FOSSIL FISHES FROM SOUTHWESTERN PENNSYLVANIA

Part I: Fishes from the Duquesne Limestones
(Conemaugh, Pennsylvanian)

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INTRODUCTION

The excellent exposures of Conemaugh, Monongahela, and Dunkard group rocks in and around Pittsburgh, Allegheny County, Pennsylvania, have been the subject of a few sporadic searches for vertebrate fossils. Beds containing fish scales and teeth were reported as early as 1876 (Stevenson, 1876: 78, 326). P. E. Raymond (1910) noted the presence of bone in the Ames limestone and underclay and in the Birmingham shale. E. C. Case (1915) described some tetrapod remains from Pitcairn, Allegheny County, and summarized earlier vertebrate fossil finds from southwestern Pennsylvania. Moran (1952) and Romer (1952) discussed all vertebrate fossil finds previous to 1952 from the Pennsylvanian of Allegheny County as well as from the Dunkard of West Virginia and Ohio. Kent (1967) and Schweinfurth (1967) repeatedly mentioned the occurrence of fish remains in the fresh-water limestones of southwestern Pennsylvania. Fossil fishes below the Conemaugh are known from two famous localities: Linton, Ohio (Newberry, 1873, 1875), and Cannelton, Pennsylvania (Westoll, 1944), within 70 miles of Pittsburgh, but are seriously in need of restudy.

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**Geologic Setting**

The Ames marine horizon of the central Conemaugh group marks a change in depositional history in this area from alternating near-shore marine and fresh-water sediments of the lower Conemaugh, to the predominantly, if not exclusively, fresh-water beds of the upper Conemaugh, Monongahela, and Dunkard groups. Fossils useful for correlation above the Ames limestone are plants, ostracods, and insect wings. Zonation of the Pennsylvanian-Permian section of western Pennsylvania is based chiefly upon plant successions (Darrah, 1934), coupled with classic applied stratigraphic principles. Little use has been made of the invertebrates, and no use of the vertebrates.

The presence of cyclical deposits throughout the Pennsylvanian and Permian of southwestern Pennsylvania indicates repetition of varied ecological and depositional conditions. A typical cyclothem in the Pittsburgh area consists of several elements. A clay zone, representing soil formation, contains scattered plant material. A carbonate zone which may contain a few teeth and denticles of *Orthacanthus*, and an occasional microsaur tooth, may occur in the clay. These carbonates thus seem to represent local flooding or standing-water conditions. Fresh-water limestone may be developed within the clay zone, usually locally. Overlying the clay is either coal or a trace of coal, with plant material only. The coal is usually succeeded by a jet-black, carbonaceous and pyritic shale, either massive or very thin-bedded, and of fresh-water origin. Massive shales may have occasional scattered fish material, while thin, evenly-bedded shales may contain many fish scales and occasional articulated vertebrates, as well as pieces of plant stem and leaf. This thin black-shale zone grades upward into gray, flaky shale, irregularly bedded, containing plants, insect wings, and conchostracans, seemingly representative of very shallow-water, mudflat facies. Above this zone lies a thick zone of plant-containing, light-gray silts and interfingering sands, upon which another clay zone is developed.

Fish remains occur, broadly speaking, in two different sedimentary types representing strikingly different ecologies. The most readily observable remains occur in the jet-black, carbonaceous siltstones and shales that frequently accompany coals or coal zones. Bones, scales,
teeth, and spines of fish, filled with pyrite, are accompanied by coprolitic material and, much more rarely, by articulated specimens or portions of specimens. Fish scales occur irregularly throughout the black shales and may be locally concentrated. Tetrapod remains are rare to nonexistent. Fresh-water limestones may contain local concentrations of fish and tetrapod remains, under somewhat specialized sets of depositional circumstances that are not well understood. Fossil vertebrate specimens, furthermore, are almost never found articulated in these limestones. While it is not unusual to find small numbers of fish teeth and scales in fresh-water limestones, only rarely are sufficient concentrations of material found to be of any paleontologic use.

