DONALD BAIRD

Studies on Carboniferous Freshwater Fishes

Studies on Carboniferous Freshwater Fishes

DONALD BAIRD[1]

ABSTRACT

New material from Nova Scotia, Illinois, and Pennsylvania casts light on certain fish taxa and faunas found in freshwater deposits of the Pennsylvanian and latest Mississippian. The earliest representative of the palaeoniscoid family Haplolepidae is described as *Haplolepis (Parahaplolepis) canadensis*, a new species distinguished from *H. tuberculata* by the shape of its frontals and from *H. anglica* by their tuberculate sculpture. The presence of *H. (P.) canadensis* in the early Pennsylvanian (Westphalian A) of Nova Scotia implies a separation of the subgenus *Parahaplolepis* from the basal haplolepid stock in Mississippian time. The lungfish genus *Ctenodus*, hitherto extremely rare in North America, is in fact represented by its three European species, each in strata of appropriate age: the primitive *C. interruptus* in the latest Mississippian (Namurian A) of Nova Scotia, the intermediate *C. cristatus* in the middle Pennsylvanian (early Westphalian D) of Illinois, and the specialized *C. murchisoni* in the late Westphalian D of Nova Scotia. *Cteno-*

dus, Conchopoma, and *Megapleuron* constitute a highly anomalous lungfish assemblage in the Mazon Creek deposits of Illinois. Pennsylvanian records of the acanthodian genus *Gyracanthus* in the Western Hemisphere, previously limited to two specimens, can now be extended by Nova Scotian finds dating from the Namurian A and Westphalian A and B. An unexpectedly late survival of *Gyracanthus* into Westphalian D time is documented by spines from Illinois; *Trichorhipis praecursor* is reinterpreted as a prepectoral spine of *Gyracanthus*. The previously unreported fish fauna of the classic locality at Cannelton, Pennsylvania, comprises the coelacanth *Rhabdoderma elegans*, the crossopterygian *Rhizodopsis* cf. *robustus*, the palaeoniscoids *Haplolepis* aff. *ovoidea* and *Elonichthys peltigerus* and a third genus resembling *Commentrya*, and the sharks *Xenacanthus compressus* and *Bandringa rayi*. The latter genus is shown to be a ctenacanthoid derivable from *Goodrichthys*, and of freshwater rather than marine habitat.

INTRODUCTION

Over the past quarter-century my search for Carboniferous tetrapods, primarily in Nova Scotia and the upper Ohio River drainage, has produced a considerable quantity of freshwater fish material, some of which provides new distribution records and affords useful additions to our knowledge of phylogeny and faunistics. The present paper selects for examination a few taxa

[1]Research Associate, the American Museum of Natural History; Director, Museum of Natural History, Princeton University.

and faunas that were previously rare or little known, noting their biogeographic significance and placing them in a biostratigraphic framework that has undergone significant refinement in recent years. Except as noted, the bone-terminologies employed are those that have been conventionally applied to the various groups of fishes discussed. This usage is intended to facilitate comparison with the previous literature and does not imply commitment as to homologies, for the deep and troublesome problems of homologies in the cranial elements of fishes are obviously beyond the scope of this paper. These studies are dedicated to my friend and colleague Dr. Rainer Zangerl in acknowledgment of his important contributions to the field of Carboniferous ichthyology.

ACKNOWLEDGMENTS

Besides the benefactors mentioned *passim* in the text, the following helped by the loan of specimens: Dr. Robert L. Carroll and Ms. Liza Alison of the Redpath Museum, Dr. A. Gordon Edmund of the Royal Ontario Museum, Mr. Donald Hoff of the William Penn Memorial Museum, Drs. Nicholas Hotton III of the National Museum of Natural History, Smithsonian Institution, Eugene S. Richardson, Jr. of the Field Museum of Natural History, Bobb Schaeffer of the American Museum of Natural History, and Keith S. Thomson of the Yale Peabody Museum. Useful information and advice has come from discussions with Drs. S. Mahala Andrews, Edward S. Belt, Mr. Gerard R. Case, Drs. Richard Lund, Eugene S. Richardson, Jr., Hans-Peter Schultze, Rainer Zangerl, and Jiri Zidek. Figures 5 and 7 were photographed by Dr. Michael Archer, figures 4 and 9A by Mr. Willard Starks; the rest and the drawings are my work.

ABBREVIATIONS

AMNH, the American Museum of Natural History
FMNH, Field Museum of Natural History
PU, Museum of Natural History, Princeton University
RM, Redpath Museum, McGill University
USNM, National Museum of Natural History, Smithsonian Institution
WPMM, William Penn Memorial Museum
YPM, Peabody Museum, Yale University

EARLIEST RECORD OF THE PALAEONISCOID *HAPLOLEPIS*

Through the courtesy of Mr. Eldon George, proprietor of the Parrsboro Rock and Mineral Shop, the Princeton University Museum of Natural History has received a second specimen of the oldest known haplolepid fish. This specimen, the major portion of a skull roof (PU 18583), was collected by him in 1962 at the same locality and within an inch or so of the same horizon as the skull roof that I described the same year under the name *Haplolepis (Parahaplolepis)* aff. *anglica*. Its source is an outcrop of steeply dipping carbonaceous shale on the west shore of Parrsboro Inlet at the mouth of Whitehall Creek, south of the town of Parrsboro, Cumberland County, Nova Scotia.

As was noted in the original publication (Baird, 1962) the source bed lies in the upper, more carbonaceous part of the Parrsboro Formation, which has been dated as Westphalian A, Early Pennsylvanian, on the basis of plant megafossils, nonmarine pelecypods, and arthropods. More recent stratigraphic revision by Belt (1964, 1965) placed the Parrsboro Formation in the Mabou Group (with which the Riversdale Group of earlier authors is synonymized), and assigned the "gray" facies of the upper Parrsboro to the later two-thirds of Westphalian A time with its uppermost part perhaps extending into the earliest Westphalian B. A dating of late Westphalian A is thus indicated for the fish fauna of the Parrsboro Inlet locality. For a recent summary of the stratigraphy, sedimentology, paleontology, and paleoecology of the Parrsboro area see Carroll et al. (1972, pp. 58-64).

When compared with the skull roof described in 1962 (PU 17058) the new specimen (fig. 1A) appears relatively narrower, but this is largely the result of its being less flattened. In other respects the two are closely comparable, the chief difference being that the posterolateral lappet of the dermopterotic in PU 18583 is sculptured with a series of long rugae, which are aligned more or less along radii from the center of the skull roof. This difference is well within the range of individual variation to be expected in a species of *Haplolepis*, as has been demonstrated by analysis of a sample of the *H. tuberculata* population from Linton, Ohio (Baird, 1962, table 1).
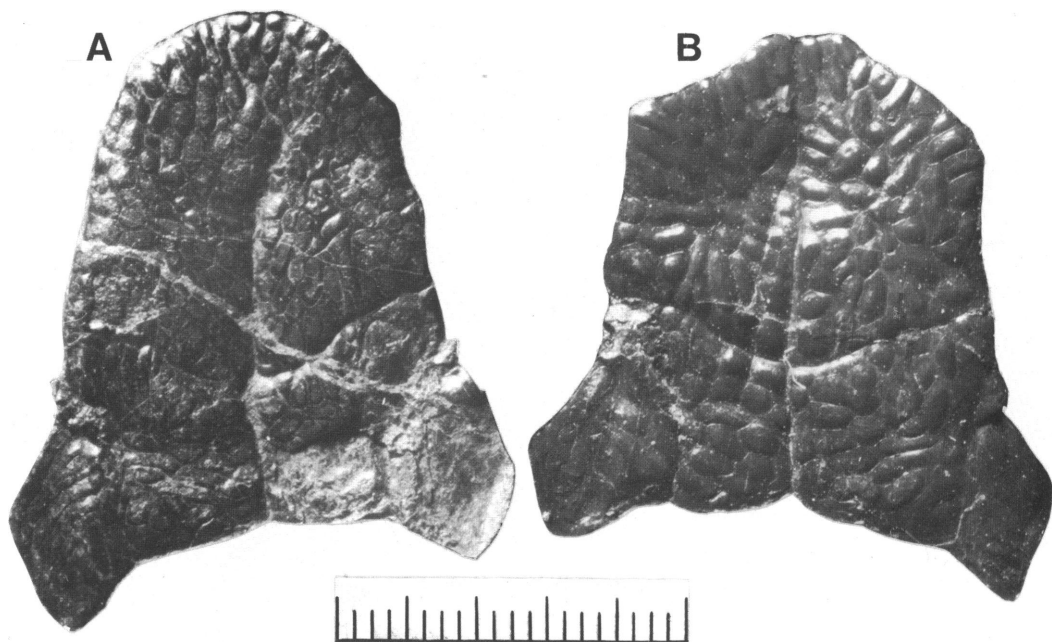
FIG. 1. A. Paratype skull roof of *Haplolepis* (*Parahaplolepis*) *canadensis*, new species, from Parrsboro (PU 18583); B. *H.* (*P.*) cf. *canadensis* from Joggins, Nova Scotia (PU 21708). Scale 5 mm. long.

A third skull roof (PU 21746), taken at the same spot by my field party in 1974, is readily identifiable as the same species but is too badly damaged to provide additional information on its morphology.

On the shore at Joggins in Cumberland County, a classic locality for fossils since the 1840s, my 1973 party found a skull roof of *Haplolepis* (PU 21708) that shows strong similarities to those from Parrsboro Inlet. Its source bed is the prominent bituminous layer about 20 feet (6 m.) above the Forty Brine coal seam. The matrix is nearly identical with that of the Parrsboro fishes: a carbonaceous shale of lacustrine origin, layered with shells of freshwater pelecypods and peppered with ostracodes—a lithology known colloquially as a "clam-coal." This new find is the second species of *Haplolepis* from Joggins, for a specimen identified tentatively as *H.* (*Haplolepis*) cf. *corrugata* (Newberry) has been found in the calcareous roof of the Forty Brine seam (Baird, 1962). The Forty Brine is a

unit of Logan's Division Four and Bell's Joggins Formation of the Cumberland Group; its age is Westphalian B, probably early Westphalian B. A current and comprehensive account of the Joggins fossil locality appears in Carroll et al. (1972, pp. 64-80).

