca. $\times 4.4$

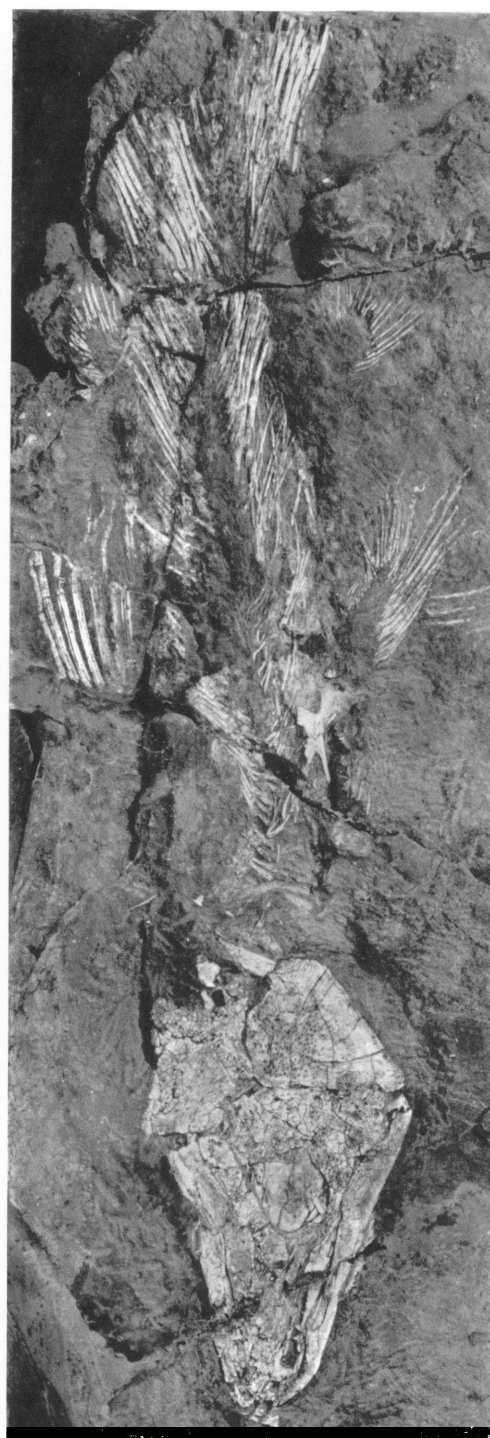
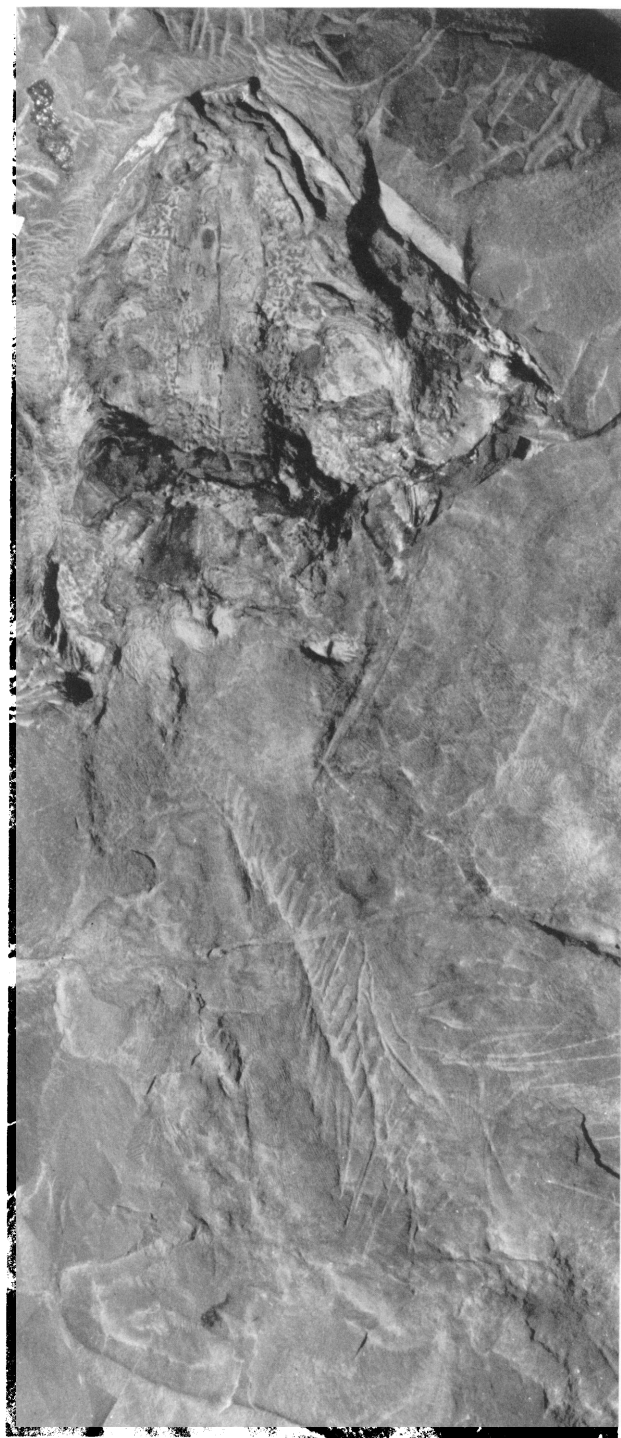
Abbreviations: cl, cleithrum; dpt, dermopterotic; dsph, dermosphenotic; esc, extrascapular; fr, frontal; inf, infraorbital; iop, interopercular; md, mandible; mx, maxilla; ?na, presumed nasal; op, opercular; pa, parietal; pop, preopercular; ?ro, presumed rostral; sbo, suborbital; scap, suprascapular; scl, supracleithrum; so, supraorbital; sop, subopercular