Stratigraphically useful invertebrate fossils are rare. But many horizons contain fossil-fish material, and it may be possible to correlate units on the basis of their vertebrate faunas when the latter are known well enough. This paper is a preliminary report on a few fresh-water fossil fish from one of these horizons, the Duquesne limestone.

The following abbreviations are used throughout: AMNH, American Museum of Natural History; CM, Carnegie Museum; DL, Duquesne limestone; CMSL, Carnegie Museum Stratigraphic Locality, Section of Invertebrate Fossils; FMNH, Field Museum of Natural History.

DUQUESNE CLAY AND LIMESTONES

The Duquesne clay occurs between the top of the Grafton shales and the base of the Duquesne coal (Johnson, 1929). In places where the Grafton shales are cut out, the Duquesne clay lies directly on the Ames limestone (Johnson, 1929: 5). The clay averages about eight feet in thickness throughout Allegheny County and contains, in its upper portion, occasional well-preserved terrestrial plant fossils standing erect (CMSL 366).

A carbonate zone occurs near the center of this clay, generally poorly developed and unfossiliferous, but persistent. North of the bluffs of the Allegheny and Ohio rivers, the carbonate zone appears in three layers of fresh-water limestone. They are dark gray to black, weathering to tan on a fresh break, and have a peculiar, foul, swamp-like odor when crushed or in contact with acid (White, 1878). Broad slabs exposed along McKnight Road, Ross Township, show many unrecognizable fragments of bone on their surfaces.

To my knowledge, the Duquesne limestones occur in only one area south of the Allegheny River, namely the west end of Mount Washing-
ton, within the city of Pittsburgh. In this area, limestones 2, 4, and 6 outcrop for almost a mile along the bluffs of the Monongahela River, and again for a short distance west of the south end of the Fort Pitt Tunnels (fig. 1). Limestone 2a, 3, and 5, however, seem to occur only for about 200 yards of outcrop east of the north portal of the Fort Pitt Tunnels. They represent small bays that extended southward from extensive marly lakes. The Duquesne limestones from this area have produced an extremely rich and varied vertebrate microfauna, part of which is described here, as well as many fragments of larger vertebrates.
The invertebrate fauna is limited to ostracods, conchostracans, and *Spirorbis*. The outcrop of these limestones at the north portal of the Fort Pitt Tunnels is in a tall, slowly sagging, slump block.

Significant quantities of varied vertebrate material occur within and between the two top limestone units and in the lowest limestone. The sedimentary character of these units is worthy of more study than presently can be devoted to them. The upper unit (DL 2) grades into gray calcareous siltstone above as well as at the east end of the outcrop. Scattered fish scales and teeth are found near the base of this siltstone. The limestone is distinctly conglomeratic, composed of dark and light lime pebbles and plates of siltstone in a calcareous and silt ground mass. The particle sizes are clearly larger toward the base of the unit, and most of the bone occurs in the lower inch of this bed. Bone occurs in all components of the rock unit, but is most common in the calcareous silt ground mass. There are associations of bony elements that indicate parts of individuals, but no articulated components. Non-carbonized but finely comminuted plant material is present throughout the unit. Fragmented tetrapod remains are common.

A very thin shale break provides an irregular plane of separation between DL 2 and DL 2a. This break, between \( \frac{1}{32} \) inch and \( \frac{1}{4} \) inch thick, has yielded scales, teeth, a partially articulated fish, and parts of a reptile.

Duquesne limestone 2a varies as greatly in composition as it does in thickness. In the thinnest parts, it is composed of thin plates of very light and very dark shale with calcareous cement. This unfossiliferous sediment may grade into either of two other types within a few inches. The more common type is a dark-brown limestone interrupted by frequent and seemingly random seams of calcareous silt. Small fossils are more prevalent in the silty fractions than in the limestones, while macrofossils are found in the limestones or crossing both silty and limestone portions. The remaining lithologic type is a massive, very dense, very black limestone with finely disseminated crystalline calcite. Macrofossils are lacking but fragmented microvertebrate fossils are common. Tetrapod material is almost totally absent in the lower of the two limestone units, and is limited to microsaur bones.