The skull roof from Joggins (fig. 1B) resembles those from Parrsboro (fig. 1A and Baird, 1962, fig. 1) in the tuberculate sculpture of its frontals but differs in having a more angular, gambrel-roof profile. As in PU 18583 the otic canal of the lateral line system divides the main body of the dermopterotic, which is ornamented with tubercles and short rugae, from the postero-lateral lappet, which bears what Westoll (1944) terms a "groove-and-terrace" ornament in echelon. Well-defined slits mark the three pairs of pit-lines (anterior, middle, and posterior), which occupy the same positions as they do in the type species of the subgenus *Parahaplolepis*, *H.* (*P.*) *tuberculata* (compare C and D, fig. 2). A thin spot, most of which lies to the left of the

interfrontal suture, represents the pineal macula.

The Parrsboro *Haplolepis* (as noted earlier) and the new specimen from Joggins belong to the subgenus *Parahaplolepis* and show close affinities with *H. (P.) anglica* (Traquair) from the Ash Coal (earliest Westphalian C) of Longton, Staffordshire—and particularly with specimens from the Low Main Coal (late Westphalian B) of Newsham, Northumberland, which Westoll (1944) described as *H. (P.) aff. anglica.* Unfortunately, taxonomic evaluation of the differences between haplolepids from these four localities in Nova Scotia and England is made difficult by the small size of the samples available, for the Longton fish is known from a single specimen and the Newsham fish from two, the better of which shows only part of the sculpture pattern.

Now that additional specimens of the Nova Scotia *Parahaplolepis* are available we have better assurance that its distinctive sculpture pattern of coarse tubercles over most of the frontal area is characteristic of the taxon. So far as one can tell the Newsham fish is similarly ornamented. The type specimen of *H. (P.) anglica* from Longton, in contrast, bears coarse rugae arranged *en chevron* on the anterior area of the frontals and longitudinally on the posterior part. In terms of the differences between established species of *Haplolepis*, the *Parahaplolepis* from Parrsboro appears to merit recognition as a distinct species.

CLASS OSTEICHTHYES

SUBCLASS ACTINOPTERYGII

INFRACLASS CHONDROSTEI

ORDER PALAEONISCIFORMES

SUBORDER PALAEONISCOIDEI

FAMILY HAPLOLEPIDAE WESTOLL, 1944

HAPLOLEPIS MILLER, 1892

SUBGENUS *PARAHAPLOLEPIS* WESTOLL, 1944

Haplolepis (Parahaplolepis) canadensis
Baird, new species

Type Specimen. PU 17058, a skull roof.

Locality and Horizon. West shore of Parrsboro Inlet near mouth of Whitehall Creek, south of Parrsboro, Cumberland County, Nova Scotia. Gray facies of the upper Parrsboro Formation, Mabou Group, Lower Pennsylvanian (Westphalian A).

Diagnosis. A *Parahaplolepis* distinguished from *H. (P.) tuberculata* by the more rounded anterior and oblique posterior margin of the frontals, and from *H. (P.) anglica* by the tuberculate sculpture of the frontals.

Referred Specimens. PU 18583 and 21746, skull roofs from the type locality and horizon.

Discussion. Because of the more angular anterior margin in the single specimen at hand, the *Parahaplolepis* from Joggins is assigned only provisionally to the same species. The specimens from Newsham described by Westoll as *H. (P.) aff. anglica* appear to be intermediate in form (as they are in time) between *H. canadensis* and *H. anglica*. Until better material becomes available their specific status cannot be determined more precisely.

As the earliest known species of its family, *Haplolepis canadensis* might be hoped to afford some clue to the morphology of the family's basal stock, the "common ancestor X" which Westoll (1944, pp. 61-63) reconstructed by retro-extrapolation. So far as the material permits comparisons (fig. 2), *H. canadensis* agrees with Westoll's "X" in having (evidently) a long dermosphenotic. The posterior embayment of its skull roof suggests that the extrascapulars and posttemporals were paired and transversely aligned as in *H. tuberculata* and in "X." On the other hand the parietal and dermopterotic are not separate elements as in the type species of the subgenus *Haplolepis*, "X," and all normal palaeoniscoids, but instead are represented by a single bone as in the subgenus *Parahaplolepis* and in *Pyritocephalus.*

Westoll called this single element the dermopterotic and postulated that loss of the parietals had caused the dermopterotics to expand medially until they met in the midline of the skull roof. However, in *Haplolepis canadensis* the posterolateral lappet (fig. 2C, lap) is conspicuously differentiated from the main body of the dermopterotic by its sculpture pattern and its thinness: it lies like a piedmont below the tubercle-hills of the central area. It looks like a neomorph, an incremental extension of the bone. This condition in the oldest known representative of *Parahaplolepis* suggests an alternative interpretation: that the so-called dermopterotics
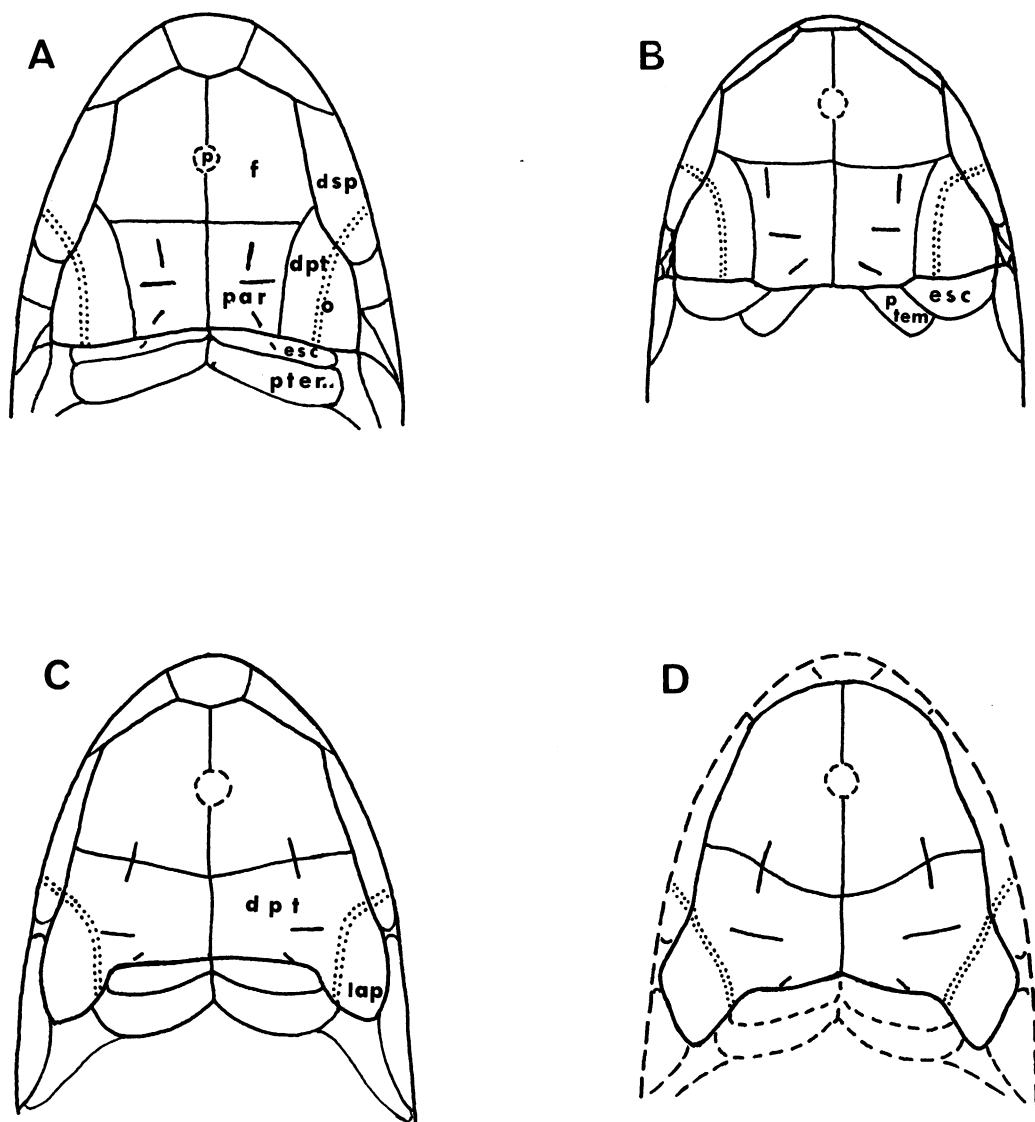
FIG. 2. Skull roof diagrams of certain Haplolepidae. A. hypothetical ancestor "X." B. *Haplolepis* (*H.*) *ovoidea*, type species of the subgenus *Haplolepis*. C. *H.* (*P.*) *tuberculata*, type species of the subgenus *Parahaplolepis* (all after Westoll). D. *H.* (*P.*) *canadensis*, new species. *dpt*, dermopterotic; *dsp*, dermosphenotic; *esc*, extrascapular; *f*, frontal; *lap*, lappet; *o*, otic canal; *par*, parietal; *p*, pineal macula; *ptem*, posttemporal.

of *Parahaplolepis* (and, by inference, of *Pyrito-cephalus* as well) are in fact parietals that have developed lappets to compensate for the loss of the true dermopterotics.

Another point perhaps worth noting is that in *Haplolepis canadensis* the anterior pit-line crosses the boundary between frontal and "dermop-terotic" (i.e., parietal as reinterpreted) as it does in *H.* (*P.*) *tuberculata* instead of being confined to the parietal as it is in other haplolepids and their hypothetical ancestor "X." These compari-sons make it clear that the subgenus *Parahaplo-*

lepis must have separated from the basal haplolepid stock and evolved its distinctive morphology a considerable time before its first appearance in the early Pennsylvanian, and therefore that the origin and radiation of the Haplolepidae must have occurred well back in Mississippian time.

AMERICAN RECORDS OF THE DIPNOAN *CTENODUS*

The extreme rarity of the lungfish genus *Ctenodus* in the American Coal Measures, in contrast to its relative abundance in those of Europe, has been pointed out by Romer and Smith (1934, p. 702). Despite frequent references to the name in the older literature, most of the specimens so assigned have proved on reexamination to belong to the related genus *Sagenodus*, the common and ubiquitous lungfish of the Carboniferous and Lower Permian. The efforts of many collectors over the subsequent decades have only reinforced the validity of Romer and Smith's observation. For this reason a new record of *Ctenodus* in the American Carboniferous merits description, along with a review (in chronological order) of the other occurrences of the genus in this hemisphere.

GRAND ETANG, NOVA SCOTIA

Diagnostic cranial material of *Ctenodus* was collected by my field party in 1969 near Grand Etang, Inverness County, on the northwest shore of Cape Breton Island, Nova Scotia. A detailed discussion of this locality and its lithologies and fauna has been published in Carroll et al. (1972, pp. 40-45) and need not be repeated here. The *Ctenodus* material was found in a hard gray dolomitic limestone of freshwater origin in which occur bones of embolomerous amphibians and crossopterygians, ctenacanthid shark spines, scraps of the eurypterid *Dunsopterus*, nonmarine pelecypods, plant fragments, and seeds. The source bed lies within the Pomquet Formation of the Mabou Group and is dated by miospores as latest Mississippian, equivalent to the Namurian A of Europe (not earliest Pennsylvanian as previously reported).

