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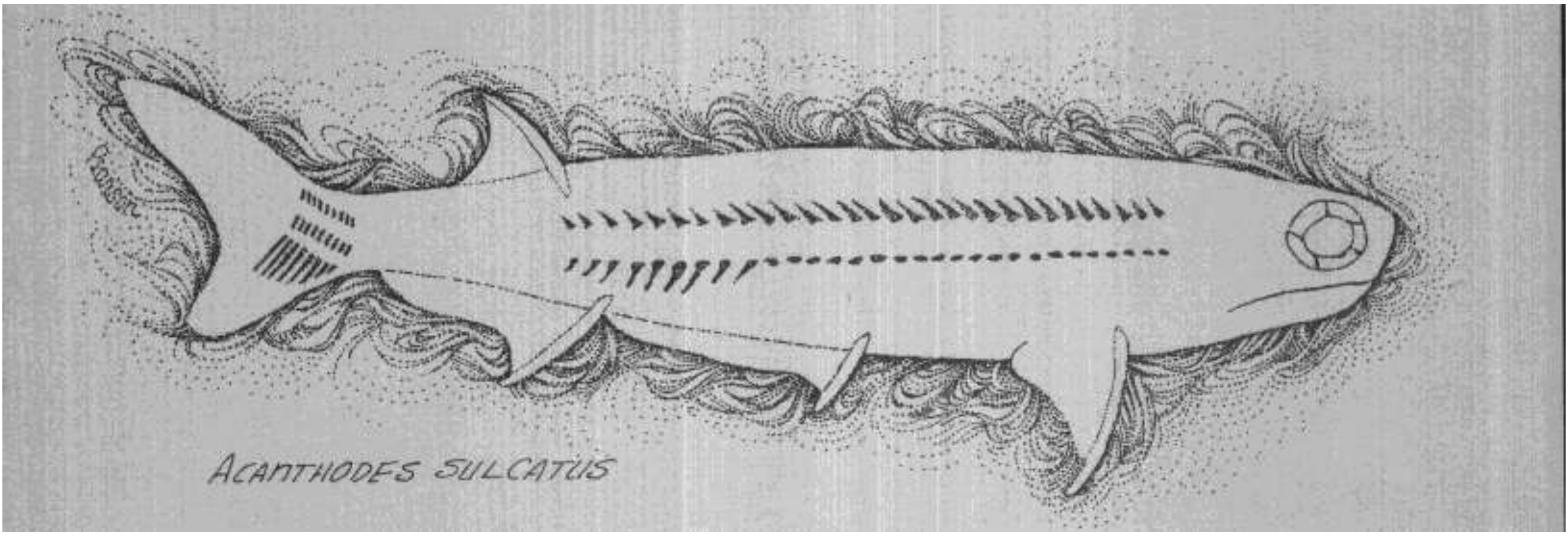

Some Fishes of the Wild Cow Formation (Pennsylvanian) Manzanita Mountains, New Mexico

by Jiri Zidek

New Mexico Bureau of Mines & Mineral Resources

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University of Oklahoma

SOCORRO 1975

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Abstract

The fish fauna in the shales of the Pine Shadow Member of the Wild Cow Formation (early Virgilian) in the Manzanita Mountains, New Mexico, has been known for over ten years but has not been described. Although this fauna includes representatives of all the higher taxa of fish known from the Late Paleozoic, few specimens can be identified generically. The Chondrichthyes are represented by the genera *Ctenoptychius, Cladodus,* and *Listracanthus,* all apparently extremely scarce. The acanthodian remains are articulated, and although none is complete, their preservation is adequate for a systematic assignment to the genus *Acanthodes.* These specimens are the first described from the Pennsylvanian of North America in which assignment to *Acanthodes* is fully warranted. The dipnoans are represented by only a single mandibular tooth plate with the prearticular attached. This dental plate belongs to the genus *Proceratodus* and is sufficiently different from the described *Proceratodus* plates that it must be regarded as a *new* species, herein designated as *P. hlavini.* The coelacanthiform remains are poorly preserved, consisting mostly of scattered scales, but they are significant because of the presence of a pelvic basal plate showing a coelacanthoid rather than a diplocercidoid affinity. The presence of this plate in the Pine Shadow Member shales offers evidence that Coelacanthidae existed during Pennsylvanian time, and consequently detached coelacanth scales can no longer be assigned arbitrarily to the Rhabdodermatinae (Diplocercidae, Diplocercidoidei) simply because they are found in rocks of Pennsylvanian age.

Introduction

From 1963 to 1974 David H. Dunkle, at that time with the U.S. National Museum, collected a large number of fish remains from the Madera Group in the Manzanita Mountains of New Mexico. (Other writers have referred to this location as the Manzano Mountains.) His collection, from the NW 1/4 SE 1/4 sec. 18, T. 9 N., R. 6 E., of Bernalillo County, was supplemented in 1967 by specimens recovered by Sergius H. Mamay, U.S. Geological Survey, from the same locality, only about 100 ft west of Dunkle's site. The specimens of both collections are deposited in the U.S. National Museum in Washington, D.C.

Dunkle's specimens are preserved in a thinly laminated yellowish-brown argillaceous, limy shale, and most of them are disarticulated. Those added later by Mamay were recovered from a carbonaceous shale and are mostly in good to excellent state of preservation. Except for the USNM 187149 specimen described below, the fish collected by Mamay belong to the Palaeonisciformes, and will be discussed in a future paper. The descriptions presented here thus pertain, with the above exception, to the older collection made by Dunkle.

Because of the fragmentary condition of most of Dunkle's material, only those specimens considered identifiable generically were chosen for discussion, although several less determinable examples are presented to include all the higher taxa present. This study will make possible the resolution of the taxonomy of some of the currently indeterminate remains in the National Museum's collection.

The names of the institutions are abbreviated as follows: USNM = U.S. National Museum; OUSM = Stovall Museum of Science and History, The University of Oklahoma; CMNH = Cleveland Museum of Natural History; MCZ = Museum of Comparative Zoology, Harvard University; PU = Princeton University.

In addition to National Museum specimens (USNM 187132-187135, 187143, 187147, 187149), I examined a lungfish tooth plate (CMNH 8311) lent by David H. Dunkle, Cleveland Museum of Natural History, and three acanthodian specimens (OUSM 00447-00449) from the Stovall Museum of Science and History of the University of Oklahoma. The acanthodian remains were obtained through an arrangement made by Gerard R. Case of Jersey City, with Thomas Lehman and John W. Prentice of Albuquerque.

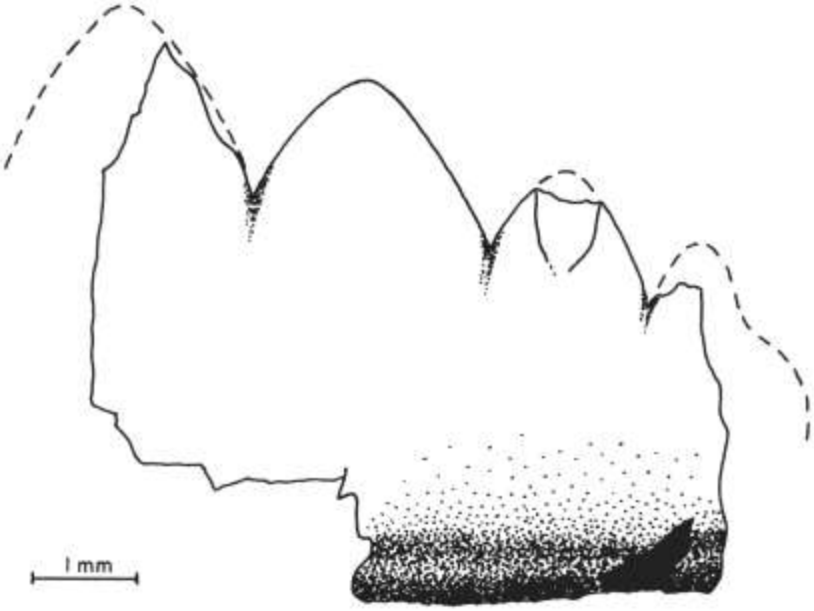
I would like to thank Robert W. Purdy of the U.S. National Museum; Donald A. Myers of the U.S. Geological Survey in Denver; and Donald Baird of Princeton University for the availability of the specimens and information pertinent to this study. Special thanks are due Robert H. Denison, Curator Emeritus of Fossil Fishes for the Field Museum of Natural History, Chicago, who reviewed my work and whose suggestions have greatly improved the manuscript. Also, I express sincere gratitude to Max V. Brown of the School of Geology and Geophysics of the University of Oklahoma for his expert photography of the specimens. Financial assistance received through the short-term visitors program of the Smithsonian Institution and through the Foundation of Geology and Geophysics of the University of Oklahoma is gratefully acknowledged.

Geologic Setting

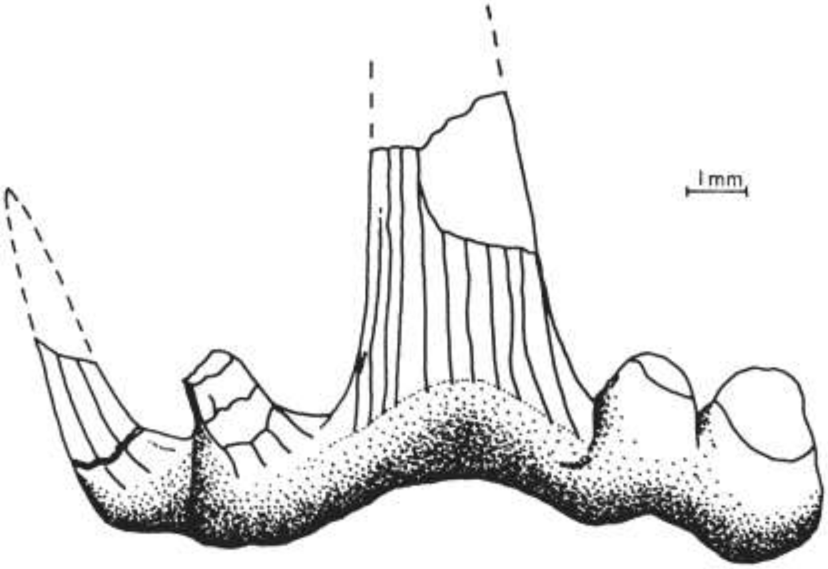
In the Manzanita Mountains area, rocks previously considered as the Madera Limestone and the Bursum Formation have been placed in the Madera Group by Myers (1973). He included the Bursum on the basis of its depositional continuity with the underlying rocks and divided the Madera Group into the following three formations, in ascending order: the Los Moyos Limestone (Desmoinesian-early Missourian); the Wild Cow Formation (Missourian-Virgilian, and possibly also earliest Wolfcampian); and a thin red-bed sequence, the Bursum Formation (Wolfcampian). The Wild Cow Formation consists in turn of three members: Sol se Mete (Missourian), Pine Shadow (early Virgilian), and La Casa (middle and late Virgilian, base (?) of Wolfcampian). According to Donald A. Myers (U.S. Geological Survey, Denver, Colorado, written communication, 1973), the fish beds are in the Pine Shadow Member (equivalent to unit C of the upper part of the upper Madera of Myers, 1966, 1967, 1969; Myers and McKay, 1970, 1971, 1972).