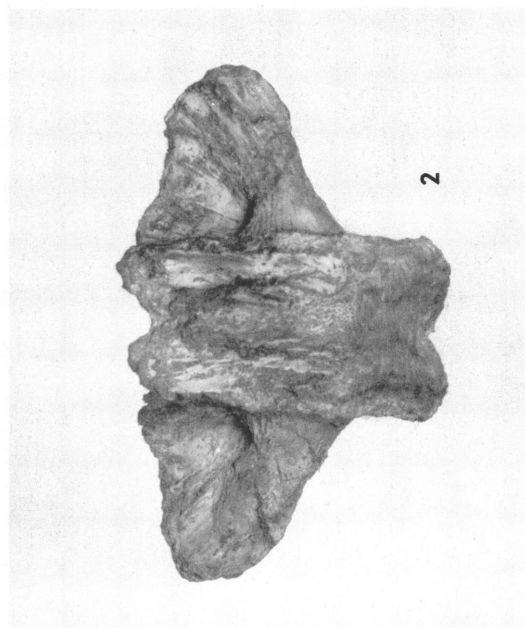
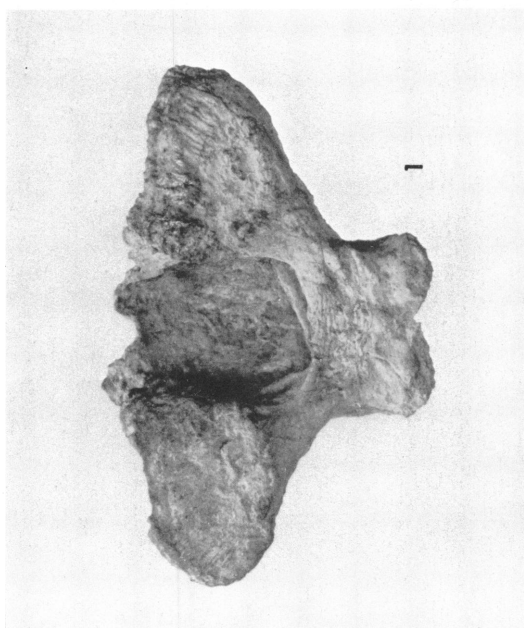
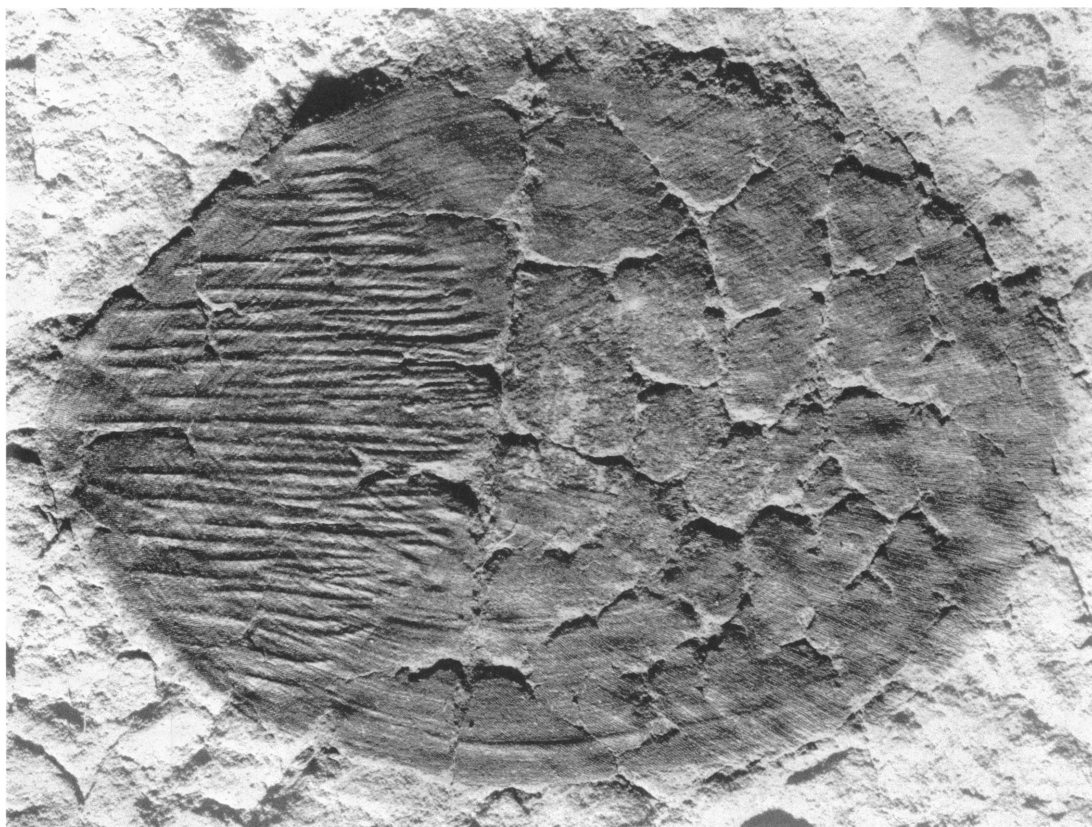
Hemicalypterus weiri, new genus and species, U.S.N.M. No. 23425, composite photograph of type specimen; retouched.
Ca. X2.1