In the following description the bone nomenclature of Westoll (1949) is used "without prejudice." White (1965) has proposed a number of modifications to Westoll's terminology for a variety of reasons: appropriateness of name (as Z for H), consistency of numerical sequence (as Y_2 for Y_1 and vice versa), and disagreement on homology (as L_2 for M). Except in cases of disputed homology, this renaming of elements in what is already a largely arbitrary system appears to provide possible clarification at the cost of certain confusion. "Therefore doth Job open his mouth in vain; he multiplieth words without knowledge" (Job 35:16). The whole question of nomenclature and homologies in dipnoan cranial bones is already more than sufficiently confused.

As shown in figure 3 the *Ctenodus* specimen (PU 20466) consists of the major elements of the left half of a skull roof together with element B of the medial series. Weathering has removed some bone from the posterior part so that all of
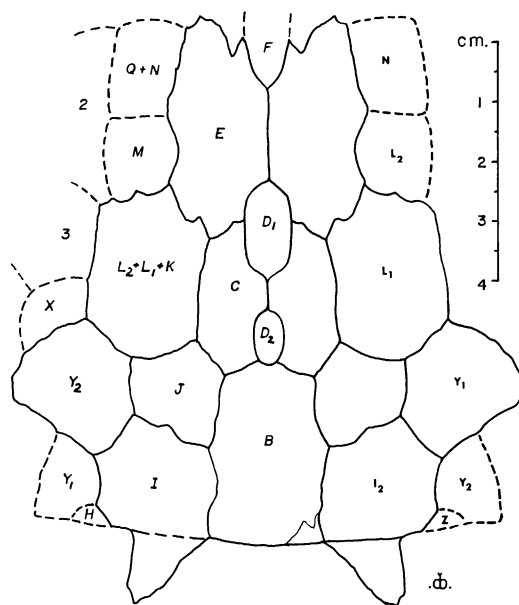

FIG. 3. Skull roof of *Ctenodus interruptus*, PU 20466, from Grand Etang, Nova Scotia. Right side restored as a mirror image of the left; restoration from other specimens indicated in dashed lines. Note supernumerary D_2 plate. Bone nomenclature of Westoll (1949) indicated on the left side, that of White (1965) on the right. (This specimen described and figured by Schultz, 1976, as *Ctenodus cristatus*.)

element J and adjacent parts of B, C, $L_2 + L_1 +$ K, Y_2, and I are represented by impressions of their ventral surfaces. For purposes of illustration the elements of the right side are restored as mirror images in figure 3; facets for articulation mark the positions of now-missing peripheral plates that are restored in dashed outline.

Comparison with the skull roofs of *Ctenodus cristatus* and *C. interruptus* illustrated by Watson and Gill (1923, figs. 21, 23; see also Thomson, 1965, fig. 2) establishes the generic identification; the species, however, could not be determined without the evidence of the toothplate described below. One anomaly, however, is conspicuous in this specimen: the posteromedial margin of plate C and the anterior margin of B are embayed to accommodate a median element of oval shape. As this supernumerary element occurs in tandem with a normal plate D, the latter may be designated D_1 and the new plate D_2.

This anomaly has not, to my knowledge, been recorded previously in *Ctenodus* (cf. Westoll, 1949, p. 152). However, several authors (Westoll, 1949, fig. 2A; White, 1965, fig. 19; Ørvig, 1961, fig. 7A) illustrated specimens of the Devonian species *Dipterus valenciennesi* (=*platycephalus*) in which an anomalous median element occupies precisely the same position as the D_2 plate in the *Ctenodus* from Grand Etang (Ørvig designated this plate C^1). A homologous plate termed the "frontal central" occurs in the earliest known ctenodontid, *Nielsenia nordica* from the Late Devonian of Greenland (Lehman, 1959, fig. 1). Although abnormalities in the cranial pattern of *Ctenodus* are rare, as Westoll pointed out, nevertheless the presence of a D_2 plate in this specimen is probably best regarded as an individual anomaly.

On the same slab with the skull roof is a clavicle ("cleithrum" of Watson and Gill) 48 mm. long. Its small size correlates with that of the skull roof (which is less than half the size of Watson and Gill's specimen) and indicates that the two probably came from the same individual.

A left pterygoid toothplate (PU 21741, fig. 4), associated with a typical scale, was found in conglomeratic limestone at the same locality by R. W. Selden in 1974. Its outer margin has been destroyed by tidal erosion, and it shows heavy premortem wear in the concave central area. Eleven denticulate ridges (the last two nearly obliterated by wear) radiate from the postero-medial apex; on each ridge the denticles are strongly compressed in the direction of the ridge axis. There appear to have been 15 or 16 denticles per ridge, though abrasion of the inner ends and loss of the outer ends of the ridges makes an exact count impossible.

The small number and radiate arrangement of the ridges, and the longitudinal compression of the denticles, distinguish this toothplate from that of the common species, *Ctenodus cristatus* Agassiz, and identify it as *Ctenodus interruptus* Barkas, a primitive species that was previously known only from the Carboniferous of Scotland. Romer and Smith (1934) made *C. interruptus* the type species of their genus *Prosagenodus*, but Westoll (1949, p. 152) found such a separation unjustified and considered Barkas's species to be "probably a very primitive *Ctenodus*." Thomson (1965), who has recently redescribed the species and illustrated additional material, concurs in this view. If the skull roof and toothplate from Grand Etang are conspecific (as seems highly probable) the American evidence supports Westoll's interpretation.

As recorded by Henrichsen (1972, p. 10) the range of *Ctenodus interruptus* in Scotland is from the Pumpherston Oil Shale of the Calciferous Sandstone Series (Lower Carboniferous, Visean) of Broxburn, West Lothian, to the South Parrot Coal (Upper Carboniferous, Namurian, Zone E_2) of Niddrie, Midlothian. The Grand Etang occurrence overlaps the upper part of this range, at a level close to the Mississippian-Pennsylvanian boundary.

JOGGINS, NOVA SCOTIA (ERRONEOUS RECORD)

The reported occurrence of *Ctenodus* in the Joggins Formation (Westphalian B) at Joggins, Cumberland County, Nova Scotia, is now known to have been based on a misidentification. The specimen in question, RM3073 in the Redpath Museum of McGill University, Montreal, was originally described by Principal Dawson (1868, pp. 209-210, fig. 53) as *Conchodus plicatus* and interpreted as a "selachian fish of considerable

FIG. 4. Upper left toothplate of *Ctenodus interruptus*, PU 21741, from Grand Etang, Nova Scotia; ×1.

size." Smith Woodward (1891, p. 255) recognized its dipnoan affinities and concluded that the species "seems to be founded upon an abraded dental plate of *Ctenodus.*" This identification was accepted by Romer and Smith (1934, p. 702), but a restudy by Sternberg (1941) has demonstrated conclusively that Dawson's specimen is in fact a left palatal (i.e., pterygoid) toothplate of *Sagenodus.* As the type specimen appears to be too fragmentary for positive specific identification, *Sagenodus plicatus* (Dawson) must be dismissed as a *nomen vanum*, a useless name—although it is the earliest name based on an American specimen of the genus.

MAZON CREEK, ILLINOIS

The classic Mazon Creek fauna occurs in nodules in the Francis Creek Shale which overlies the Number 2 (Wilmington or Colchester) Coal of the Carbondale Formation. This seam is corre-

lated with the Lower Kittanning Coal of Pennsylvania (Smith et al. 1970, p. 61); its time-stratigraphic position is early Westphalian D, Middle Pennsylvanian (Darrah, 1969, p. 64). Three genera of dipnoans are represented in the fauna but their geographic distribution is not uniform. *Ctenodus* is the common (indeed, if not the only) lungfish found in the old collecting area along Mazon Creek in Grundy County; *Conchopoma* predominates in the Braidwood area in Will County, where scales of large lungfishes are infrequent (Denison, 1969); and *Sagenodus* appears to be absent, its niche being occupied by *Megapleuron* (Schultze, 1976).

The polynominal history of the large Mazon Creek lungfish has been reviewed by Romer and Smith (1924, p. 702) and Olson (1946, p. 297). As many as nine nominal species, which had been based on isolated scales, were synonymized by Romer and Smith under the name *Sagenodus occidentalis* (Newberry and Worthen); but a spe-

cies based on such material has minimal validity and even the generic assignment is extremely doubtful, since the scales of *Sagenodus* and *Ctenodus* are virtually indistinguishable. *Sagenodus occidentalis* is therefore no better than a *nomen vanum*, useless in taxonomy. As all the large-sized cranial material is identifiable as *Ctenodus*, the large scales probably pertain to that genus rather than to *Sagenodus*.

Undoubted *Ctenodus* is represented by several diagnostic specimens collected along Mazon Creek. A left palatal toothplate, YPM 3261 in the Peabody Museum of Yale University, constitutes the type specimen of "*Sagenodus*" *cristatus* Eastman (1903). This toothplate is not distinguishable from that of the type species, *Ctenodus cristatus* Agassiz: thus the two specific names are synonymous homonyms. A much larger individual is represented by a left mandibular toothplate in the National Museum of Natural History (USNM 14834). Other identifiable elements include a quadrate (PU 19515) and a characteristic *E* plate (YPM 3262) that is evidently the "narrow and elongate cranial plate, having the dimensions of 5 by 10 cm., and belonging to the same [Yale] collection," which Eastman (1903, p. 189) referred to his species "*S.*" *cristatus*.

In summary, the dipnoan fauna of the Mazon Creek deposits (*sensu lato*) is highly anomalous. It includes, as a not-uncommon element, the aberrant genus *Conchopoma* which is known from only two other localities in the Carboniferous, the canneloid shale of Linton, Ohio, and the Danville Bonebed of Illinois (Schultze, 1975). *Sagenodus*, which one would expect to be common, is not in evidence; its place is taken by *Megapleuron*, which has been found nowhere else in the Western Hemisphere. *Ctenodus*, which is known from only two other localities in the American Carboniferous, is relatively common at Mazon Creek.