Myers' (1973) dating is based on fusulinid evidence, although for the Pine Shadow Member the Virgilian age assignment appears to be supported also by the megaflora recovered from the locality in question by Mamay (written communication, 1973). Mamay states, however, that he is unable to ascertain what part of the Virgil is represented.

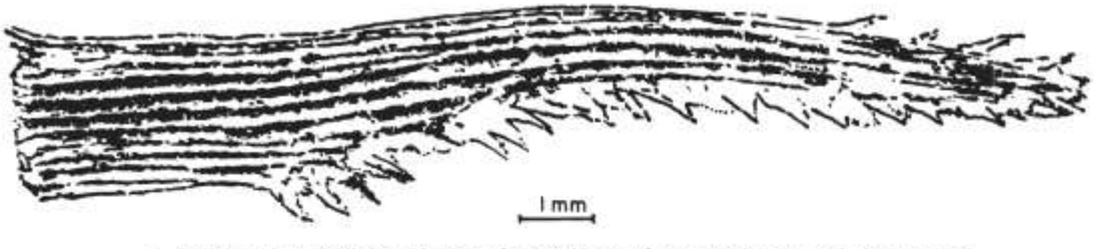
The paleoecology of the site in question has been discussed by Berman (1973, p. 944), who concluded that the deposition was in near-shore, calm, probably lagoonal waters, with periodic discharge from silt-laden streams being responsible for transport of terrestrial organisms to the site. A stage of aerial exposure is suggested by deeply penetrating, rectangular shrinkage marks, according to Berman. Other evidence of aerial exposure comes from a palynological analysis of the yellowish-brown shale, furnished by Leonard R. Wilson, University of Oklahoma. This analysis shows the cuticules macerated beyond recognition, thus indicating such an erosional surface.



A, *Ctenoptychius* sp. indet., USNM 187133, labial view of partial "crown."



B, *Cladodus* sp. indet., USNM 187135, tooth in labial view.



C, *Listracanthus eliasi,* lateral view of spine (drawn from photograph of holotype published by Hibbard, 1938, pl. 19).

FIGURE 1—ELASMOBRANCHII.

Systematic **Descriptions**

Class CHONDRICHTHYES
Subclass ELASMOBRANCHII
Order BRADYODONTI
Family PETALODONTIDAE
GENUS *CTENOPTYCHIUS* Agassiz, 1838
(Fig. 1A)

USNM 187133

Labial face of the right half (or less) of the "crown." The surface is smooth, the upper margin is coarsely lobate. The part preserved exhibits four lobes that increase in size toward the midline of the tooth. The lobes are apically rounded in the labio-lingual plane, and their cutting edges are not serrated.

Because of the fragmentary state of preservation of the specimen, no species identification has been attempted here. A specimen described by Martin (1913), however, as coming from the Permian of Kansas (a dubious stratigraphic placement), has a "crown" morphology similar to the specimen under consideration, with the exception of having a total of only five lobes. Martin identified his specimen as *C. semicircularis,* but his illustration (1913, pl. 21) bears little resemblance to the original illustration of that species (Newberry and Worthen, 1866, pl. 4, fig. 18). Martin's specimen resembles more closely another Pennsylvanian species, *C. andersoni* of St. John and Worthen (1875, pl. 12, figs. 15 a, b).

ELASMOBRANCHII incertae sedis
GENUS *CLADODUS* Agassiz, 1843 (Fig. 1B)

USNM 187135

A tooth exposed by its labial face, showing the proximal half of the principal cusp and the bases of two pairs of the accessory cusps. The cross sections can be seen in the principal cusp and in the left outer accessory cusp, where they are shown to be lenticular and to have well-developed cutting edges. Striation is clearly apparent in the cusps, but because the cusps are incomplete the distal extent of the striae cannot be determined. The striae do not anastomose, and this, plus the number and the relative size of the cusps, their lenticular cross section, and their close spacing, are features found in *C. occidentalis* Leidy (Zidek, 1973a, p. 91-93). However, the fossil is enclosed inseparably in the matrix, and the character of the lingual striation, the distal extent of the labial striation, and the extent of the lingual curvature of the tooth base cannot be determined, making identification of the specimen impossible except as to genus.

GENUS *LISTRACANTHUS* Newberry and Worthen, 1870

USNM 187132 (counterparts)

A spine complete lengthwise but split along the midline so that its surface is not exposed for examination, nor can the extent of the denticulation be established. The fossil is only 15 mm long, thus corresponding in length to *L. eliasi* described by Hibbard (1938, pl. 19; Fig. 1C of this paper) from the Upper Pennsylvanian of Missouri. However, here also too few morphological characteristics are determinable to allow a species assignment.

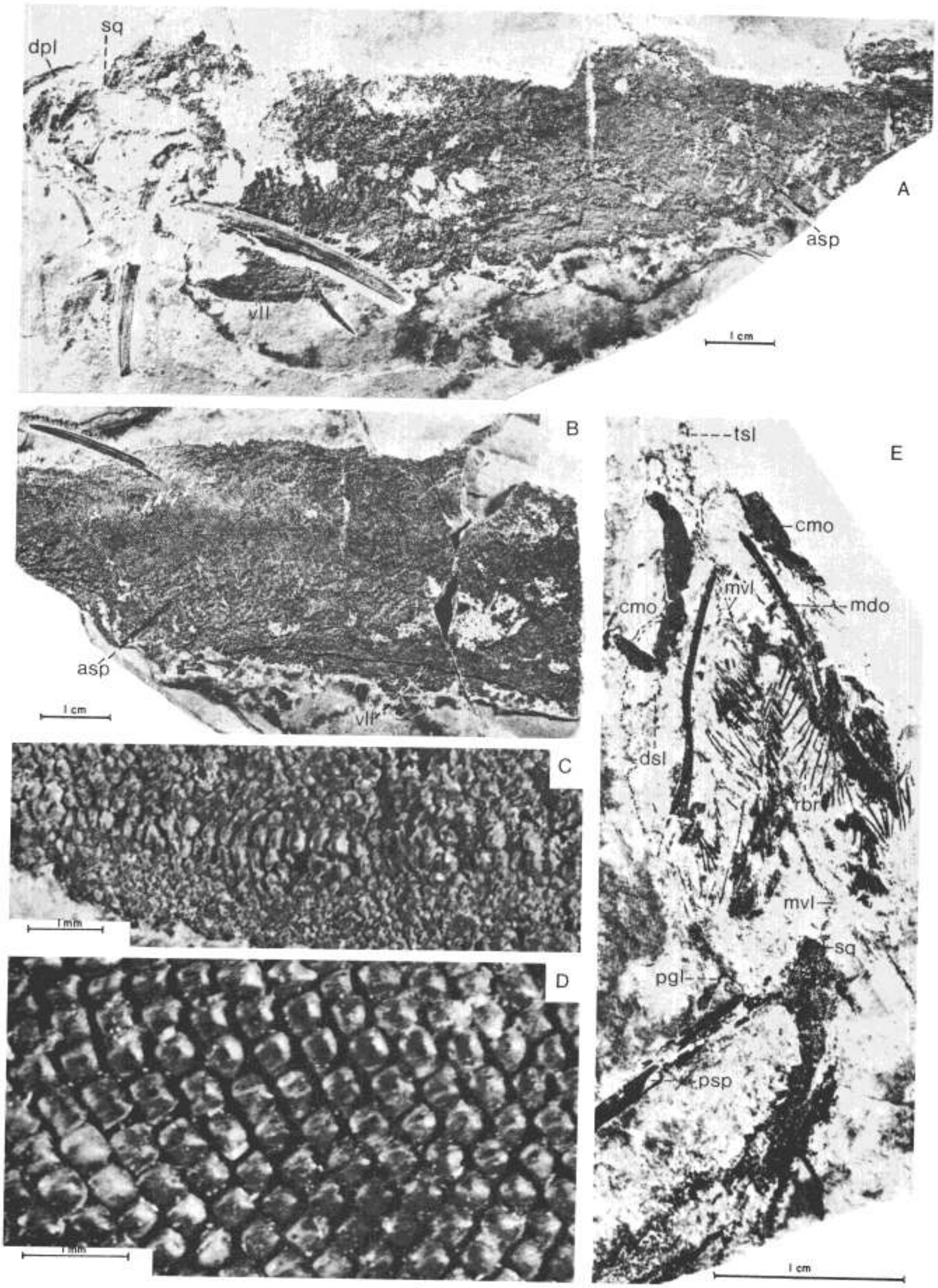
Remarks on the Elasmobranchs

All three of the elasmobranch genera are marine elements that, from the evidence of their previous occurrences, may be considered indicators of either shallow-water marine, deltaic, or lagoonal depositional environments.