Hemicalypterus weiri, new genus and species. 1. Skull impression of type specimen, U.S.N.M. No. 23425. Ca. $\times 2.6$. 2, 3. Fluorescence photomicrographs. 2. U.S.N.M. No. 23427. Ca. $\times 1.6$. 3. M.C.Z. No. 9034, showing ventral ridge scales. Ca. $\times 1.3$. 4. Isolated premaxilla from U.S.N.M. No. 23427. Ca. $\times 32.6$. 5. Pectoral fin impression in U.S.N.M. No. 23428. Ca. $\times 1.5$



Chinlea sorensoni, new genus and species. 1. Partial specimen with skull in dorsal aspect, also impressions of neural arches, ribs, and scales, A.M.N.H. No. 5654. Ca. $\times 1$. 2. Fluorescence photograph of type specimen, A.M.N.H. No. 5652. Ca. $\times 1.2$



Chinlea sorenseni, new genus and species. 1, 2. Basisphenoid, A.M.N.H. No. 5656. Ca. $\times 2.7$. 2. Ventral aspect. Ca. $\times 2.7$. 3. Impression of scale, A.M.N.H. No. 5655; note mud cracks. Ca. $\times 6$

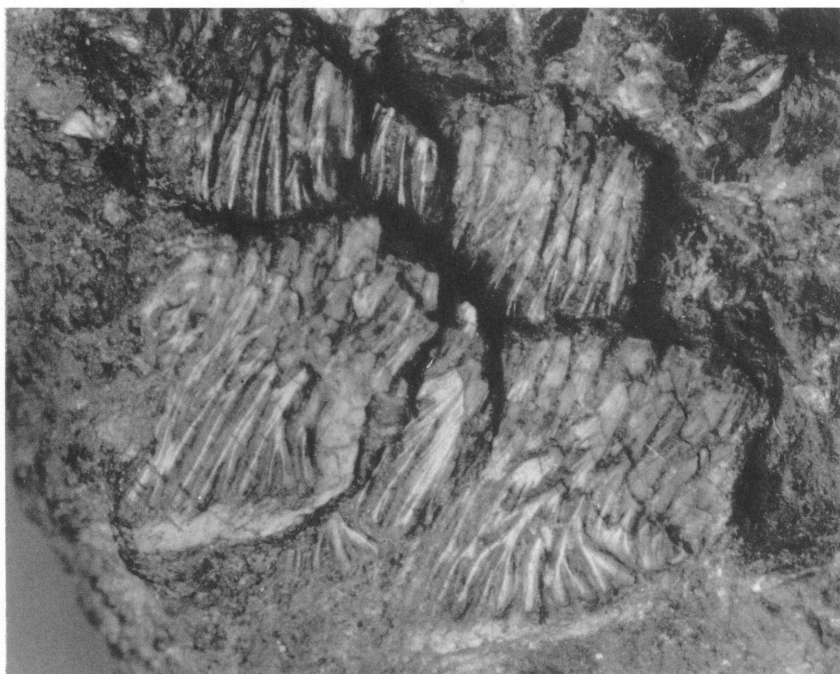


1



2

Chinlea sorenseni, new genus and species. 1. A.M.N.H. No. 5653, isolated skull. *Ca.* $\times 1.1$. 2. Fluorescence photograph of type specimen, A.M.N.H. No. 5652. *Ca.* $\times 2.8$