GLACE BAY, NOVA SCOTIA

The third and geologically youngest occurrence of *Ctenodus* in this hemisphere consists of dental plates and head bones of an individual collected in the roof shales of the Phalen Coal at Glace Bay in the Sydney coalfield of Cape Breton County, Nova Scotia. This specimen (Geological Survey of Canada no. 8813) has been described and illustrated by Sternberg (1941), to whose account little need be added. An additional toothplate from Sydney is no. 1976.37 in the Royal Scottish Museum, Edinburgh. The species represented is *Ctenodus murchisoni* Agassiz *in* Ward (1890), an advanced form in which the toothplates bear as many as 20 subparallel ridges, in contrast to the more radiate arrangement of 12 to 14 ridges which characterizes the type species *C. cristatus*.

The Phalen Coal falls in the lower subzone of Bell's *Ptychocarpus unitus* Zone, which is equated approximately by Bell (1938, p. 1) with the Westphalian D of Europe. This assignment is supported by the abundant presence of the freshwater pelecypod *Anthraconauta phillipsii* (the eponymous species of the Phillipsii Zone) in the roof shale from which the lungfish was collected.

In North America, then, *Ctenodus* is seen to range from late Mississippian to somewhat past the middle of Pennsylvanian time (Westphalian D) and to be represented by three species that also occur in beds of approximately equivalent age in Europe. These three species—*interruptus*, *cristatus*, and *murchisoni*—occur in a temporal sequence that reflects their phylogenetic status of primitive, "normal," and advanced. Despite this evolutionary diversity and despite the considerable time-span represented, however, the known record of the genus in the Western Hemisphere is limited to eight diagnostic specimens from only three localities.

NEW OCCURRENCES OF THE ACANTHODIAN *GYRACANTHUS* IN NOVA SCOTIA

In 1962 I described a fin-spine of *Gyracanthus* from the Parrsboro fish locality, noting it as the second (and the first unequivocal) record of this genus in the Pennsylvanian of North America. Since that date *Gyracanthus* has been found at two additional localities in Nova Scotia, and the type specimen of Dawson's disputed species *G. duplicatus* has been made available for study by the Redpath Museum. These occurrences, which will be surveyed in ascending stratigraphic sequence, constitute the total known record of *Gyracanthus* in the Upper Carboniferous of the Western Hemisphere.

GRAND ETANG, INVERNESS COUNTY

As noted above (p. 6) the Pomquet Formation exposed along the Grand Etang shore is dated as latest Mississippian, equivalent to the Namurian A of Europe. The presence of *Gyracanthus* spines in the gray conglomeratic limestone was first reported by me in Carroll et al. (1972, p. 42) and additional material has since been collected.

The best specimen, the small spine (PU 18806) shown in figure 5, is rather water-worn and slightly distorted by compression. If the missing proximal and distal ends were present its total length would be about 160 mm.; its anteroposterior diameter is 15 mm. at mid-length. The denticulate ridges are spaced at 1 mm. intervals in the central area, more widely in the proximal part of the ornamented surface and more closely toward the tip. On the posterior edge the medullary cavity communicates with the exterior by a slit that runs nearly the full length of the spine as preserved. Larger spines from the same layer include PU 21738, which is 172 mm. long as preserved and was probably at least 230 mm. long originally, and isolated fragments (PU 18806 A,B). These spines are morphologically typical of the genus *Gyracanthus* but at present they cannot be assigned to species in any biologically meaningful way.

PARRSBORO, CUMBERLAND COUNTY

The small spine I described in 1962 (pp. 25-26, fig. 2) was found in association with the type specimen of *Haplolepis canadensis* described above. Its source bed in the upper or "gray" facies of the Parrsboro Formation is dated as late Westphalian A.

MARGAREE HARBOUR, INVERNESS COUNTY

The fish faunule of Margaree Harbour occurs in a platy, buff-colored sheet sandstone that crops out immediately southwest of the neck connecting the mainland with a rocky promontory known locally as "The Monster." This sandstone forms part of the Port Hood Formation, which has been dated as Westphalian A on paleobotanical evidence. Belt (in Carroll et al. 1972, pp. 37-39) attributed a fluvial origin to the Port Hood sandstones: in some cases upriver sedimentation is postulated, in others, splay-sand deposition by distributary streams in a deltaic environment. Appreciable transportation before burial is indicated by the complete dissociation of the fish debris.

The first *Gyracanthus* spine from Margaree Harbour (PU 18732) was discovered in 1964 by a vacationer, Jeremy Bonner of Princeton, who generously presented it to the museum. A second spine (PU 19329) was similarly donated by James Alexander Munro. Under Mr. Bonner's guidance my field party collected a third pectoral spine and a prepectoral spine (PU 21739, 21740).

Of the two more nearly complete spines PU 21739 (fig. 6A) shows the slightly curved, elongate-conical form typically seen in *Gyracanthus*, whereas PU 19329 (fig. 6B) resembles the spine
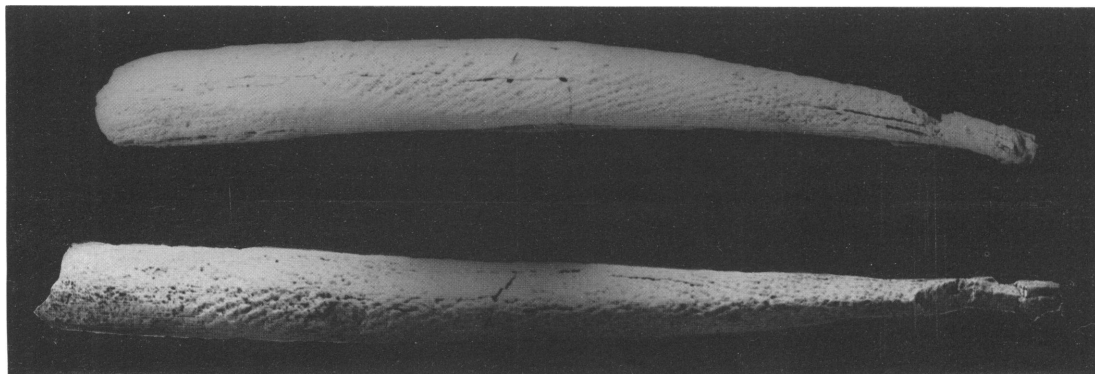

FIG. 5. Pectoral spine of *Gyracanthus* sp., PU 18806, from Grand Etang, Nova Scotia. Length 136 mm. as preserved.
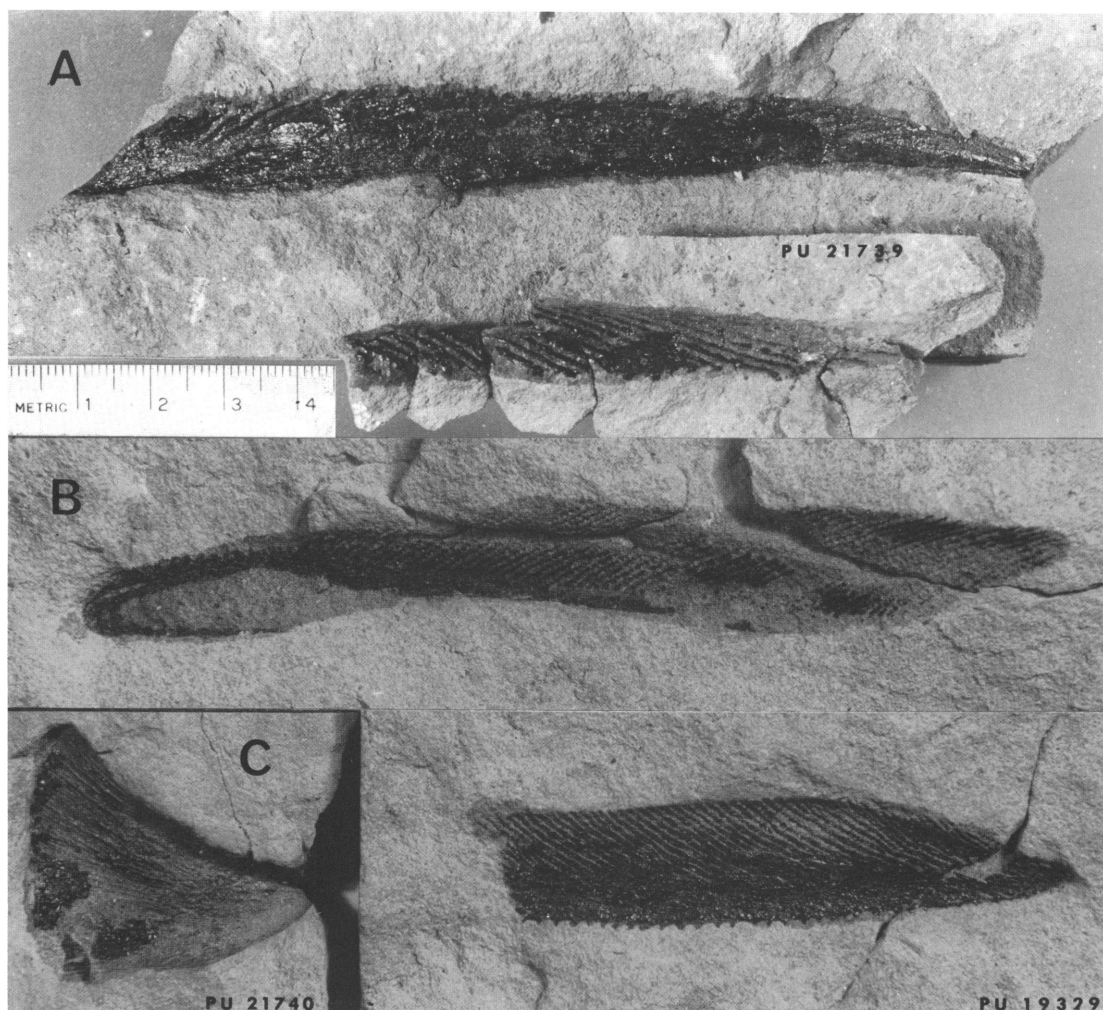
FIG. 6. Pectoral spines (A, B, both in partial counterpart) and prepectoral spine (C) of *Gyracanthus* sp. from Margaree Harbour, Nova Scotia.

from Parrsboro (PU 17059) in being dorsoventrally compressed with a more abruptly tapering point resembling that of a slant-point knife or scramasax. The prepectoral spine (fig. 6C) is of low conical form, laterally compressed and with a concave posterior margin. Except in the region near the tip, where a few scattered tubercles are visible, its surface is ornamented with fine ridges and grooves. In his recent revision of the Gyracanthidae, Miles (1973, pp. 185-190) interpreted this element in both *Gyracanthus* and *Gyracanthides* as the homologue of paired prepectoral

spine 3 in climatioids. Although the systematic position of the Gyracanthidae remains uncertain, their closest affinities appear to lie with the suborder Climatioidea.