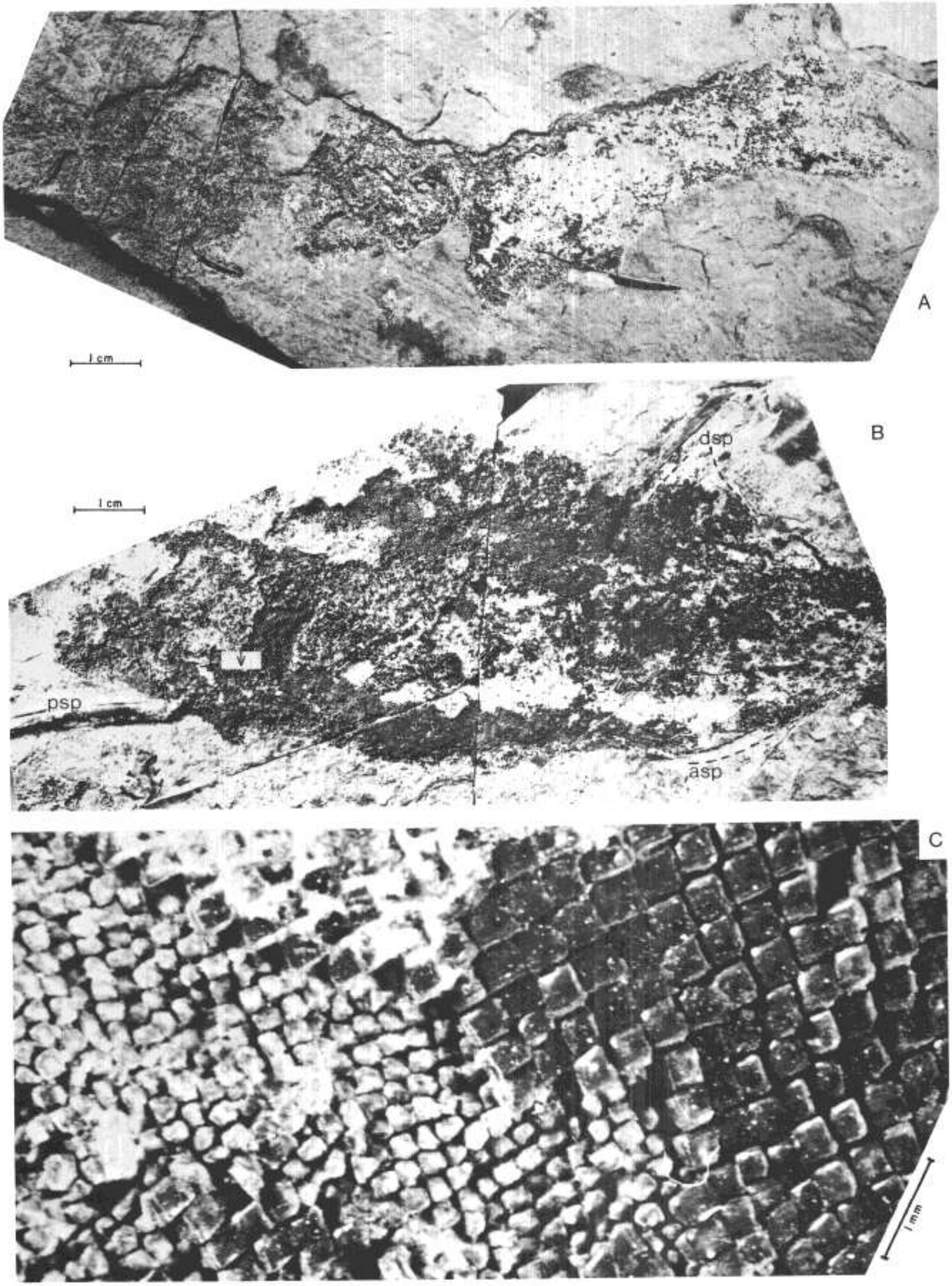
Ctenoptychius, known only from isolated teeth whose morphology justifies a taxonomic assignment to the family Petalodontidae, is more likely to be determined a form rather than an organ genus of that family. The vertical time range of *Ctenoptychius* has been given as Mississippian-Permian, but the Permian occurrences (Martin, 1913; Obrutchev, 1964, p. 249) are doubtful. Most species occur in the Upper Mississippian, and the genus thus cannot be regarded as characteristic of the Pennsylvanian even though there are often occurrences in sediments of that period.

Occurrences of detached teeth of the *Cladodus* type are known from the Middle Devonian into the Upper Permian. In the Pennsylvanian, such teeth are quite common in some zones, but at the present state of our knowledge not much can be said of them. In these teeth the characters that could be of value in classification into higher taxonomic categories are either lacking or remain unrecognized so far, and so even categories as general as the levels of elasmobranch organization of Schaeffer (1967; the cladodont and hybodont levels, in this case) cannot be recognized with any degree of confidence (Zidek, 1973a, p. 88-89). Obviously, under such circumstances *Cladodus* must be regarded as a form genus in part (as long as identified from detached teeth only), and the profusion of species names given in the past to such detached teeth (or, worse, to fragments of teeth) is of limited value. *C. occidentalis,* for instance, although one of the better known species, has been recorded in the literature from almost all levels of the Pennsylvanian, from Morrowan into Virgilian. Unfortunately, many of the specimens assigned to this species cannot be located today, but the available descriptions and illustrations alone (and the unlikely vertical range as well) indicate that in fact this "species" includes a variety of sharks—plus a number of indeterminables.

Listracanthus ranges from the Mississippian into and throughout the Pennsylvanian, but is found in abundance only in some Pennsylvanian zones. It has never been reported from the Permian. This is an organ genus known only from delicate spines that have been regarded by some students as being of cochliodontid derivation (Romer, 1966, p. 351), but such a taxonomic assignment is without factual basis. The *Listracanthus* spines commonly occur in association with another organ genus, *Petrodus* dermal denticles, which has led some authors (Bradley, 1870; Demanet, 1941) to link the two as elements that may have belonged to the same



ACANTHODII:
PLATE 1—*ACANTHODES* (*explanation on page 11*).



ACANTHODII:
PLATE 2—*ACANTHODES* (*explanation on page 11*).

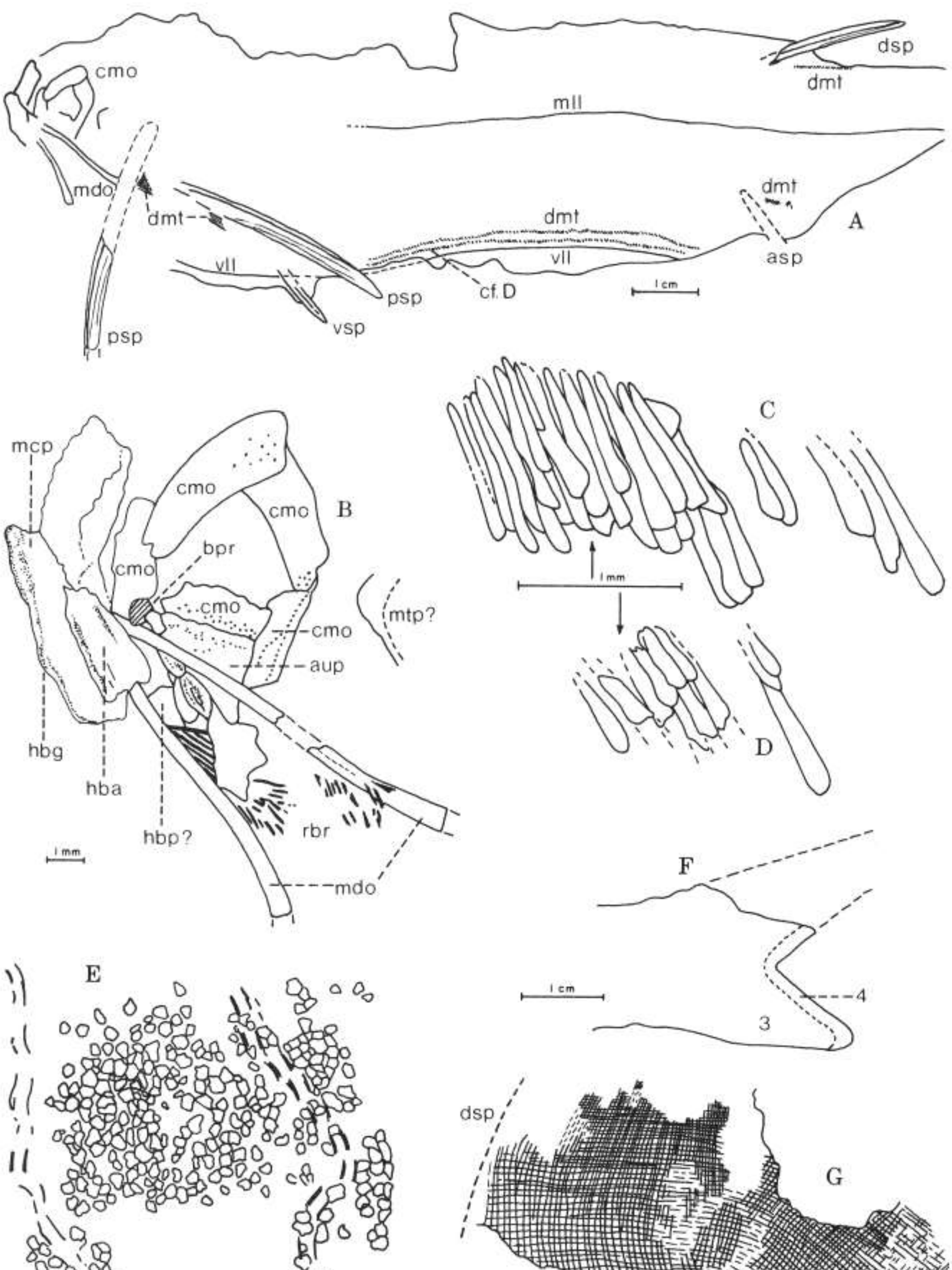


FIGURE 2—ACANTHODII (*explanation on opposite page*).

PLATE 1-ACANTHODII: *Acanthodes*

Acanthodes, OUSM 00447 (A-D) and USNM 187147 (E) specimens. A and B, preservation of the counterparts (see Fig. 2A for a composite illustration). With the exception of a few scales the squamation is exposed in the interior view only. **C,** scales of the anterior portion of the ventrolateral sensory line (interior view); D, squamation around the main lateral sensory line in the dorsal fin area (interior view); E, ventral view of the head and the pectoral girdle region of the USNM specimen (a mosaic of minute dermal plates is preserved only in the counterpart, and is illustrated in Fig. 2E). Parts of sensory lines retouched.