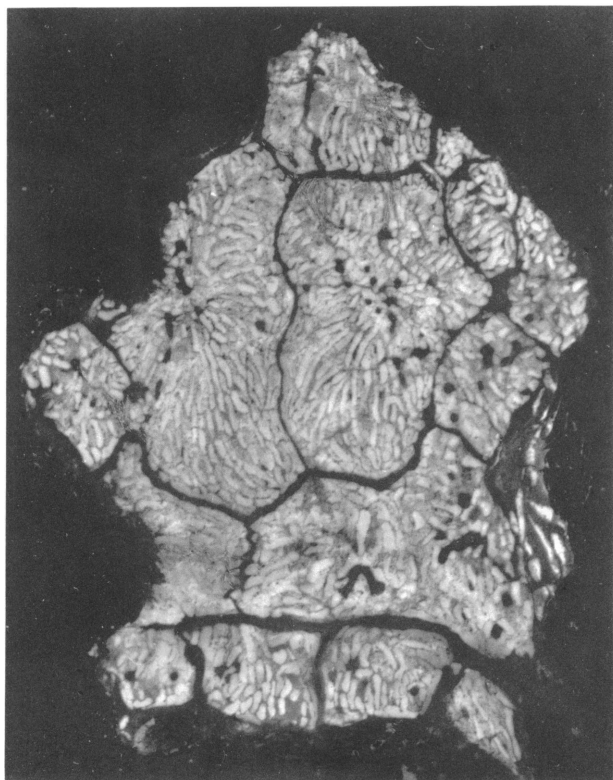


1

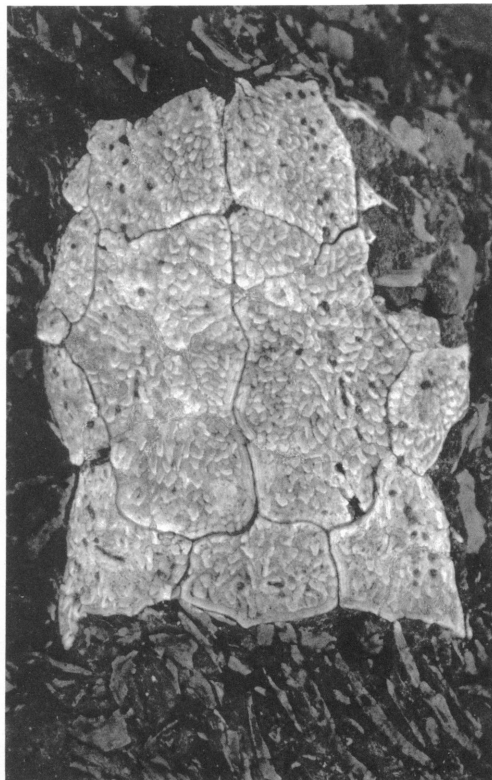


2

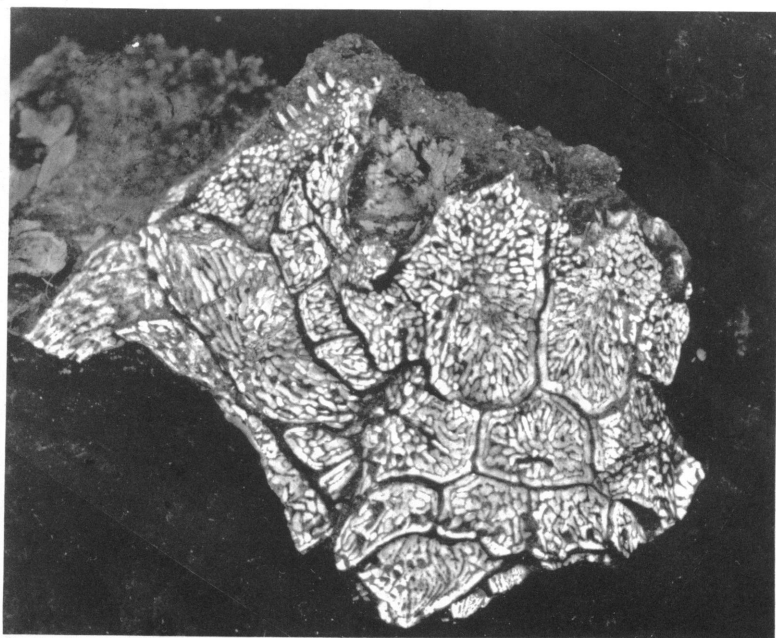
A.M.N.H. No. 5720, indeterminate palaeonisciform scales from the Dockum Group near Otis Chalk, Howard County, Texas. 1, *ca.* $\times 12$; 2, *ca.* $\times 11.3$



1



2



3

Indeterminate palaeonisciform, A.M.N.H. No. 5662, from the Dockum Group near Otis Chalk, Howard County, Texas. 1. Skull roof in dorsal aspect, showing fusion of median parietal and right dermopterotic. 2. Skull roof in dorsal aspect. 3. Specimen including most of cheek region. All *ca.* $\times 4.2$