Scattered over the same sandstone surfaces as the *Gyracanthus* spines were found scales and an operculum of the lungfish *Sagenodus* (PU 19351); a maxilla and other bones and scales of a rhizodontid crossopterygian, probably *Rhizodopsis* ("*Strepsodus*" of Dawson) (PU 18811); debris of *Megalichthys* and palaeoniscoids; and carbonized plant fragments.

JOGGINS, CUMBERLAND COUNTY

Dawson described the species *Gyracanthus duplicatus* in 1868 (p. 210, fig. 55), illustrating it with a woodcut which is impressionistic rather than carefully drawn. As a result Newberry (1889, p. 124) was understandably skeptical about the generic assignment. Restudy of the type specimen, however, confirms Dawson's identification.

As shown in figure 7, the spine (RM3074) in the Redpath Museum of McGill University is preserved in a layer of coaly shale which exhibits a rectangular fracture and an abundance of finely disseminated pyrite. Pyrite has evidently infiltrated the medullary cavity of the spine itself, and the expansion caused by its chemical breakdown has disrupted the specimen somewhat. Below the coaly layer (or perhaps above, one cannot be sure) the matrix consists of a brownish gray calcareous shale containing nonmarine pelecypods, ostracodes, and a little plant debris. This matrix resembles (for example) the roofing shale of the Forty Brine coal seam; and Dawson (1868, p. 209) stated that his fish material was found "usually in the roof-shales"; but he failed to specify the stratigraphic position of *Gyracanthus*

duplicatus within the Joggins section. In any case it comes from the Joggins Formation and is Westphalian B, probably early Westphalian B, in age.

The spine lies one-third embedded with its proximal end to the left and is 10 cm. long as preserved, a centimeter or more of the distal end being broken away. The anteroposterior diameter, much exaggerated in Dawson's drawing, is 13 mm. For the distal half of its length the posterior edge has become broken and displaced upward since burial, producing an artificial groove along the side. Along the leading edge there are five ridge-apices per centimeter. At mid-length the ridges make an angle of about 30 degrees with the long axis of the spine; more distally this angle decreases and is about 20 degrees for the last clearly defined ridge. In proportion to its size this spine is appreciably more coarsely ridged than the other spines described above, but the taxonomic significance of this feature cannot be assessed. Until much more is known about the anatomy of *Gyracanthus* its various nominal species, based on the typology of spines, will have little biological significance. For the present, then, we may as well let Dawson's form-species stand.
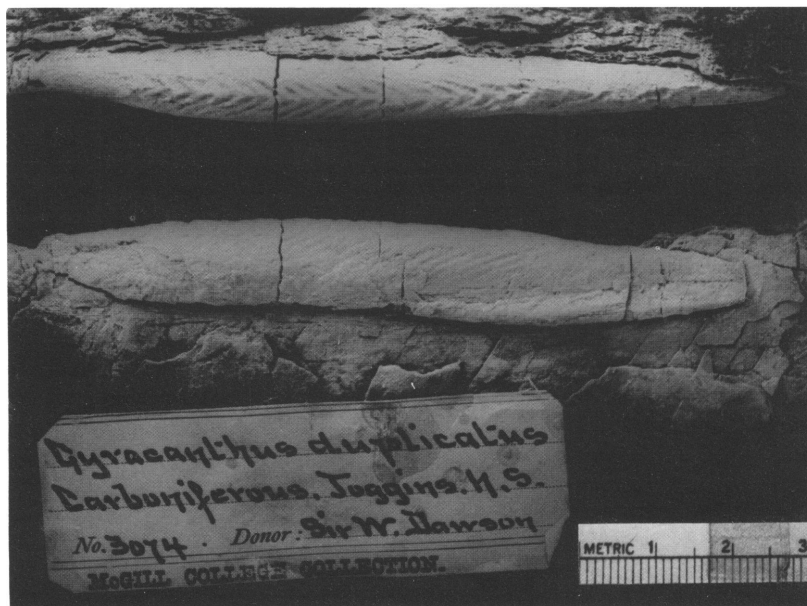

FIG. 7. Type specimen of *Gyracanthus duplicatus* Dawson, RM 3074, from Joggins, Nova Scotia.

On a 1972 visit to the Fundy Museum in Joggins, I identified a short section of a large *Gyracanthus* spine among the fossils on display. While the precise source of this specimen is not recorded, there seems to be no doubt that it was found locally and thus, like Dawson's specimen, comes from the Joggins Formation.

ADDENDUM

Gyracanthus in the Carbondale Formation of Illinois

After this manuscript was submitted a suite of 13 *Gyracanthus* spines, marking the latest occurrence of the genus in North America, came to light at the Field Museum of Natural History. Neither time nor space permits an adequate description of this material here, but its existence and significance should be recorded. The specimens are catalogued as FMNH PF 2127 and PF 8358-8368, all but the first being from the great collection donated by Mr. Jerry Herdina shortly before his death. I am obliged to Eugene S. Richardson, Jr., for the following source data:

"These Gyracanthi are from [Peabody Coal Company] Pit 15, which is in Sec. 19, T. 31 N., R. 9 E., Kankakee County. On [W. H.] Smith's map (1968, Illinois Survey Circular 419) this would seem to be Coal 2, so that the shale would be Mecca Quarry shale [as described by Zangerl and Richardson, 1963].... The wedge of deltaic Francis Creek Shale has pinched out this far south, so the Mecca Quarry Shale should be present over Coal 2. The Gyracanthi occur in a humulite facies such as we had at Garrard Quarry ... an inland fresh-water deposit. *Megalichthys* is associated."

The spines, three of which are prepectorals, are dissociated and variably crushed but otherwise excellently preserved. On slab PF 8358 a prepectoral and a pectoral spine lie touching, but as the latter had been split lengthwise and somewhat abraded before burial the association between them is fortuitous rather than organic. The date of this occurrence, early Westphalian D, is significantly later than the Nova Scotia records described above.

The recognition that undoubted *Gyracanthus* occurs in some numbers in the Carbondale Formation of Illinois prompts a re-examination of the specimen from Mazon Creek upon which Zangerl (1973, p. 13, pl. 1) based the nominal genus and species *Trichorhipis praecursor*. With some reservations Zangerl interpreted this specimen (FMNH PF 5729) as the pectoral fin of a phalacanthous shark which foreshadows the modern level of elasmobranch organization. The advent of a modern type of shark so early as the Middle Pennsylvanian would be as significant as it is unexpected, and strong substantiating evidence for it may reasonably be called for.

The specimen, preserved as a natural mold in ironstone, is a flattened, roughly triangular object that bears fine striae radiating from apex to base and a shagreen of denticles concentrated toward the apex. Although the radii have been interpreted as ceratotrichia there is no evidence that they are discrete rods rather than superficial features on a unitary element. By the describer's admission "the cartilaginous fin skeleton cannot be made out in any detail": in my opinion it cannot be made out at all.

Comparison with the prepectoral spines of equivalent age from Pit 15, with the example from Nova Scotia (fig. 6C), and with the type species of *Gyracanthides murrayi* Woodward (1906, pl. II, fig. 1a) convinces me that the type of *Trichorhipis praecursor* is not a shark fin but a gyracanthid prepectoral spine. The misinterpretation of this specimen is understandable in view of the fact that, at the time it was described, only two occurrences of *Gyracanthus* (one questionable, and both stratigraphically low) had been reported for the entire Pennsylvanian of North America.

These additional records extend the range of *Gyracanthus* in North America past the middle of Pennsylvanian time and demonstrate (if demonstration were needed) how little we really know about the distribution or morphology of this elusive acanthodian.

ADDITIONS TO THE FAUNA OF CANNELTON, PENNSYLVANIA

This classic fauna is known entirely from specimens collected a century ago by I. F. Mansfield at his mine near Cannelton in Darlington Township, Beaver County, Pennsylvania. Unlike Mazon Creek and Linton the Cannelton fossil locality is no longer productive, for the coal "is

now mined out, and all entrances to the many mines in the deposit have collapsed" (Patterson, 1963, p. A9). As the shale disintegrates when exposed to water, anything left on the mine dump has been lost to science.

References in the literature to the stratigraphic position of the fossil-bearing carbonaceous shale may appear confusing, for Moodie (1916, p. 15) stated that "the Cannelton slate, in which the fossils occur, forms the roof of the Middle Kittanning Coal"; whereas Hall (1884, p. 23) quoted I. F. Mansfield about a eurypterid "found by him in the shale immediately beneath the Darlington cannel coal bed." The fact of the matter is that at Cannelton the Upper Kittanning (Darlington) Coal consists of bituminous coal up to three and one-half feet thick, overlain by up to 12 feet of cannel coal beneath a thick roof of cannel slate; the fossils were found, as Mansfield stated, beneath the cannel coal. "Extensive mining and prospecting has shown that the deposit apparently occupies an old oxbow shaped channel. The length of the channel is about 3-1/2 miles; its width, about 600 feet" (DeWolf, 1929, pp. 41, 119).

The Upper Kittanning coal is a member of the Kittanning Formation of the Allegheny Group. It is intermediate in age between the Colchester Coal (=Lower Kittanning Coal) of Mazon Creek and the Upper Freeport Coal of Linton, Ohio. Its age is about middle Westphalian D.

Besides an abundant compression-flora the Cannelton locality has yielded a number of insects (much in need of restudy) and two genera of eurypterids: the rare *Mycterops ordinatus* and the common *Adelophthalmus mansfieldi* (Kjellesvig-Waering, 1963, pp. 95, 104). Vertebrate fossils are so few in number that the sample preserved cannot be considered truly representative of the fauna: many of the taxa are known from a single specimen. The only lepospondylous amphibian present is the snakelike aïstopod *Ophiderpeton* cf. *amphiuminum* (Baird, 1964, p. 12; PU 17293). [The nectridean, *Ctenerpeton*, which occurs only in the Linton fauna, was erroneously attributed to Cannelton in Cope's (1897) original description on the authority of an incorrect museum label.] Moodie has named a number of small labyrinthodonts but all prove on examination to belong to the trimerorhachoid genus *Saurerpeton*, which (as at Linton) is rela-

tively common; pending detailed study the specimens can be referred to a single species for which the name *Saurerpeton* [*Tuditanus*] *minimum* (Moodie), new combination, has priority. The fishes, however, are what concern us here.