Duquesne limestone 6, averaging almost one foot in thickness, is a massive unit high in clay, locally high in iron compounds, and containing some gypsum crystals as well as an irregular mesh of calcite tubules, possibly from burrow fillings. *Orthacanthus* and *Xenacanthus* teeth,
paleoniscoid scales, and small tetrapod bones are irregularly distributed throughout and may be locally concentrated near the base of the unit. Lungfish remains are present but rare.

Transport of bone seems to have been significant in DL 2, but minimal in DL 2a and DL 6. Reworking of the unconsolidated substrate by burrowing organisms may have been the most important factor in disarticulating specimens in these units.

Deformation of bones prior to lithification can be seen in certain specimens from all fossiliferous limestone units. Small microsaurian vertebrae are generally skewed to one side. A large portion of an Orthacanthus spine was bent to the point of shattering individual longitudinal bony spicules. A large Sagenodus cf. S. periprion operculum was crushed from above, fragmented, and spread out to occupy almost twice its intact area. These examples, however, are exceptions, for most bones, large and small, show no trace of the effects of fossilization.

The distinctly fresh-water nature of the deposits is indicated by the presence of Orthacanthus sp., Sagenodus periprion, and another dipnoan, as well as by the several tetrapod remains.

The assignment of the name Duquesne limestone to these beds (Johnson, 1929: 60) recognizes their proximity to the overlying Duquesne coal and/or black shale. This stratigraphic proximity is deceiving, for the limestones occur in the midst of a clay representing a soil zone, a gap in deposition of unknown duration. At least one layer of erect, fossil land plants occurs between the definitive Duquesne coal horizon and the underlying limestone-coal sequence (fig. 2). The six-inch coal overlying the limestone sequence at the Fort Pitt Tunnels is not the Duquesne coal of Johnson (1929), which is represented by a trace at the base of the Birmingham shales at this place.

The elapsed time between the faunas of the Duquesne limestone and

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**Fig. 2.** Outcrop of Duquesne limestone 100 feet east of north portal of Fort Pitt Tunnels prior to removal of layer 2a. At the top is a zone containing upright plant fruiting bodies. 1. Coal zone. Six inches of well-developed coal, underlain by soft gray siltstone. 2. Soft, laminated gray siltstone grades downward and laterally into a graded limestone conglomerate. Fossil vertebrates chiefly near base. A thin shale break at bottom contains occasional bones. 2a. Limestone interbedded with shale. Variable in composition, very rich in bones. Underlain by clay-shale. 3. Thin, silicified layer, with occasional pleuracanth teeth, underlain by clay. 4. Thick, limy clay, with some fine silicate sand. Very few fossil vertebrates. Ostracods, Spirorhitis, pleuracanth present. Underlain by clay. 5. Varially developed limy clay. No known fossils. Slight clay break underneath. 6. Thick, persistent layer. Limy clay mixed with areas richer in lime. Fossils in scattered concentrations near bottom of layer. Significant quantity of tetrapod material as well as a good representation of fish.
the overlying Duquesne shale may be significant. The time elapsed, however, in deposition of each of the two principal fossil-bearing limestones (DL 2 and DL 2a), is geologically very short. Neither bed shows any interruption or change in the nature of deposition vertically. Particle-size distribution suggests that DL 2 is a single, graded bed. Larger pieces of tetrapod bone are abraded and occur at the base of the bed, suggesting transportation of these chunks along with the plates of hardened silt. The small bones of fish and microsaurs are, for the most part, unworn and uninjured in spite of their great fragility. The remains of these aquatic vertebrates, found in the lime-silt ground mass, probably represent an in situ fauna. The peculiarities of this bed can be compared to a dried swamp bed flooded with silt-laden water.