Abbreviations: asp, impression of anal spine; cmo, circumorbital plates; dpl, mosaic of minute dermal plates; dsl, sensory lines from dorsal surface of head; mdo, mandibular bones; mvl, median ventral sensory line; pgl, fragment of pectoral girdle; psp, pectoral spine; rbr, branchiostegal rays; sq, the most anterior extent of squamation; tsl, transverse sensory line commissure in snout; vll, ventrolateral sensory line.

PLATE 2 —ACANTHODII: *Acanthodes*

Acanthodes, OUSM 00448 (A) and **OUSM 00449 (B,** C) specimens. The enlarged portion of squamation (C) is from the area marked with an arrow in B. In Fig. C the exposure of both sides of the flank is well demonstrated due to a vertical slip that brought together the large scales of the left side (crowns showing) and smaller, more ventral scales of the right side (bases showing).

Abbreviations: asp, impression of anal spine; dsp, impression of dorsal spine and partial dorsal fin (Fig. 2G for detail); psp, pectoral spine.

FIGURE 2—ACANTHODII

Acanthodes, OUSM 00447 (A-D), USNM 187147 (E), OUSM 00448 (F), and OUSM 00449 (G) specimens. A, composite illustration of the counterparts (P1 1A, B); B, detail of the visceral skeleton and circumorbital plates; C, dermotrichia of the anal fin; D, ventrolateral dermotrichia of the area specified in Fig. A; **E,** mosaic of minute dermal plates and sensory canals composed of semicylindrical elements; **F,** zones of scales in the caudal fin; **G,** orientation of scale rows in the dorsal fin.

Abbreviations: asp, anal spine; aup, autopalatine ossification; bpr, basal process of autopalatine ossification; cmo, circumorbital plates; dmt, dermotrichia; dsp, dorsal spine; hba, anterior ossification of hyoid bar; hbg, groove on mesial surface of Meckel's cartilage for hyoid bar; hbp?, fragment of posterior ossification of hyoid bar; mcp, posterior ossification of Meckel's cartilage; mdo, mandibular bones; mll, main lateral sensory line; mtp?, fragment of metapterygoid ossification; psp, pectoral spine; rbr, branchiostegal rays; v11, ventrolateral sensory line; vsp, pelvic spine; 3, 4, zones of scales in caudal fin.

organism. However, Zangerl and Richardson (1963, p. 148, fig. 32), basing their interpretation on an analysis of the fossil content of the Mecca quarry, Indiana, concluded that despite certain similarities in occurrence, the vertical distribution of the two genera seems to rule out such a possibility. The *Listracanthus* spines are mainly characteristic of dark, carbonaceous shales and, together with *Petrodus,* indicate low-energy depositional environments—evidenced by the lack of orientation and by the intact preservation of the delicate spines (Zangerl and Richardson, 1963). This is not the case of our locality, however, which has so far produced only one shattered *Listracanthus* spine that, as well as the other two elasmobranch genera, comes from the light-yellowish-brown shale.

Class ACANTHODII
Order ACANTHODIFORMES
Family ACANTHODIDAE
GENUS *ACANTHODES* Agassiz, 1833
(Pls. 1, 2; Fig. 2)

USNM 187147 (counterparts), OUSM 00447 (counterparts) through 00449; circumorbital bones (plates), mandibular bones, mosaic of minute dermal plates, fragments of visceral skeleton, scattered gill-rakers, squamation, sensory lines, fragmentary pectoral girdle, partial fins, fin spines.

OUSM 00448 (Pl. 2A and Fig. 2F) and 00449 (Pl. 2B, C and Fig. 2G) consist only of squamation, partial fins, and fin spines, but they provide additional information about the squamation of both the flank and the fins.

OUSM 00447 (Pl. IA-D and Fig. 2A-D) is exposed laterally, and neither the circumorbital plates nor the elements of the visceral skeleton are quite *in situ.* The circumorbital ring was displaced slightly posteriorly as a unit and with little distortion and fragmentation of its plates. In the visceral skeleton, however, occurred an upward compression, bending, and crushing. For this reason the visceral skeleton is fragmentary, and its elements are difficult to identify.

The USNM specimen (Pl. 1E and Fig. 2E), projecting its dimensions from the size of the parts preserved, was only about two-thirds as large as OUSM 00447. It is exposed ventrally; its preservation is similar to that of the *Acanthodes bronni* specimen illustrated by Miles (1966, fig. 4).

There are five circumorbital plates (cmo) with the two dorsal ones being the longest and broadest. The ornamentation (OUSM 00447) consists of minute tubercles and is visible only in the outer portions of the ventral plates and in the ventral end of the posterior dorsal plate. Even in the ventral plates the ornamentation is indistinct, and a pattern, a branching line of well-separated tubercles, can be detected only in the posterior ventral plate. In the USNM specimen only the inner surfaces of the circumorbital plates are exposed; therefore no ornamentation can be seen.

The mandibular bones (mdo; mandibular splints of Watson, 1937) are preserved in the posterior two-thirds to three-quarters of their estimated total length in the OUSM 00447 specimen, and throughout their length in the USNM specimen. They are gently curved sinusoidally, and, as is usual in *Acanthodes* (except in *A. sulcatus,* Miles, 1966, p. 154), they lack ornamentation of any sort. In the USNM specimen they have well preserved the dorsal groove for the ventral margin of the Meckel's cartilage.

Except for the circumorbital and mandibular bones, the exoskeleton of the head is represented only by a mosaic of minute polygonal plates and by elements surrounding the lateral line sensory canals. In the OUSM 00447 specimen a mass of delicate plates is found above the orbit, and additional plates are embedded deep in the matrix under the left mandibular bone, so that their individual shape and original position cannot be established (Pl. 1A, dpl). In one of the counterparts of the USNM specimen, however, these plates are well exposed between the circumorbital rings and around the front ends of the mandibular bones. Apparently the dermal plates were on an average only 0.3 mm in diameter and were excessively thin, with translucent margins (Fig. 2E). All these plates are exposed with their inner, concave side up, but examination of their convex outer surfaces revealed no ornamentation. Watson (1937, p. 107, 108) found a mosaic of dermal plates in what he called "a rarer type" of *Acanthodes* from Lebach, Germany, in which "the squamation extends forward on to the head, passing into a continuous shield of very thin polygonal bones just as it does in the earlier Acanthodians, *Climatius, Mesacanthus* and *Diplacanthus.* This region lies entirely dorsal to the main lateral line and orbit and does not continue over the snout . . . Reis, 1896, fig. 2 is a good representative of this type." Except for the reference to Reis' figure (1896, fig. 2 on p. 195) showing the plates extending well behind the orbit, Watson's description is in accord with what was found in our specimens. In the OUSM 00447 specimen, the squamation clearly extends more forward, reaching the posterior margin of the circumorbital ring.

The palatoquadrate (OUSM 00447) is represented by a fairly complete autopalatine ossification (aup) with the basal process (bpr), and perhaps also by a small fragment of the metapterygoid ossification (mtp?). Nowhere is a structure preserved that could be identified as a remnant of the quadrate ossification.

The Meckel's cartilage (OUSM 00447) is represented by its larger, posterior (articular) ossification (mcp). Its surface is gently concave, and at the ventral margin is a clearly discernible groove for the hyoid bar (hbg). Consequently, the element is the right one with its mesial face showing. Its preglenoid process is covered by an element that may best be identified as the anterior ossification of the hyoid bar (hba).

In addition to the anterior, and possibly also posterior, ossification of the hyoid bar (hba, hbp?), the OUSM 00447 specimen exhibits some indeterminable fragments of the post-hyoid elements, along with scattered fragments of brachiostegal rays and gill rakers. The branchiostegal rays are better preserved in the USNM specimen (Pl. E, rbr), where there are approximately 20 rays, most of them complete, with some of the more anterior ones maintaining their sinusoidal shape.

The main lateral (m11) and ventrolateral (v11) sensory lines are preserved in the OUSM 00447 specimen; the USNM specimen exhibits the median ventral sensory line (my!), parts of the sensory lines from the dorsal surface of the head (dsl), and the transverse sensory line commissure in the snout (tsl). The labeling of the latter two lines (dsl, tsl) follows Miles' (1966, fig. 4) interpretation of an *A. bronni* specimen, the preservation of which matches in almost every detail that of the USNM specimen. The transverse sensory line commissure in the snout can be seen also in a number of specimens from the Autunian of France ("commissure ethmoidienne" of Heyler, 1969, p. 34-46, fig. 2C; pl. 4, fig. 1; pl. 5, figs. 6, 7; pl. 8, figs. 1, 3-6), where it is better preserved, evidently because the specimens are exposed with the dorsal side up. In the USNM specimen only a small part of this commissure is present, and, as is the case in Miles' and Heyler's specimens, it consists of minute elements whose shape cannot be determined. Immediately posterior of the transverse sensory line commissure in the snout, in the proximity of the left circumorbital ring, there is a closely spaced pair of longitudinal canals, in which the canal closer to the midline appears to be quite short and curved mesiad. Although the existing material does not permit drawing definite conclusions, due to the above-noted exposure of the specimen, the short, seemingly mesiad-curved canal probably could not represent the profundus sensory line. A more plausible explanation is that the close spacing of the two canals is the result of such distortion during fossilization that each of the canals actually belongs to one side of what is here cumulatively termed "sensory lines from dorsal surface of head" (dsl). For the most part these canals consist of elements described as "pieces hemi-cylindriques" by Heyler (1969, pl. 6, fig. 5; Fig. 2E of this paper), and they may be tentatively interpreted as the suborbital and postorbital branches of the infraorbital sensory line, plus possibly also a part of the supermaxillary sensory line.

The actual point of branching of the median ventral sensory line into the paired ventrolateral line in the pectoral girdle region (Miles, 1966, p. 153, footnote on *A. gracilis)* is not preserved. The two branches of the ventrolateral line are known to come together (or nearly so) posteriorly, before the line ends in the area of the anal fin (Troschel, 1857, pl. 1, figs. 1, 3; Watson, 1937, p. 111). In the OUSM 00447 specimen each counterpart exhibits a part of the ventrolateral sensory line. From the smaller counterpart (Pl. 1B), which shows the more posterior portion of this line, apparently the joining of its branches takes place about 15 mm in front of the anal fin. The main lateral and the ventrolateral sensory lines are described in more detail in connection with the squamation.