CLASS OSTEICHTHYES

ORDER CROSSOPTERYGII

SUBORDER COELACANTHINI

FAMILY COELACANTHIDAE

Rhabdoderma elegans (Newberry)

The first coelacanth from Cannelton—the first Carboniferous coelacanth from Pennsylvania—was collected by Mansfield about 1877 but lay unrecognized in the collections of the Second Pennsylvania Geological Survey. Transfer of these collections from dead storage to the William Penn Memorial Museum in Harrisburg, Pennsylvania, has enabled the curator, Donald T. Hoff, to make them accessible to scientists for the first time in decades. On an exploratory visit in 1966 I recognized the coelacanth specimen (WPMM 10970) and was permitted to borrow it for study.

Little bone is preserved, the specimen consisting largely of a natural mold in siltstone. My description is therefore based on a high-fidelity cast in red latex (fig. 8), prepared as described in Baird (1955). The most conspicuous element present is the right palatoquadrate complex, which is directly comparable with that of *R. elegans* as illustrated by Schaeffer and Gregory (1961, fig. 6B; PU 17170). Parallel to and slightly overlapped by the ventral margin of the palatoquadrate is one of the gular plates; across these two elements lies the right lacrimojugal.

Both angulars are present, the right one in articulation with the quadrate, the left one transposed end-for-end so that its sculptured labial surface lies uppermost. These angulars show the prominently humped dorsal profile, which is seen in the type (AMNH 503) and topotype specimens of *Rhabdoderma elegans* from Linton, Ohio—but not in the reconstruction by Moy-Thomas (1937, fig. 1), which purports to represent that species. Behind the palatoquadrate lie the cleithra, the right one rotated 180 degrees on its long axis, the left one (labeled *cl* in fig. 8)
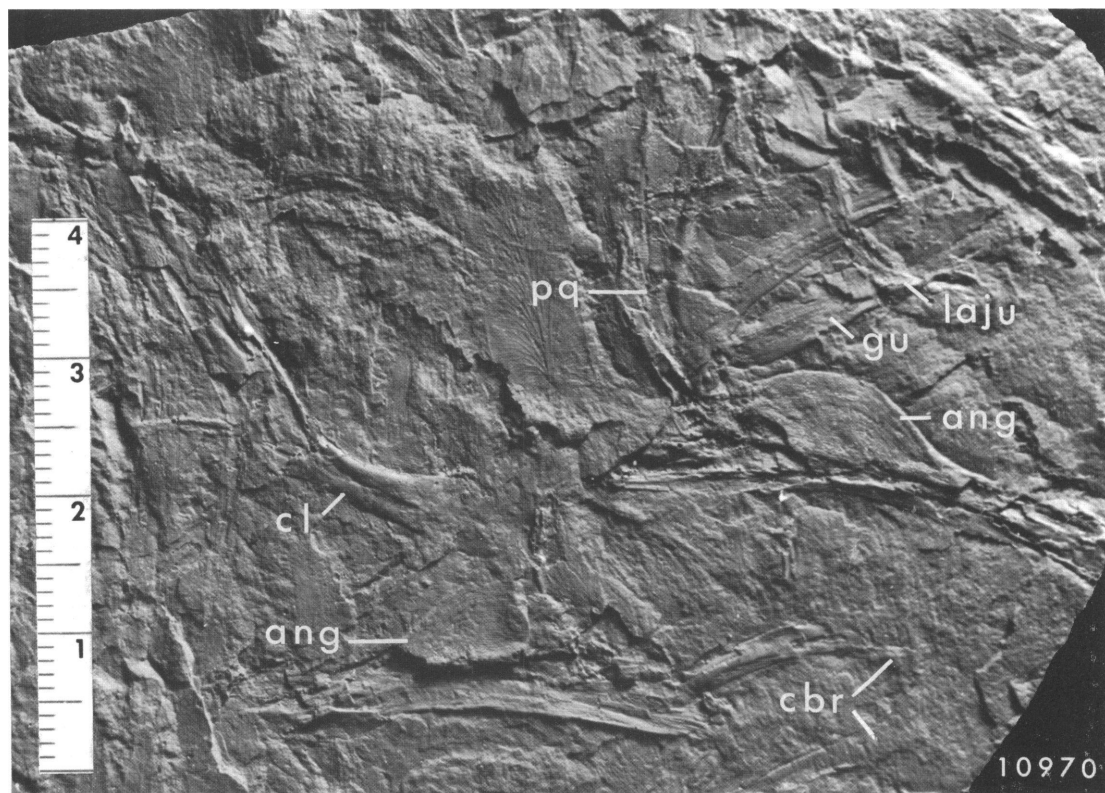
FIG. 8. *Rhabdoderma elegans* from the Upper Kittanning Coal at Cannelton, Pennsylvania; WPMM (SGSP) 10970. Scale 4 cm. long. *ang*, angular; *cbr*, ceratobranchials; *cl*, cleithrum; *gu*, gular; *laju*, lacrimojugal; *pq*, palatoquadrate complex.

reversed and inverted so that its dorsal blade points ventrally with respect to the other elements. Two hockey-stick-shaped ceratobranchials can be seen to the right of the left angular.

The Cannelton coelacanth is intermediate in age between the nominal species *R. exiguum* (Eastman, 1902, p. 538) from Mazon Creek and *R. elegans.* It is readily assignable to the latter species and probably represents a population ancestral to that at Linton.

ORDER CROSSOPTERYGII

SUBORDER RHIPIDISTIA

FAMILY RHIZODONTIDAE

Rhizodopsis cf. *R. robustus* (Roemer)

A rhizodontid fish of small to medium size is represented by a macerated and incomplete indi-

vidual (USNM 4564), an operculum (USNM 4538), and isolated oval scales (USNM 4540, 4565/69). The scales are closely comparable with those of *Rhizodopsis* from Margaree Harbour mentioned above on page 11 and may be referred to that genus provisionally. A similar scale from Mazon Creek (USNM 4337) was described by Hay (1900, pp. 110-111) as *Rhizodopsis mazonius*, and identical-appearing scales from the Essex fauna of the Mazon Creek deposits have recently been described by Schultze (1974, p. 38) as *Rhizodopsis* cf. *R. robustus* (Roemer). Of course such fragmentary material must be identified with caution. The point of interest here is that *Rhizodopsis* is present at Mazon Creek and Cannelton but absent at Linton, where the rhipidistians appear to have been excluded from their niche by a variety of aquatic labyrinthodont predators.

ORDER PALAEONISCIFORMES

SUBORDER PALAEONISCOIDEI

Palaeoniscoids of the families Haplolepidae and Palaeoniscidae are present in the Cannelton fauna. *Haplolepis* (*H.*) aff. *ovoidea* was described by Westoll (1944, pp. 23-24) on the basis of a single, poorly preserved specimen (USNM 4560); he found it to differ slightly from typical *H. ovoidea* in scale count and possibly in the larger size of its subopercular.

Elonichthys (or what passes for that genus in our current state of knowledge) is represented by a coprolitic mass of scales (PU 18061) that are striated exactly like those of *E. peltigerus* from Linton, Ohio.

A larger palaeoniscid, which I refrain from describing here, is the most common fish in the fauna. Parts of several fragmentary individuals are catalogued as USNM 4561/62, 4566, 4567/74, 4572, and PU 12361/62, 12363, 12364/65 (compound numbers mean separately numbered counterparts). Most of these are patches of scales, evidently severed by the bites of predators (see Zangerl and Richardson, 1963, p. 137), but USNM 4566 and 4567/74 are regurgitated masses that include head elements. So far as I can see this fish conforms to *Commentrya* as redescribed by Blot (1966), a genus known from the late Stephanian of Commentry, France. In view of its trans-Atlantic locale and earlier (late Westphalian) date, the Cannelton species clearly merits detailed description and comparison with the French one.

CLASS CHONDRICHTHYES

ORDER PLEURACANTHODII

FAMILY XENACANTHIDAE

The ubiquitous unicorn-shark *Xenacanthus*, whose characteristic tricuspid teeth are often the commonest elements in Pennsylvanian and early Permian bone-bearing deposits of freshwater origin, is represented in the sample from Cannelton by a single tooth, USNM 4547. It is indistinguishable from *X. compressus* (Newberry) from the type locality at Linton, Ohio.

ORDER SELACHII

SUBORDER CTENACANTHOIDEA

FAMILY BANDRINGIDAE

Bandringa rayi Zangerl

The polymorphic array of Carboniferous elasmobranchs received a bizarre addition in 1969 when Zangerl described a new genus and species of spoonbill dogfish from the Essex fauna of the Mazon Creek deposits. Based on a nearly complete but extremely juvenile individual (FMNH PF 5686), *Bandringa rayi* was shown to be a ctenacanthoid shark with an elongate and spatulate rostrum that is superficially similar to that of the spoonbill catfish, *Polyodon spathula*. What appears to be an additional specimen of this shark, obtained by I. F. Mansfield in 1877, has come to light in the Princeton paleobotanical collection and has been catalogued among the fossil vertebrates as PU 19814. Despite poor preservation, its relative maturity (more than five times the linear size of the type individual) permits additions to our knowledge of the head morphology and teeth of *Bandringa*.

As shown in figure 9A the specimen consists of a head, probably amputated by the bite of a predator, which is dorsoventrally crushed, and considerably broken in the otic region of the chondrocranium. The rostrum is disrupted by a woody stem of *Artisia* which has pressed down across it. As morphological features in calcified cartilage are difficult to make out even under favorable conditions of preservation (which is hardly the case here), the following observations should be considered tentative.