DL 2a contained a major portion of the skull of one individual of Sagenodus cf. S. periprion (CM 19127). The bones were disarticulated but closely associated, and in some cases extended from the top to the bottom of the stratum. The bed itself is quite limited in area and probably represents the product of a single season of deposition of calcium carbonate in a shallow and algal-filled body of water.

Certain vertebrate elements in the fauna of the Duquesne limestones lend themselves readily to identification; others, such as the isolated paleoniscoid scales, cannot presently be treated.

**Systematics**

*Class Acanthodii*
*Family Acanthodidae*
*Genus Acanthodes Agassiz*
*Acanthodes* cf. *A. marshi* Eastman, 1902

Certain fin spines found in the Pennsylvanian and Permian of south western Pennsylvania have been referred by Romer (1952:49) to *Acanthodes* cf. *A. marshi* Eastman. Neither spines nor scales are ornamented. Although spines and scales have been found in association (CM 21549, Fishpot, Monongahela group, upper Pennsylvanian), not enough is known of this form to render a valid comparison with *Acanthodes marshi* Eastman.

*Class Elasmobranchii*
*Family Xenacanthidae*
*Genus Orthacanthus Agassiz, 1843*

*Orthacanthus* Agassiz, 1837-1843.  
*Diplodus* Agassiz, 1843.
Xenacanthus Newberry, 1856.
Orthacanthus Fritsch, 1889.
Xenacanthus Olson, 1946.
Xenacanthus Hotton, 1952.
Xenacanthus Romer, 1952.
Acondylacanthus Romer, 1952.

Diagnosis: See von Fritsch, 1889: 100.

Orthacanthus compressus (Newberry)

Figure 3

Diplodus compressus Newberry, 1875.
Xenacanthus compressus Hotton, 1952.

Description: Several hundred teeth, ranging in height from 1/2 mm. to 3 cm., plus parts of two fin spines, have been found within the limited volume (5 cubic feet) of rock dissolved from DL 2a. These teeth, while varying in size and proportions of the two main cusps, are perfectly uniform in characteristics. Each tooth has two large, blade-like serrated cusps, and a tiny central, generally unserrated, cusp upon a prominent rounded base. The basal surface of the tooth is cupped for attachment to the jaw, and a prominent boss is present lingual to the cusps on the denticulated surface. The two major cusps are almost of equal size in teeth that seem to be from near the symphysis, while on other teeth there is progressive proportional difference in the height of the two cusps. This feature, together with strong angling of the smaller cusp, seems to be indicative of teeth located far back along the jaws. The spines (fig. 3) are rounded in cross-section, thick, composed of longitudinal bony fibers reflected externally as fine striae, and bear a double row of small, sharply downcurved denticles proximally along a cupped rear margin. No complete spines have been found.

Discussion: Hotton (1952) suggested that only one genus (Xenacanthus) of North American pleuracanth shark is known. Gluckman (1964: 211-212) reproduced the superb illustrations of von Fritsch (1889). These illustrations (von Fritsch, 1889, figs. 173-175) clearly indicate that the teeth named Diplodus (Agassiz, 1843) are associated with the spine named Orthacanthus (Agassiz, 1843, pl. 45, figs. 7-9), while the spine named Pleuracanthus (Agassiz, 1843, pl. 45, figs. 4-6), which is a senior synonym for Xenacanthus (Byrich, 1848), is associated with distinctly different teeth built upon the same general plan as those of Orthacanthus (Diplodus).

Almost all reported North American pleuracanth teeth are of the Diplodus type, corresponding to the genus Arthacanthus. North American spines of the genus Xenacanthus have been uniformly assigned
(incorrectly) to the genus *Orthacanthus* (Newberry, 1873, pl. 40, fig. 4, for example). True *Orthacanthus* spines have been assigned incorrectly to the “genus” *Acondylacanthus* (Romer, 1952: 51). North American *Xenacanthus* teeth are rarely reported and tend to be overlooked principally because of their small size.