In the area between the pelvic and anal spines of the OUSM 00447 specimen are ventro-caudad oriented rod-shaped elements; these are only 0.5-1.0 mm long and maximum 0.2 mm thick, broadly oval-to-circular in cross section, with smooth, compact surfaces, and with the greatest thickness concentrated at their distal (lower) ends (Fig. 2A, dmt, 2D). Apparently in life these elements formed a continuous, ventrolaterally situated, paired line that followed closely the course of the ventrolateral sensory line above it, and ended some distance before the anal fin. Although preservation of such elements only in the specimen under discussion seems unlikely, I have not found any previous mention of them or detected them in any other specimen of *Acanthodes*. Obviously they supported a long pelvic fin. In regard to their position in the body wall rather than proximally in the fin, and also in regard to their morphology, they resemble miniature radialia more than dermotrichia. Viewed in sharply diagonal light, the OUSM 00447 specimen exhibits a series of regularly repeated shallow grooves that are parallel to each other and follow a course similar to the course of the myomeres seen in Watson's (1959, pl. 1) specimen of *Cheiracanthus*. Such grooves can hardly be considered the accidental result of post-mortem folding of the skin. It seems more reasonable to assume rather that they actually represent boundaries between the individual myomeres. If so, each myomere would be 2.5 to 3.0 mm wide (in Watson's specimen the myomeres are 3.5 to 4.0 mm wide, which, corresponding to the larger size of his specimen, is approximately one-fourth larger than OUSM 00447), and not two, but over twenty ventrolateral rods would correspond to one such myomere. Jarvik (1965, p. 156, fig. 7A) drew attention to the often-overlooked fact that one supporting endoskeletal rod (primary radial) develops between each dorsal and ventral radial muscle, and, therefore, that two such radials are in each metamere. Even if the above interpretation of the grooves as myomeric boundaries should prove incorrect, expecting the myomeres in a specimen 230 mm long (table p. 15 presents total length estimates) to be so narrow as to accommodate only two radials 0.2 mm thick would be unreasonable. The elements in question thus show discrepancy with the radial muscles in regard to their arrangement. Such a discrepancy should not be surprising; it occurs frequently in both the median and paired fins in sharks (Osburn, 1907, p. 179-180, fig. 15; Goodrich, 1930, p. 9192, 133 of Dover edition). However, the extent and consistency of this discrepancy, instead of being restricted to the ends of the fin, occur throughout its course, and would thus require multiplication rather than just secondary duplication of the radials, making the endoskeletal derivation of the elements extremely unlikely; consequently, they have to be interpreted as the proximal, ossified parts of the dermal fin rays (dermotrichia). A number of authors have noted the dermotrichia in the pectoral, anal, and dorsal fins of acanthodians, particularly in species of the genus *Acanthodes* (Miles, 1965, p. 245-246, 1966, p. 188, 1970, p. 358-359). A long pelvic fin was described and/or illustrated in *Acanthodes* and related forms by Fritsch (1893, pl. 108, fig. 252D), Davis (1894, pl. 27, fig. 1), and Miles (1970, fig. 5, 1971, fig. 4.4). Of these authors only Fritsch depicts the dermotrichia in the fin of *"Protacanthodes" pinnatus* (1893, fig. 252D). In Fritsch's specimen of *"Protacanthodes" Pseudacanthodes)* the rays differ from the ones in question in two important respects: 1) the rays are split longitudinally, except for their proximal terminations, which are smooth, undivided and as broad as the scale rows overlying them on the ventral side of the fin and 2) the rays are arranged in one layer only. In the OUSM 00447 specimen the rays are smooth, compact rods corresponding to only about one-fourth of the breadth of the overlying scale rows and are arranged in two layers. Excluding the tail, the dermotrichia of acanthodian fins are deeply-seated and can be regarded as early generations of scale rows sunk into the dermis and overlaid by the existing squamation (Jarvik, 1959; Miles, 1965, 1970). Thus, the upper layer of the rays corresponds ontogenetically to the modified early scale rows from the dorsal surface of the fin and the lower layer, to those from the ventral surface (Fig. 2D). In all the specimens I could examine, the deeply seated fin rays are invariably narrower than the scale rows covering them, and I am, therefore, inclined to regard the relationship of the scales and fin rays shown in Fritsch's illustration as a case of erroneous interpretation rather than as an unusual development. In the OUSM 00447 specimen the rods are somewhat thicker at their distal ends. This may be taken as an indication of the extent of ossification of the rays, known to ossify only proximally in the Acanthodii (Watson, 1937; Schaeffer, 1968; Miles, 1970).

Rays of a size and morphology similar to those just described are also preserved in the dorsal and anal fins of the OUSM 00447 specimen, as well as in the dorsal fin of the OUSM 00449 specimen. In the dorsal fin, the preservation of the rods does not allow accurate observation of their morphology nor identification of layered arrangement. Clearly, however, their proximal, ossified parts were restricted to the very base of the fin (Fig. 2A, G). In the anal fin (Fig. 2A, C) the dermotrichia are slightly larger than the ventrolateral and dorsal dermotrichia but are otherwise similar to them. I have found no evidence of "a single basal bone" (Watson, 1937, p. 113) supporting the dorsal fin.

The squamation consists of oblique rows of minute, rhomboidal, unornamented scales. All the specimens are fully scaled, and even in the smallest one (USNM 187147) the squamation appears to have extended as far anteriorly as into the pectoral girdle region (Pl. 1E, sq). The largest scales (Pls. 1D, 2C) occupy the flank around and above the midline on both the sides of the main lateral sensory line (situated above the midline of the flank), and extend posteriorly onto the caudal fin (OUSM 00448). The size of scales measured along the rows, are: 4 scales per mm in the OUSM 00447 specimen (only 3 scales per mm in the area beneath the dorsal fin; P1. 1D); 6 scales per mm in the OUSM 00448 specimen (beneath the dorsal fin the squamation is not preserved); and 3 scales per mm in the OUSM 00449 specimen (only 2 scales per mm beneath the dorsal fin). The size of scales decreases gradually toward the head and the belly and more abruptly toward the back, so that eventually in these areas the scales are only about half the size of the large scales on the flank. In the craniad direction the decrease in size becomes apparent approximately halfway between the anal and pectoral regions. Scales can be detected as far anteriorly as between the hind portions of the mandibular bones and dorsally behind the orbits (OUSM 00447; P1. IA, sq).

The OUSM 00447 specimen is split in the sagittal plane so that in both the counterparts only the interior view of the squamation is visible (P1. 1A-D); in the other two OUSM specimens both the scale crowns of the left flank and the scale bases of the right flank are exposed (Pl. 2A-C). Although the preservation of the 00447 specimen might seem to make its squamation quite distinct, few scales are preserved with their crowns exposed and these crowns are identical to those in the OUSM 00448 and 00449 specimens (P1. 2C). All the scales have short crowns with practically no overlap over the bases; the scale counts listed above are not affected by the inside-out exposure of the squamation.

As can be inferred from the bases exposed, the scales bordering the main lateral sensory line do not differ in size and orientation from the rest of the large flank scales (Pl. ID). Nevertheless, the line can be traced because its scales are farther apart and appear not to lie in exactly the same plane as the scales surrounding them. This observation is in accord with the findings of other authors, with the exception of Dean (1907, p. 219, fig. 35), who described the scales bordering the lateral line in *A. bronni* as enlarged and prosalient. Through the kindness of H. Remy, Geologisch-palaontologisches Institut of the Friedrich Wilhelms-Universität, Bonn, I have been able to examine specimens of *A. bronni* from Lebach and found the scales of the main lateral sensory line to be no different from those in the New Mexico material. Dean (1907) treated the neuromast system in only general terms; his "lateral line" is a term not necessarily restricted to the main lateral line. His fig. 35 (labelled "detail of lateral line") apparently does not pertain to the main, but to the ventrolateral line.

The ventrolateral sensory line is much more distinct than the main lateral line because its scales are significantly larger than the scales of the pectoral and pelvic regions surrounding them (Pl. IC). As an exception to the general rule that acanthodian scales do not imbricate, the scales of the ventrolateral line do imbricate, appearing broader than long. In these scales the two members of each pair (the dorsal and ventral scale) are packed close together, indicating that the ventrolateral sensory line probably was a partially enclosed canal that opened on the surface either by an alternately narrowing and broadening fissure or by pores between the rounded corners of the scales.

In the anal fin (OUSM 00448; Pl. 2A) the scale rows are straight and run parallel to the fin spine, except at the fin base, where they are gently curved caudad. Measured along the rows, there are 12 scales per mm close to the fin base. The margin of the fin is not preserved, but judging from the rate of decrease in size, the count could be as high as 20 to 24 scales per mm.

The squamation of the dorsal fin is preserved only in the OUSM 00449 specimen (Pl. 2B, Fig. 2G), and, conforming to its larger size, there are only 5 scales per mm at the fin base. At the base the anterior scale rows curve caudad, but further up, toward the margin of the fin, they bend and eventually become parallel with the fin spine. In about midlength of the fin the orientation of the scale rows changes and they no longer curve caudad at the fin base but instead are almost straight and run parallel to the fin spine throughout their preserved length. Closer to the posterior end of the fin the rows remain straight but become more inclined, so that the angle between them and the trunk is more acute than the angle of the fin spine.

In the caudal fin (OUSM 00448; P1. 2A, Fig. 2F) the squamation is disturbed and the scale zones nos. 1, 2, 2", and the part of zone 4 in the axial lobe (Heyler, 1969 and earlier works; Miles, 1970) cannot be identified. Judging from what is preserved of the squamation, there does not seem to be any difference in orientation, size, and morphology *between* the scales of zone 3 in the ventral division of the hypochordal lobe (Miles, 1970, p. 355) and the scale rows of the flank. The longitudinal division of the hypochordal lobe appears to be somewhat more extensive than is indicated by Miles (1970, fig. 7). In the specimen in question the zone 4 scales extend from the postero-superior margin of the lobe onto its very tip. It might be argued that the two zones (3 and 4) pass gradually into one another and, if so, the small scales of the tip of the hypochordal lobe actually belong to the ventral division of it. However, the zone of truly minute scales at the tip of the lobe (these scales are similar in size to those in the anal fin of the same individual) is too wide to support the belief that all of them belong to the ventral division.