As I interpret it the head is seen in ventral aspect with the left palatoquadrate folded out to one side and mandibular fragments on the other; an additional piece of mandible lies between the orbits. The orbits are semicircular embayments in the chondrocranium. Distance between orbits is about equal to orbit length, i.e., somewhat greater than it is in the juvenile type specimen, as might be expected. Unlike other Paleozoic sharks the postorbital process is not short anteroposteriorly but instead merges into the laterally expanded dorsal otic ridge to form a boxlike temporal region, the posterolateral corner of
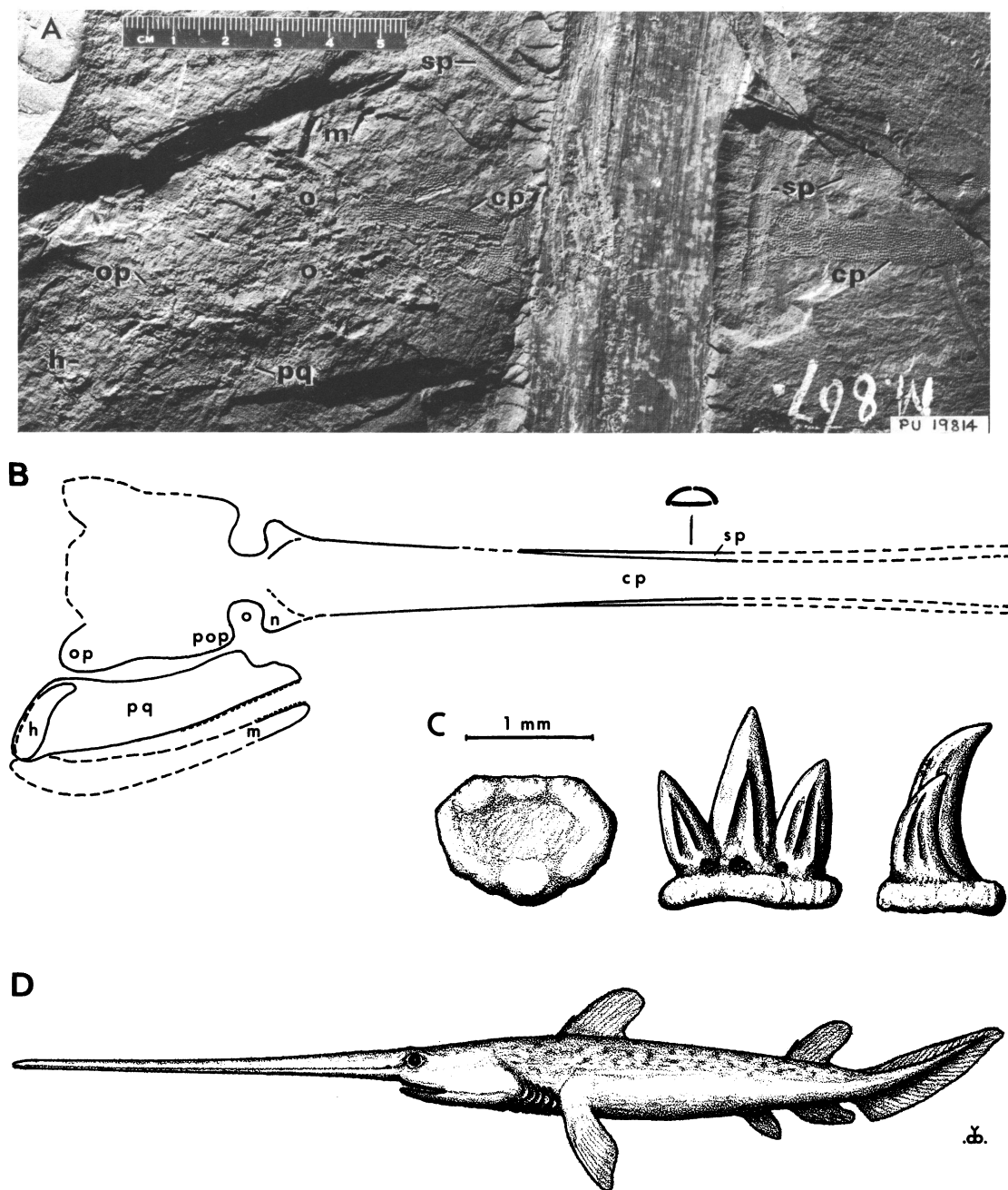
FIG. 9. *Bandringa rayi* from the Upper Kittanning Coal at Cannelton, Pennsylvania. A. Head as preserved, PU 19814. B. Attempted diagrammatic reconstruction of chondrocranium in ventral view and jaws in medial view, with inferred cross-section of rostrum (to the same scale as A). C. Tooth in basal, labial, and anterior views. D. Restoration of the fish with body proportions based on Zangerl's projection of the adult configuration. *cp*, cultriform process; *h*, hyomandibular; *m*, mandible fragment; *n*, nasal capsule; *o*, orbit; *op*, otic process; *pop*, postorbital process; *pq*, palatoquadrate; *sp*, selinoid processes.

which projects as an otic process similar to that of *Xenacanthus* (Romer, 1966, fig. 63). The rest of the otic region is so crushed and disrupted that its morphology and length cannot be made out. As in *Xenacanthus* the nasal capsule extends laterally to form an antorbital process. Into this process the flared base of the rostrum appears to merge.

The rostrum is a tripartite structure consisting of a broad cultriform process and a pair of shallow gutter-like elements which I propose to call the selinoid processes because they resemble celery stalks. These paired elements are broken and disarticulated but there can be no doubt of their identity with the "fringes" that border the cultriform process in the type specimen. They lie with their concave surfaces up, i.e., ventral. The proximal portion of the cultriform process must have been bowed in cross-section, as crushing has caused it to crack longitudinally; more distally it becomes flat. Histologically the rostral elements are distinctive, being composed of irregular ranks and files of calcified cells shaped like vertebral centra or spools strung lengthwise. The body of the chondrocranium and the palatoquadrate, in contrast, are formed of more typical mosaics of polygonal cells.

The palatoquadrate shows an extremely long, low profile which, peculiar though it is, appears to be conformable to the peculiar chondro-cranium. Its ventral margin (with a few teeth still adhering) is gently convex, turning downward at the posterior end to form the oblique suspenso-rium. Close to the anterior end the dorsal margin is embayed by the lower rim of the orbit. Instead of rising high behind the orbit to form a vertical process for articulation with a restricted post-orbital process on the chondrocranium, the mar-gin turns caudad in a gentle festoon, rising slightly to meet the conjoined heads of the quadrate buttress and the hyomandibular. Ap-parently the otic articulation of the palato-quadrate was extended rather than restricted.

Little can be said of the fragmentary mandible except that it appears to be sturdy in cross-section but long and low in profile, like that of *Cladoselache.*

Teeth are strewn about the surface from a point behind the quadrate condyle to the base of

the rostrum. This distribution supports the evi-dence of the type specimen that the mouth occupies a normal position and is not involved in the rostrum. The teeth (fig. 9C), although charac-teristically cladodont in form, are distinctive. From an oval platform arise three stout, incurved cusps broadly fluted on their labial faces but smoothly rounded lingually. The teeth are, of course, somewhat variable: in some examples the lateral denticles are relatively smaller than in the illustration or more divergent or apparently lack-ing. Although these teeth are remotely similar to some from the Devonian and Mississippian that have been referred to the form-genus *Phoebodus*, they are distinct from anything known to me. Their closest resemblance is to the smaller teeth of *Goodrichthys eskdalensis* (Moy-Thomas, 1936, pl. 1c), and indeed they could be derived from that type by the suppression of one pair of lateral denticles.

Its teeth are the only feature of the Cannelton specimen which might militate against its identi-fication as *Bandringa rayi*, since those of the type specimen are described as acuminately mono-cuspid. We must bear in mind, however, that the type is an extremely juvenile individual with teeth that are preserved as the merest pinpricks in the ironstone matrix, the largest being only 30.4 microns in height. Thus we may invoke incomplete ossification, imperfect preservation, and difficulties of observation to account for the appearance of the teeth in the Mazon Creek specimen. In all other (observable) respects the two specimens are morphologically congruent if allowance is made for the difference in onto-genetic age. As less than the full thickness of the Kittanning coal-group separates them strati-graphically, there is no reason to assume a spe-cific difference on temporal grounds.

While the new specimen adds appreciably to our understanding of *Bandringa*, several features of this peculiar shark still remain to be eluci-dated. For example, what are the homologies of the rostral cartilages? The major median element, the cultriform process, is most probably an ex-tension of the stout rostral process that projects from the floor of the chondrocranium in clado-donts and many later sharks; the paired selinoid elements are plausibly interpreted as outgrowths

of the nasal capsules. Such is the situation in the living long-snouted shark *Mitsukurina owstoni*, in which the "rostral cartilage [is] posteriorly in three branches, two upper and one lower, as in *Carcharias*" (Garman, 1913, p. 28, pl. 51 fig. 1). On this basis I reconstruct the rostrum of *Bandringa* as a hemi-tubular structure, consisting of a ventral cultriform process with an arched roof formed by the selinoid processes.

Zangerl's restoration of the type specimen, however, envisages the "fringe" structures (selinoid processes) as lying lateral and ventral to the cultriform process. Which of these antipodal interpretations is correct? Perhaps the discrepancy arises from the difficulty of distinguishing top from bottom in the type specimen, in which dorsal and ventral features have been compressed into a single plane. If the head in the half-nodule shown in Zangerl's figure 84 (top) is seen as dorsal-side-up, then the proximal part of the right selinoid cartilage does appear to bend *under*, and thus must be ventral to, the cultriform process. But in the counterpart half-nodule the relationship looks exactly the same, in which case the right selinoid cartilage must bend *over* the cultriform process. It cannot go both ways, and the second alternative is as plausible as the first. Thus, depending on how you look at it, the type specimen can be reconciled with the reconstruction shown in figure 9B.

In figure 9D an attempt is made to restore the appearance in life of the *Bandringa* from Cannelton. The body proportions shown are intended to reflect the greater maturity of the Cannelton individual; they are derived from Zangerl's figure 88d, a cartesian distortion of the type specimen based on allometric differences between juvenile and adult individuals of *Mitsukurina owstoni*. That the head differs from Zangerl's restoration in resembling *Polyodon* rather than *Xiphias* is a matter of interpreter's bias. My impression of *Bandringa* is one of a bottom-dwelling fish that fed on organisms stirred up from the mud by the rostrum.

Within the very small group of ctenacanthoid genera of which we have adequate knowledge, *Goodrichthys* from the Visean of Scotland seems to have most in common with *Bandringa*. The similarity in teeth has been noted. In both genera

the dorsal fins are semi-elliptical with the free portions of the fins extending well above the tips of the relatively diminutive fin-spines; this contrasts with the triangular, heavy-spined dorsal fins of *Tristychius* and *Ctenacanthus costellatus*. Without overstressing the comparison we may plausibly postulate that *Goodrichthys* represents the stock from which the highly specialized *Bandringa* evolved.

One previously unsuspected fact about *Bandringa* is revealed by the Cannelton occurrence: the spoonbill dogfish was a freshwater shark. Nothing positive could have been said about the preferred ecology of the type specimen, for the Essex fauna in which it occurs, while predominantly an assemblage of marine and euryhaline animals, is associated with an appreciable number of "strays" from the freshwater environment. The Cannelton biota, on the other hand, is exclusively an assemblage of coal-swamp plants and animals, deposited in an abandoned oxbow of a stream channel during the coal-forming episode of the Upper Kittanning sedimentary cycle. Presence of the eurypterid *Adelophthalmus* [*Lepidoderma*] might indeed tempt the nonpaleontologist to infer a marine or euryhaline element in the fauna, but Kjellesvig-Waering (1948, p. 9) categorically rebuts that notion: "The fact that *Lepidoderma* is a fresh water animal has been known for a considerable time, and no longer is doubted. . . ."