In DL 2a, two robust spines of *Orthacanthus* accompany many teeth of comparable size. *Orthacanthus* teeth are also known from DL 2, 3, and 6.

Genus *Xenacanthus* (Beyrich, 1848)

*Pleuracanthus* Agassiz, 1843.

*Orthacanthus* Newberry, 1873.
Xenacanthus sp.
Figure 4

One almost complete spine, plus a fragment of a second spine of this genus, is known from DL 2a. Teeth associated with spines of this size and delicacy have not been found in the same bed. However, *Xenacanthus* teeth have been retrieved from DL 6 and are quite common in the Dunkard series of southwestern Pennsylvania.

The spine (fig. 4) is quite thin, evenly tapered to the tip, and bears a row of depressed, recurved denticles on each side nearly throughout its length. The spine is nearly oval in cross section distally where the denticle rows are borne midlaterally, and is more highly arched proximally along its presumed dorsal surface than its somewhat flattened ventral surface. The denticle rows are ventrolaterally placed near the proximal end.

The teeth of Duquesne limestone *Xenacanthus* are diminutive, and differ strikingly from those of *Orthacanthus*. The two major cusps are subequal in size, approximately twice the length of the central cusp, thin, and circular in cross-section throughout their length. The two major cusps each bear six to eight thin vertical ridges along their distal halves from *Orthacanthus* in lacking a prominent labial process. The lingual "button" is quite variable in development. Little angular deviation of the cusps from each other is present. There is no difficulty in distinguishing the teeth of *Xenacanthus* from teeth in the same size range of *Orthacanthus*. The spine of *Xenacanthus arcuatus* (Newberry, 1873, pl. 40, fig. 4) from Linton, Ohio, Upper Allegheny series, differs from the Duquesne specimen in having a concave ventral face. No differences in spine shape are known between Conemaugh and Dunkard *Xenacanthus* (to be reported on at a later date). It is not presently possible to make species assignments based on the small samples available.

Order Hybodontida
Family Hybodontidae
Genus *Hybodus* Agassiz

*Hybodus allegheniensis*, new species
Figure 5

Hybodont shark: Romer, 1952, p. 49.

*Agassizodus variabilis* Romer, 1952: 49.

**Definition:** A small, fresh-water hybodont shark, distinguishable from others by the following characters: the teeth bear a robust central crown flanked by 2 to 3
Fig. 5. *Hybodus* sp. A. Spine fragment, lateral view. B. Spine fragment, posterior view. CM 19134. C. Tooth, lingual view. CM 19135. D. Dentine dorsal view. E. Dentine, lateral view. CM 19136. Units = 1 mm.

progressively smaller crowns on each side; all crowns bear vertical, radiating crenulations, and a central ridge unites the cusps; tooth bases are produced inward into a strong roughened ridge. Denticles are large with a smooth, slightly convex internal surface, and an external portion consisting of two major lateral cusps and one to two smaller, central cusps, projecting backwards. The dorsal-fin spine is
greatly compressed, slightly curved and strongly tapering, ornamented with a few strong, narrow, longitudinal ridges laterally. Denticles along the posterior edge are directed basally, but alternately point to left and right, as do the teeth of a saw.

HORIZON AND LOCALITY: Duquesne limestone 2a, Conemaugh, Pennsylvania, 200 feet east of north portal, Fort Pitt Tunnels; Pittsburgh, Allegheny County.

TYPE SPECIMEN: CM 19134, distal portion of a dorsal spine, Duquesne limestone 2a.

REFERRED SPECIMENS: CM 19136, dermal denticles; CM 19135, teeth, from the Duquesne Limestone.

A considerably broader spine fragment, equally severely compressed but showing more rapid tapering and no left-right alternation of dentine direction, comes from the Mason shale at Sample, Allegheny County. This spine (CM 21565) is regarded as a pectoral spine of the same "species" of hybodont shark.