Based on the examination of specimens in various states of growth, Watson (1937) described the development of the squamation in *Acanthodes,* concluding that its mode accounts for "the remarkable fact that the scales of large specimens of *Acanthodes* may be no larger than those of small individuals" (p. 112), and, consequently, that "the scales seem to reach their maximum size early in the life of the fish and growth takes place by the addition of new scales" (p. 117). However, this conclusion does not appear to be in accord with the scale counts in the specimens under discussion.

The fin spines are gently arcuate, laterally compressed rods of asymmetrical cross section in the paired fins and bilaterally symmetrical in the median fins. The length of their inserted bases is considerable, comprising perhaps as much as one-fourth of the total spine length. The pelvic, anal, and dorsal spines narrow toward their tips more or less gradually. However, the pectoral spines narrow progressively, or, to be more precise, the lowering of their height as seen in cross section takes place mainly in the most distal fifth of their length. All the spines have a deep main longitudinal groove on each side that divides the spine into an anterior keel (the anterior margin is nevertheless rounded) and a higher and broader posterior part. This groove is situated close to the spine's midheight proximally, and toward the tip gradually approaches the anterior margin. Another more posteriorly situated, rather indistinct, shallow groove begins at the posterior margin of the proximal fourth and crosses the spine wall, approaching the main longitudinal groove distally but not joining it. In the pelvic spines (OUSM 00447, 00448) only a trace of this more posterior groove can be found at the distal ends. In the pectoral spines there are, in addition to the grooves just noted, two to three shallow posterior grooves that distally spread and interrupt. All the grooves posterior to the main longitudinal groove have the character of attachment impressions rather than of true ornament.

In *Acanthodes* the single dorsal and the anal spines are situated far back, close to the tail; the anal spine is somewhat longer than the dorsal spine and somewhat in front of it. The pectoral spines are by far the biggest; the pelvic spines are the smallest and are placed close behind the pectoral fins. This characteristic distribution and size relation can be seen in the OUSM 00447 and 00448 specimens (Pls. IA, 2A, Fig. 2A). In the available material the only measurable proportion, besides the size of the spines, is the distance between the pelvic and anal spines. Based chiefly on Fritsch's and Watson's restorations, the distance between the pelvic and anal spines multiplied by 3.3 appears to correspond roughly to the total length of the fish. (Tabulated below.)
Considering the total length estimates for OUSM 00447 and 00448, apparently the dorsal spine is smaller than the anal, although not as small as indicated by Watson (1937, fig. 21) nor as large as indicated by Fritsch (1893, fig. 254).

Spines similar in appearance to those found in the specimens discussed have been described previously in *Acanthodes* by several authors. Unfortunately, with rare exceptions (Fritsch, 1893), the descriptions lack detail, and the question of whether spine morphology alone can be considered diagnostic of the genus (not to speak about species) cannot be answered here. Under these circumstances the distribution of the spines and their size in relation to each other become important considerations. In some older illustrations (Reis, 1895, pl. 6, fig. 5, 1896, pl. 6, fig. 11) the pectoral spines of *Acanthodes (A. bronni)* are shown as being highest in their distal fifth. Although impossible to determine (from the figures cited) whether the distal bladelike expansion is an outgrowth or is simply the result of a post-mortem deformation, this expansion is certainly not typical of *Acanthodes,* or, for that matter, of spines of any other acanthodian. The above statement characterizing the more posterior grooves as having the appearance of attachment impressions implies that they had to do with the fin web attachment; if this is true, the restorations showing the fin web connected only with the proximal half of the pectoral spine (Jaekel, 1899, fig. 2) are unlikely. However, not all pectoral spines of *Acanthodes* can be so characterized, and the above statement should not be considered applicable to the genus as a whole.

Remarks on Acanthodes

This genus ranges from the Mississippian (Miles, 1966, p. 174) into the Lower Permian (Beyrich, 1848; Roemer, 1857; Troschel, 1857; Kner, 1868; Rzehak, 1881; Sauvage, 1883; Fritsch, 1893; Reis, 1896 and earlier works; Watson, 1937; Augusta, 1939; Miles, 1966, 1973b; Heyler, 1969; Simpson, 1973a, 1974;

MEASUREMENTS OF SPECIMENS, IN MM
(? denotes unmeasurable, ϕ denotes absent)

Specimen	Length/height of spine				Distance between pelvic and anal spines	Estimated total length
	Pectoral	Pelvic	Anal	Dorsal		
USNM 187147	?/1.4	ϕ	ϕ	ϕ	ϕ	150 (±)
OUSM 00447	36/2.5	9/1	?	22/1.5	70	231
OUSM 00448	?	8/1	22/1.5	ϕ	55	181.5
OUSM 00449	?/3.5	ϕ	?	?	100 (+)	330 (+)

Zidek, 1973b). Miles (1966) recognized *Acanthodes sulcatus* from the Lower Carboniferous of Scotland and remarked that several other Lower Carboniferous species assigned to this genus need revision urgently.

A suite of acanthodian fragments from the Horton Bluff Formation (Lower Mississippian) of Nova Scotia, Canada (PU, MCZ, and OUSM specimens), may contain some of the oldest fossils assignable to the genus *Acanthodes.* The Horton Bluff material has been noted as including *Gyracanthus* and an unidentified long-spined genus (Carroll and others, 1972, p. 20). From the specimens loaned by Donald Baird (PU 19348 and unnumbered) more than two genera may be present. One of the remains (PU 19348) is an isolated large mandible with bluntly conical teeth anchylosed in its posterior part and small teeth, evidently from the lining of the mouth cavity, on its inner wall. The jaw is broken off anteriorly; therefore, separate ossifications cannot be determined. Because *Gyracanthus* spines are common in the Horton Bluff Formation, one could speculate on the possible affinity of this mandible to that genus, in which the head is entirely unknown (Donald Baird, written communication, 1974). However, the Gyracanthidae have been referred to the Climatioidei by Miles (1973a); the mandible in question appears to be more ischnacanthid-like. The "unidentified long-spined genus" is represented only by detached spines that (with the exception of a single specimen OUSM 00403, donated by Baird) appear accidentally associated in the slabs with fragments of pectoral girdles—most of which are climatioid, as far as is determinable from their exoskeletal parts, but which are too small for, and structurally different from *Gyracanthus.* The spines are remarkably *Acanthodes-like,* and, although some of them are unusually large for *Acanthodes,* nothing in their morphology precludes assignment to this genus. The OUSM 00403 specimen is the only example in the Horton Bluff material of a pectoral spine attached to the girdle. The specimen is well within the usual *Acanthodes* size range; the girdle closely resembles that described in *Acanthodes* (Miles, 1971, p. 71, fig. 4.12; 1973a, p. 151-155, figs. 19, 21). Although this specimen and the detached spines are not conclusive of the presence of *Acanthodes* in the Horton Bluff Formation, they demonstrate that the family Acanthodidae was extant by Lower Mississippian (Tournaisian) time.

The Lower Permian of Europe has produced more numerous and better preserved specimens of *A canthodes* (Germany, France, and, to a lesser degree, Czechoslovakia) than have the Permian deposits of North America, where most finds are exceedingly fragmentary and where the number of occurrences is probably even fewer than was previously thought (Simpson, 1973a; Zidek, 1973b). A new collection, as yet undescribed, is known from the Texas Permian, where *Acanthodes* is common in many microvertebrate samples recovered below the Clyde-Lueders contact (Gary D. Johnson, Southern Methodist University, Dallas, written communication, 1973). Inasmuch as this material consists only of detached spines and scales, it is assigned to *Acanthodes* solely because no other acanthodian genus is "supposed" to cross the Pennsylvanian-Permian boundary.

The Pennsylvanian record of *Acanthodes* is based chiefly on European occurrences (Fritsch, 1893)—not (as is the case in the European Permian) because of a greater number and higher quality of European specimens, but because significant collections recovered in North America have yet to be described. Among these are materials taken from the Virgilian deposits in the Hamilton quarry of Kansas and reposited at Kansas State Teachers College in Emporia, Kansas; and the Field Museum of Natural History collection from the Desmoinesian of Indiana in the Mecca and Logan quarries (Zangerl and Richardson, 1963).

The North American finds so far recorded in the literature are from Mazon Creek, Illinois, and were described under the names of *Acanthodes marshi* and *A. beecheri* by Eastman (1902). These two species, and also *Cercariomorphus parvisquamis* Cope from Linton, Ohio (regarded as an amphibian by Cope, 1885, and as a xenacanth shark by Romer, 1930), were later commented upon by Gregory (1951), who concluded that the scaleless *A. beecheri* specimens are immature and possibly represent the young of *A. marshi,* and that the squamation of *C. parvisquamis (as* illustrated by Moodie, 1916, pl. 24, fig. 2) reveals a strong resemblance to acanthodian scales such as those in *A. marshi.* The fact that the mutual positions and proportions of the fin spines remained stable throughout ontogeny of *Acanthodes* is well documented in the Kansas Hamilton quarry collection. Eastman's (1902, p. 95) observation is also noted: "The most marked characteristic of the present form *(A. beecheri)* consists in the small size of the pectorals as compared with the pelvic, dorsal, and anal fins." Either Eastman underestimated the total size of the imperfectly preserved pectoral spines, or the specimens labelled as *Acanthodes beecheri* do not belong to this genus. As for *A. marshi,* both Eastman's and Gregory's specimens are too poorly preserved to allow comment other than that they belong to a large acanthodian, possibly *A canthodes.*