That ctenacanthoid sharks were customary inhabitants of streams and lakes during the Carboniferous and Permian is a fact ignored in nearly all the literature, where nonxenacanthid sharks are simply assumed to have been marine. We have already noted (p. 6) *Ctenacanthus* in a typical freshwater assemblage at Grand Etang in Nova Scotia, a province noted for its utter lack of marine sediments throughout the Pennsylvanian sequence (Carroll et al. 1972, p. 17). Nor is this a local aberration in distribution. The ctenacanthoid sharks whose pictures appear in every textbook—*Ctenacanthus costellatus*, *Goodrichthys eskdalensis*, and *Tristychius arcuatus* from the Lower Carboniferous of Glencartholm, Scotland—were also members of an extensive freshwater fauna. Stomach contents of *C. costellatus* included coelacanth and palaeoniscoid re-

mains (Moy-Thomas, 1936, p. 765), showing plainly the environment in which it made its living. Clearly it is time to abandon unthinking assumptions about the paleoecology of these Carboniferous sharks.

LITERATURE CITED

Baird, D.
  1955. Latex micro-molding and latex-plaster molding mixture. Science, vol. 122, p. 202.
  1962. A haplolepid fish fauna in the early Pennsylvanian of Nova Scotia. Palaeontology, vol. 5, pp. 22-29.
  1964. The aïstopod amphibians surveyed. Breviora Mus. Comparative Zool., vol. 206, pp. 1-17.
Bell, W. A.
  1938. Fossil flora of the Sydney coalfield, Nova Scotia. Mem. Geol. Survey Canada, no. 215, pp. 1-334.
Belt, E. S.
  1964. Revision of Nova Scotia Middle Carboniferous units. Amer. Jour. Sci., vol. 262, pp. 653-673.
  1965. Stratigraphy and paleogeography of Mabou Group and related Middle Carboniferous facies, Nova Scotia, Canada. Bull Geol. Soc. America, vol. 76, pp. 777-802.
Blot, J.
  1966. Étude des Palaeonisciformes du bassin houiller de Commentry (Allier, France). Cahiers de Paléontologie, pp. 1-99, pls. 1-18.
Carroll, R. L., E. S. Belt, D. L. Dineley, D. Baird, and D. C. McGregor
  1972. Field excursion A59, vertebrate paleontology of eastern Canada. Guidebook, 24th Int. Geol. Congress, pp. 1-113.
Cope, E. D.
  1897. On new Paleozoic vertebrata from Illinois, Ohio and Pennsylvania. Proc. Amer. Phil. Soc., vol. 36, pp. 71-91, pls. 1-3.
Darrah, W. C.
  1969. A critical review of the Upper Pennsylvanian floras of eastern United States with notes on the Mazon Creek flora of Illinois. Gettysburg, Pennsylvania, author, viii + 220 pp., 80 pls.
Dawson, J. W.
  1868. Acadian geology, 2d ed. London; Macmillan, xxvii + 694 pp.

Denison, R. H.
  1969. New Pennsylvanian lungfishes from Illinois. Fieldiana: Geol., vol. 12, pp. 193-211.
DeWolf, F. W.
  1929. New Castle quadrangle. Pennsylvania Geol. Survey, Topog. Geol. Atlas, no. 5, 238 pp., 18 pls.
Eastman, C. R.
  1902. The Carboniferous fish-fauna of Mazon Creek, Illinois. Jour. Geol., vol. 10, pp. 535-541.
  1903. Carboniferous fishes from the central western states. Bull. Mus. Comparative Zool., vol. 39, pp. 163-226, pls. 1-5.
Garman, S.
  1913. The Plagiostomia (sharks, skates, and rays). Mem. Mus. Comparative Zool., vol. 36, xiii + 515 pp., 75 pls.
Hall, J.
  1884. Eurypteridae from the Lower Productive Coal Measures in Beaver County. Rept. Progress, vol. PPP, Second Geol. Survey Pennsylvania, pp. 23-39, pls. 3-8.
Hay, O. P.
  1900. Descriptions of some vertebrates of the Carboniferous Age. Proc. Amer. Phil. Soc., vol. 39, pp. 96-123.
Henrichsen, I. G. C.
  1972. A catalogue of fossil vertebrates in the Royal Scottish Museum, Edinburgh; pt. 3, Actinistia & Dipnoi. Roy. Scottish Mus. Inform. Ser., Geol. 3, pp. i-v + 1-26.
Kjellesvig-Waering, E. N.
  1948. The Mazon Creek eurypterid: a revision of the genus Lepidoderma. State of Illinois Sci. Papers, vol. 3, no. 4, 48 pp., 8 pls.
  1963. Pennsylvanian invertebrates of the Mazon Creek area, Illinois: Eurypterida. Fieldiana: Geol., vol. 12, pp. 83-106.
Lehman, J.-P.
  1959. Les dipneustes du Dévonien supérieur du Groenland. Meddelelser om Groenland, vol. 160, Nr. 4, pp. 1-58, pls. 1-21.
Miles, R. S.
  1973. Articulated acanthodian fishes from the Old Red Sandstone of England, with a review of the structure and evolution of the acanthodian shoulder-girdle. Bull. British Mus. (Nat. Hist.), Geol., vol. 24, pp. 111-213, 21 pls.

Miller, S. A.
1892. First appendix to North American geology and palaeontology for the use of amateurs, students and scientists. Cincinnati, Ohio (author), pp. 665-718.

Moodie, R. L.
1916. The Coal Measures Amphibia of North America. Carnegie Inst. Washington, Pub. no. 238, x + 222 pp., 26 pls.

Moy-Thomas, J. A.
1936. On the structure and affinities of the fossil elasmobranch fishes from the Lower Carboniferous rocks of Glencartholm, Eskdale. Proc. Zool. Soc. London, 1936, pp. 761-788, pls. 1-2.
1937. The Carboniferous coelacanth fishes of Great Britain and Ireland. Proc. Zool. Soc. London, ser. B, pp. 383-415, pls. 1-4.

Newberry, J. S.
1889. The Palaeozoic fishes of North America. Mon. U. S. Geol. Survey, vol. 16, 340 pp., 53 pls.

Ørvig, T.
1961. New finds of acanthodians, arthrodires, crossopterygians, ganoids and dipnoans in the Upper Middle Devonian calcareous flags (Oberer Plattenkalk) of the Bergisch Gladbach-Paffrath trough, pt. 2. Paläont. Z., vol. 35, pp. 10-27, pls. 1-6.

Olson, E. C.
1946. Fresh- and brackish-water vertebrate-bearing deposits of the Pennsylvanian of Illinois. Jour. Geol., vol. 54, pp. 281-305.

Patterson, E. D.
1963. Coal resources of Beaver County, Pennsylvania. Bull. U. S. Geol. Survey, vol. 1143-A, iv + 33 pp., 5 pls.

Romer, A. S.
1966. Vertebrate paleontology, 3d ed. Chicago, Univ. Chicago Press, ix + 468 pp.

Romer, A. S., and H. J. Smith
1934. American Carboniferous dipnoans. Jour. Geol., vol. 42, pp. 700-719.

Schaeffer, B., and J. T. Gregory
1961. Coelacanth fishes from the continental Triassic of the western United States. Amer. Mus. Novitates, no. 2036, pp. 1-18.

Schultze, H.-P.
1974. Osteolepidide Rhipidistia (Pisces) aus dem Pennsylvanian von Illinois/USA. Neues Jahrb. Geol. Paläont. Abh., vol. 146, pp. 29-50.

1975. Die Lungenfisch-Gattung Conchopoma (Pisces, Dipnoi). Senckenbergiana Lethaea, vol. 56, pp. 191-231.
1976. Megapleuron zangerli, a new dipnoan from the Pennsylvanian, Illinois. Fieldiana: Geology, vol. 33, no. 21, pp. 375-396.

Smith, W. H., R. B. Nance, M. E. Hopkins, R. G. Johnson, C. W. Shabica, et al.
1970. Depositional environments in parts of the Carbondale Formation, western and northern Illinois. Illinois Geol. Survey Guidebook, vol. 8, 125 pp.

Sternberg, R. M.
1941. Carboniferous dipnoans from Nova Scotia. Amer. Jour. Sci., vol. 239, pp. 836-838, pl. 1.

Thomson, K. S.
1965. On the relationships of certain Carboniferous Dipnoi; with descriptions of four new forms. Proc. Roy. Soc. Edinburgh, vol. 69, B, pp. 221-245, pls. 1-4.

Ward, J.
1890. The geological features of the North Staffordshire coal fields, their organic remains, their range and distribution; with a catalogue of the fossils of the Carboniferous system of North Staffordshire. Trans. North Staffordshire Mining and Mechan. Engineers, vol. 10, pp. 1-189 + i-ix, pls. 1-9.

Watson, D. M. S., and E. L. Gill
1923. The structure of certain Palaeozoic Dipnoi. Jour. Linnean Soc., Zool., vol. 35, pp. 163-216.

Westoll, T. S.
1944. The Haplolepidae, a new family of Late Carboniferous bony fishes. Bull. Amer. Mus. Nat. Hist., vol. 83, pp. 1-122, pls. 1-10.
1949. On the evolution of the Dipnoi. In Jepsen, G. L., E. Mayr, and G. G. Simpson (eds.), Genetics, Paleontology, and Evolution. Princeton, Princeton Univ. Press. pp. 121-184.

White, E. I.
1965. The head of Dipterus valenciennesi Sedgwick & Murchison. Bull. British Mus. (Nat. Hist.), Geol., vol. 11, pp. 1-45, pls. 1-3.

Woodward, A. Smith
1891. Catalogue of the fossil fishes in the British Museum (Natural History), pt. 2. London, xliv+567 pp., 16 pls.
1906. On a Carboniferous fish fauna from the Mansfield District, Victoria. Mem. Natl.

Mus. Melbourne, vol. 1, 32 pp., 11 pls.

Zangerl, R.
1969. *Bandringa rayi*, a new ctenacanthoid shark from the Pennsylvanian Essex Fauna of Illinois. Fieldiana: Geol., vol. 12, pp. 157-169.
1973. Interrelationships of early chondrichthyans. *In* Greenwood, P. H., R. S. Miles, and C. Patterson (eds.), Interrelationships of fishes. Zool. Jour. Linnean Soc., vol. 53, supp. 1, xvi + 536 pp.

Zangerl, R., and E. S. Richardson, Jr.
1963. The paleoecological history of two Pennsylvanian black shales. Fieldiana: Geol. Mem., vol. 4, xii + 352 pp.