DISCUSSION: The teeth originally referred to Agassizodus variabilis by Romer (1952) were, in fact, not related to the marine Pennsylvanian fish bearing the original name. The teeth and spine fragments mentioned by Romer are those of a fresh-water fish, and lack the broad, rounded cusps and the characteristic bradyodont structure of typical Agassizodus teeth.

Order Dipnoi
Family Ctenodontidae Woodward, 1891
Genus Sagenodus Owen, 1867
Sagenodus cf. S. periprion
Figures 6-9

Sagenodus cf. S. periprion have previously been described from the uppermost Conemaugh and the Greene of this region by Romer (1952: 52). Remains from DL 2a consist of two opercula, two tabulars, a parietal, parapophyseal, numerous cheek and snout bones, ribs, and right pterygoid and vomerine tooth plates, all pertaining to one individual (CM 19127). This specimen has an associated vomerine tooth (fig. 6), the first such tooth reported for this genus.

The forms of the cranial bones are apparently unchanged from the upper Conemaugh through the Dunkard and are relatively undistinguishable from the Texas Permian Sagenodus periprion (Romer, 1952: 54).

The vomerine tooth (fig. 6) is remarkable in its similarity to the form illustrated in figure 9 from the Duquesne horizon. Differences between these vomerine teeth are almost exclusively a reflection of the differences in size of the forms. The similarity between these teeth is in
Fig. 6. *Sagenodus* cf. *S. peripron*. CM 19127. Left vomerine tooth. A. Anterior view. B. Ventral view. Unit is 1 mm.
strong contrast to the differences between the tooth plates of large (fig. 7A) and small (figs. 7B, 8) forms. The tiny vomerine teeth pro-
vided the first indication that a series of very tiny *Sagenodus* were preserved in the Duquesne limestone. This was confirmed only after a number of intermediate-size specimens were found in Monongahela- and Dunkard-group rocks. The latter specimens are currently under study.

**EARLY GROWTH:** The Duquesne limestone *Sagenodus* provide an insight into the ontogeny of the jaws of this form. The most immature specimen, CM 19465, bears four rows of teeth on a flat, simple, bony plate. The four rows contain five, five, five, and three, teeth respectively, beginning with the most anterior row, which measures 86 mm. in length. Each tooth in each row is almost double the size of the tooth mesial to it.

In CM 19471, the first row of teeth is missing, but the specimen bears a ventral ridge of bone that presumably lay mesial to Meckel's cartilage. The tooth rows show some fusion with growth of the individual teeth, so although there are five, four, and one, cusps respectively, the innermost cusps have been almost completely incorporated into the bases of the cusps next lateral.

CM 19467, which shows a well-developed ventral ridge, also bears a first cusp-row of 1 mm. length. It has four rows, bearing three, two, two, and two, cusps respectively. All traces of the tiniest mesial teeth have vanished, while the remaining teeth in individual rows have grown into hefty, well-rounded cusps united at the base. The most anterior tooth row maintains a sharply bladed series of cusps. In all three specimens where the first tooth row measures more than 1 mm., or where the splenial bone is well-developed vertically, there are four tooth rows, with a maximum of three cusps in each row.

CM 19468 (fig. 7) is the largest of the small Duquesne limestone *Sagenodus*, and the only specimen with five tooth rows. Evidence from Dunkard group specimens indicates that two additional cusps are added to each row before additional tooth rows are added to the splenial element.

One right palatal element is known that corresponds in size range with these splenials (CM 19469; fig. 7B). It is a broad, rounded element in a poor state of preservation which bears teeth or tooth bases indicating the presence of six rows. The most anterior row is compressed and blade-like, while teeth in succeeding rows decrease in compression, in tooth size, and in basal proximity. The superficial glossy layer of the teeth seems to extend at least across the anterior two valleys between tooth ridges. The remarkable thinness of tooth walls, dramatically
Fig. 8. Sagenodus cf. S. periprion. CM 19468. Right splenial. A. Dorsal view. B. Labial view. Unit is 1 mm.