The Manzanita Mountains specimens are the first described from the Pennsylvanian of North America in which the assignment to the genus *Acanthodes* is fully warranted. Species assignment for these specimens, however, is impossible; perhaps they belong to more than one species. Their imperfect preservation is one reason for identifying them only generically; the primary reason is our inadequate knowledge of the genus, in spite of *Acanthodes* being the best known acanthodian, with the consequent lack of criteria for species assignments. In describing the specimens, I could find nothing that would distinguish them from *A. bronni* or *A. gracilis* (if one chooses to consider these distinct; but see Woodward, 1891, p. 6). However, from Watson's (1937) account of *A. bronni* from Lebach near Saar-bracken (Rhineland, Germany) the Lebach material appears to include specimens with such wide proportional variations, unaccountable for by growth, that doubtless several *Acanthodes* species are present. Because Agassiz's syntypes of *A. bronni* cannot be identified in the Lebach material, and because his description is inadequate for determination as to on which one of the variations recorded by Watson the species had been based, erecting a neotype is impossible; accordingly, *A. bronni* should be regarded *as nomen dubium.*

The similarity in structure should not be used to infer

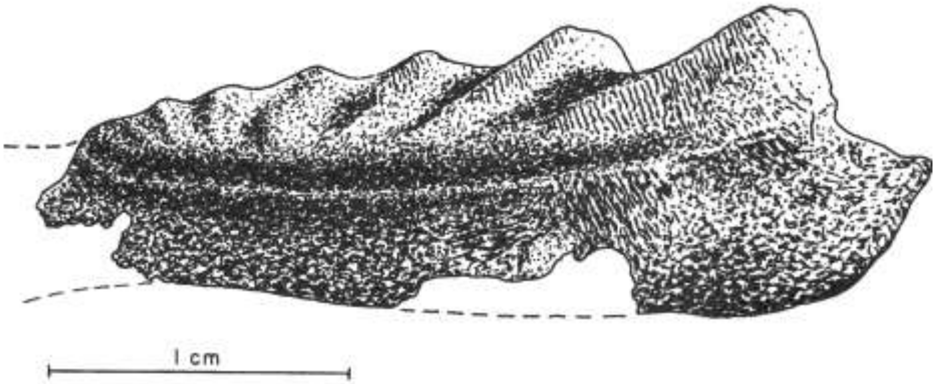


FIGURE 3—DIPNOI.
Proceratodus hlavini, n. sp., CMNH 8311, left mandibular tooth plate with incomplete prearticular; lingual and slightly superior view.

that the Manzanita Mountains specimens are conspecific with one of the species found in the Rothliegenden in Lebach, nor with the specimens known from the Autunian of France. There is a time gap of 10 million years or more between the New Mexico and the European occurrences, and the favorable paleogeographic situation during the Late Paleozoic cannot thus be operated with. In terms of chronotypy and chorotypy, the Manzanita Mountains *Acanthodes* ought to differ from those in Germany and France, but the structure preserved fails to demonstrate such a difference.

Class DIPNOI
Order ?CERATODONTIFORMES
Family ?CERATODONTIDAE
GENUS *PROCERATODUS* Romer and Smith, 1934
Proceratodus hlavini, n. sp.

(Fig. 3)

ETYMOLOGY—Named for Dr. William J. Hlavin, who collected the holotype.

HOLOTYPE—CMNH 8311, left mandibular tooth plate with prearticular bone attached. No other material. ZONE AND LOCALITY—See Introduction.

DIAGNOSIS—Mandibular plate narrow, with seven ridges; sharp crests only on the anterior ridges; no tuberculation or crenulation on ridges; lingual margin only gently arched; obtuse angle and no sharp edge between occlusal and lingual faces.

DESCRIPTION AND DISCUSSION—The left mandibular tooth plate with the prearticular bone attached. In the prearticular (in terminology of Watson and Gill, 1923) the anterior, mesiad expanded portion by which it joins the prearticular of the other side is well preserved. Posteriorly this bone is incomplete (the part posterior to the tooth plate is missing). As the specimen is fractured perpendicularly in several places, no attempt has been made to remove it from the matrix. Only a minor amount of preparation was done in order to examine the labial curvature of the plate's ridges and to search for tuberculation on their distal parts.

The tooth plate is 26 mm long, with the length to width ratio approximately 3:1. The occlusal face bears seven ridges, the length, height, and sharpness of which decrease posteriorly. The most posterior of the ridges is very small and indistinct, situated on a "heel." The center of the outward (labiad) radiation of the ridges lies linguad of the fourth ridge. On the labial side of the plate the ridges curve strongly downward, and the indentations (lacunae, clefts) between them extend over less than one-fourth of the plate's width. Linguad, the ridges extend almost to the margin of the plate. The three anterior ridges have sharp crests; in the remaining ridges the crests are oblique in profile. All the ridges are devoid of tubercles or crenulation. Instead, the transition from the occlusal to the labial face is somewhat angular (a heel between the two faces), and the labial margin is bounded by horizontal bands (growth zones) of enameloid. Inasmuch as the specimen is not abraded, the profiles of the ridges and the lack of tuberculation on them cannot be regarded as accidental. The lingual margin is only gently arched, more so in the anterior than in the posterior half of the plate. The transition from the occlusal to the lingual surface is oblique (the lingual margin does not form a sharp edge). The two faces meet at an obtuse angle (about 100°).

An overall resemblance might lead to the consideration of the genus *Sagenodus;* if so, a comparison could best be made with *S. porrectus* (Romer and Smith, 1934, fig. 7A). However, the specimen in question is somewhat broader (4 to 1 in *S. porrectus)* and is less curved in the labiolingual plane. The transition from the occlusal to the lingual face is oblique, and the angle between the two faces is obtuse, whereas angular and acute in *S. porrectus.* The first ridge is somewhat shorter than in *S. porrectus,* and throughout its length the highest of all the ridges. Most significantly, the ridges lack the tuberculation otherwise found in all the *Sagenodus* species of which I am aware, the bands of enameloid are present on the labial margin of the tooth plate, implying that the growth of the plate was apparently accomplished in a way somewhat different from that found in *Sagenodus* (Denison, 1974, p. 52-53). The prearticular appears to be unusually narrow for *Sagenodus,* particularly beneath the posterior part of the tooth plate, where one would expect a downward expansion of the bone.

The genus *Proceratodus* was established by Romer and Smith (1934, p. 715) "to include forms seemingly ancestral to *Ceratodus*, but differing from that genus in the more pronounced development of the tooth ridges on the dental plates." For the type species, *P. carlinvillensis,* a pterygoid tooth plate from the Pennsylvanian of Illinois, these authors list as diagnostic features seven fairly well-marked ridges that extend inward nearly to the lingual margin and show no evidence of tuberculation; the plate has only narrow labial indentations, and there are numerous bands of 'enamel' (= enameloid; Denison, 1974, p. 34) on its labial margin. Also, *Ctenodus wagneri* of the Cleveland Shale (Newberry, 1889, p. 172, pl. 27, fig. 30) and *Ceratodus favosus* of the Texas Permian (Cope, 1884, p. 28; Hussakof, 1911, p. 167, pl. 27, fig. 11, 11a), both lacking tubercles on ridges, having only shallow labial indentations, with the labial bands of enameloid present, are referred to *Proceratodus* by Romer and Smith *(C. favosus*, with some doubt). The absence of tuberculation, the relatively shallow labial indentations, and the presence of growth zones (bands) of enameloid on the labial side of the dental plates are considered diagnostic of the genus, and consequently, the specimen in question is here identified as *Proceratodus.* Of the three species just named, only *"Ceratodus" favosus* is based on a mandibular tooth plate (only a small fragment offering no clue concerning the overall shape of the plate). *Proceratodus carlinvillensis* and *"Ctenodus" wagneri* are known only from pterygoid tooth plates. Unfortunately, nothing compares more closely with our specimen.

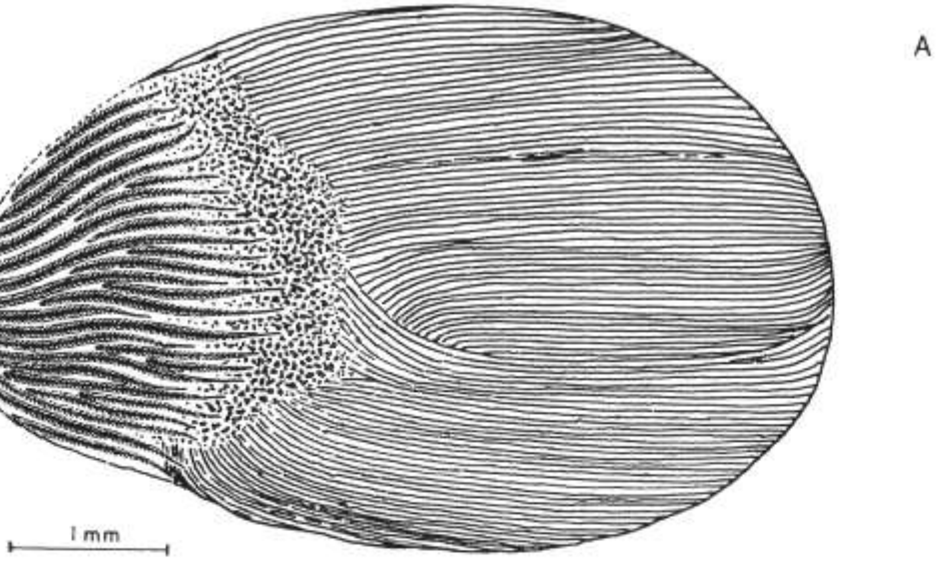
The position of *Proceratodus* in the dipnoan system is uncertain. The genus was first described as a ceratodontid by Romer and Smith (1934), but was placed later by Romer (1966, p. 362), with a question mark, in the family Sagenodontidae. Yet, in their 1934 paper (p. 714-715) Romer and Smith state: "Though it is perhaps theoretically possible to derive a ceratodont type of tooth from that of *Sagenodus*, there is little evidence of `drift' in such a direction in the members of the last genus. Further, plates suggesting the ceratodont type are found occasionally in late Paleozoic deposits." Characterizing *Sagenodus porrectus,* Romer and Smith (1934, p. 712-714) state: "in this species we perhaps are not far from the point of origin of the line leading to the existing *Epiceratodus.* Whether, however, *Ceratodus* proper has had a like origin seems to us more than doubtful. In this last genus the tendency seems to be toward the retention of a broad crushing plate and lack of any great development of deep ridge terminations. This suggests an origin from some type much more primitive in nature." Because *Sagenodus* and *Proceratodus* are contemporaries and because in the latter genus, as in *Ceratodus* and in contradistinction to *Sagenodus,* the labial indentations are shallow and there is a tendency to retain broad dental plates (as evidenced by the pterygoid plates), grouping of the two under the same family heading does not seem appropriate. Rather, the two genera could be regarded as members of two lineages, *a Sagenodus-Neoceratodus (Epiceratodus)* lineage, and a side, sterile *Proceratodus-Ceratodus* lineage. If so, the question arises whether any sharp distinction can truly be made between the ctenodontid (including Sagenodontidae) and ceratodontid dipnoans.

Class CROSSOPTERYGII
Order COELACANTHIFORMES
Suborder COELACANTHOIDEI
Family COELACANTHIDAE, g. et sp. indet.
(Fig. 4)

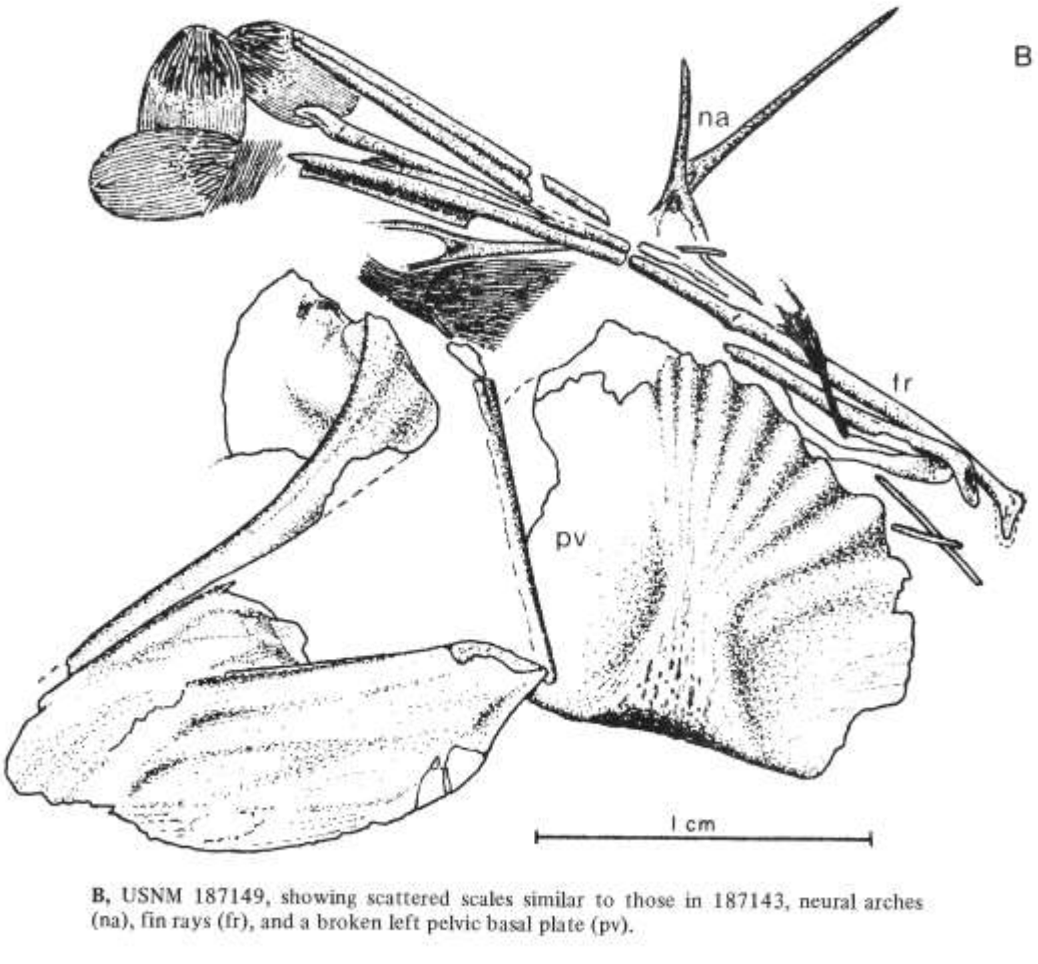
USNM 187143 (counterparts), a mass of crushed fin rays and scattered scales. Imprints of scales of similar morphology are present also in the USNM 187149 specimen, which otherwise consists of scattered neural arches, fin rays, and a remnant of the pelvic girdle.

The scales (Fig. 4A) are of the cycloid type, thin, ovate in shape (approximately 3:2), 5 to 6 mm long, and broadest in the anterior third. The overlapped surface comprises roughly the anterior two-thirds of the scale length and consists of thin dentinal tubes (striae or fibrils of other authors) oriented parallel with the long axis of the scales. The exposed, ornamented part is restricted to the narrower posterior third of the scales, with the ornamentation consisting of over 20 closely spaced, undulating, and posteriorly converging ridges, and of a narrow zone of exceedingly small tubercles anterior to the ridges. The ridges are rounded in cross section; from a few broken ones it is apparent that they have large, undivided pulp cavities. The tops of the ridges are smooth; the sides bear closely spaced, short wrinkles that converge posteriorly toward the midline of each ridge. The anterior extent of the ridges is greatest along the long axis of the scales, but the mesial ridges are shorter than the lateral ones. This seeming discrepancy is due to an alternating pattern of the mesial ridges that occupy either only the more posterior or the more anterior part of the exposed portion of the scales, with the overlap between adjacent ridges being approximately one-third of the ridge length. The tuberculated zone is roughly semilunar in outline, except for a small V-shaped area off the center (evidently the point of contact of the overlapping scales), where the tubercles extend farther anteriorly. The boundary between the zone of tubercles and the overlapped portion of the scale is quite sharp, whereas posteriorly there is a transitional area in which the ridges gradually thin out among the tubercles. The tubercles are closely spaced, slightly inclined backwards, uniform in size, and much smaller than the smallest (first generation) tubercles described by Orvig (1957, figs. 4A, C, 7C, 8C) in the porolepiform *(Glyptolepis, Porolepis)* and the struniiform *(Onychodus)* crossopterygians. Also, in the scales of the genera discussed by Orvig the tubercles show an orderly pattern in their distribution and relation to the ridges. No such pattern can be detected in the scales in question; therefore, whether their tubercles can be related to those in the non-coelacanthiform crossopterygians is doubtful.

Ornamentation of ridges with wrinkles has not been recorded previously in the coelacanth scales. Wrinkles on ridges were described in the three above-named porolepiform and struniiform genera by Orvig (1957, p. 386, 395, 400, and tabulated characters, figs. 4D, 7C, 8B, C), who observed that they continue as creases across the grooves between the ridges, and concluded that the wrinkles actually represent demarcation lines between dentine tubercles (presumably lepidomorial crowns)



Coelacanthidae indet. **A,** USNM 187143, detail of a scale.



B, USNM 187149, showing scattered scales similar to those in 187143, neural arches (na), fin rays (fr), and a broken left pelvic basal plate (pv).

FIGURE 4—Crossopterygii.

that have fused to form ridges. Particularly in *Glyptolepis* the wrinkles appear similar to the ones noted in the foregoing description. To account for the large, undivided pulp cavities present in the ridges of the scales in question, one must assume *complete* fusion of the dentine tubercles, as proposed by Orvig.

The scarcity and jumbled preservation of the scales precluded examination of their microstructure; their morphology alone provides adequate grounds for recognizing coelacanth derivation. Scale morphology as a sole taxonomic criterion has been shown to be unreliable on the specific and generic levels for the coelacanths (Moy-Thomas, 1937, p. 385; Schaeffer, 1952, p. 51; Echols, 1963, p. 495), and in the USNM 187143 specimen the scales are the only usable criterion of identification. The specimen could thus be identified only as a coelacanth that, with regard to its age, would be tentatively assignable to the subfamily Rhabdodermatinae (Diplocercidae, Diplocercidoidei), established by Echols (1963, p. 478, 497) for the Carboniferous genera *Rhabdoderma* and *Synaptotylus.* However, in the USNM 187149 specimen (Fig. 4B) scales similar to those in USNM 187143 are associated with a pelvic basal plate (pv) that, although incomplete, shows enough to indicate clearly that it is neither from *Rhabdoderma* nor from *Synaptotylus.* This plate is more closely comparable to a pelvic basal plate of *Coelacanthus* (Moy-Thomas and Westoll, 1935, fig. 9; MoyThomas, 1937, fig. 10B; Schaeffer, 1941, fig. 6C), but at the same time differs from that genus in characteristics important enough to preclude such generic assignment. The ridges and grooves of the mesial process of the plate are more numerous and more profoundly radiating than is the case in *Coelacanthus;* even more significantly, the mesial process is webbed with bone both anteriorly and posteriorly (the webbing is present only at the anterior margin of the process in *Coelacanthus).* Consequently, the mesial, grooved part does not project as a true process.

In conclusion, the pelvic basal plate indicates coelacanthoid rather than diplocercidoid affinity; the scales of the other USNM specimen correspond to those associated with that basal plate. Accordingly, both the USNM specimens are here identified as Coelacanthidae indet. The pelvic plate may represent a new genus, but to erect a genus on a broken and rarely found skeletal element is impracticable. Besides, the untestable possibility exists that the plate belongs to *Spermatodus.* This genus has been regarded by Westoll (1939) as being closer to *Coelacanthus* than to any other coelacanth, but, unfortunately, its pelvic girdle is unknown, and the few poorly preserved scales mentioned by Westoll (p. 15) allow no comparison. Concerning its occurrence Westoll stated that the provenances of the type and referred specimen of *Spermatodus pustulosus* are uncertain, but that the basisphenoids lent to him by Romer are from the Admiral Formation of the Wichita Group in Archer County, Texas. The Wichita Group is Wolfcampian in age, and its top has recently been correlated with the top of the Gearyan Series (Upper Pennsylvanian) in Oklahoma (Simpson, 1973b). However unorthodox this may seem, indications are strong that this concept is essentially correct, and, consequently, Westoll's using "Permian" for *Spermatodus* appears to have been justified.

The Manzanita Mountains coelacanth remains, poor as they are, indicate the presence of the Coelacanthidae in pre-Permian deposits; thus, detached coelacanth scales should not be assigned to the Rhabdodermatinae merely because they happen to occur in rocks of Pennsylvanian age.

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