Illustrated in this specimen, corresponds to the condition in several of the splenials.
The blade-like anterior ridge of the palate and splenial evidently were piercing and chopping ridges. The large, rounded, and yet thin-walled teeth of the posterior ridges seem incapable of masticating anything firmer than soft plant tissue or soft-bodied invertebrates. A generally vertical action of the splenial-dental ridges between those of the palate seems to be the only possible way of masticating.

The vomerine teeth assigned to this group (fig. 9) have been placed here on the basis of two observations. The first is that they closely resemble the vomerine tooth of Sagenodus cf. S. periprion (fig. 6), to which the tooth rows on the jaws also bear some resemblance. The second is the assignment of vomerines illustrated by Berman (1968) to Gnathorhiza, which, if correct, strongly suggests that vomerines such as that in figure 12 belong with a genus more closely related to Gnathorhiza.

Vomerine teeth of this size generally lack strong, bony bases. The bases, where seen, consist of highly spongy bone, spicular in construc-

![Fig. 9. Sagenodus cf. S. periprion. CM 19431. Right vomerine tooth. Anterior view. Unit is .25 mm.](image-url)
tion and probably endochondral in origin. The teeth themselves vary only in the degree of development of secondary cusps, which are not constant in number, proportion, or size. Few cusps, gradually increasing in size away from the midline, plus a slight anterior convexity, describe this form. Only two features distinguish this vomerine from that of large Sagenodus: its minuscule size and a lack of evident wear on the sides of the more mesial cusps.

At the growth stages represented by the small Sagenodus specimens, there is no evident tooth wear. Addition of tooth rows and cusps with age is indicated in the Duquesne limestone Sagenodus where numbers of cusps per row is decreased by the incorporation of the smallest teeth into the bases of adjacent ones. Growth of individual teeth seems indicated, not only by this observation but by the tendency of larger splenials to have the teeth united at their bases, producing rows of cusps.

The small specimens of Sagenodus provides a remarkable insight into the ontogeny of this form.

Family Lepidosirenidae Bonaparte, 1841
Genus Monongahela\(^1\), new genus
Type species: Monongahela stenodonta, new species

_Provisional diagnosis:_ Lungfish, related to Gnathoriza, and known only from toothed elements recognizable on the basis of the following criteria: pterygoid element with four laterally divergent tooth ridges, the anterior three ridges divergent from an apex, the most posterior ridge originating lateral to the apex from the side of the ridge next anterior; all ridges slightly convex anteriorly; palatal bone broad and thin, not extending under lateral ends of posterior three ridges, and with a long horizontal symphysis; mandibular element with three tooth ridges divergent laterally, the anterior ridge longest, transverse ridge shortest, and originating posterior to apex of other two ridges; bone vertically developed with a posterior coronoid enlargement.

Monongahela stenodonta\(^2\), new species
Figures 10-15

_Horizon:_ Duquesne limestone, Conemaugh group, upper Pennsylvanian.

_Locality:_ North face of Mount Washington, 200 feet east of the north portal of the Fort Pitt Tunnels, Allegheny County, Pittsburgh, Pennsylvania.

_Type:_ CM 19450, right pterygoid element, from DL 2a.

_Referred specimens:_ Mandibles CM 19412-19419, CM 19434-19442, CM 19445-19448, CM 19459-19461, CM 19473-19476, CM 19478-19484, AMNH

\(^1\) Name is taken from the site where the first representatives were found, the bluffs at the mouth of the Monongahela River, Pittsburgh, Pennsylvania.

\(^2\) From the extreme narrowness of the tooth rows.
4665; pterygoids, CM 19420-19430, CM 19449-19458, AMNH 4664; partial skull with two pterygoids and mandible, CM 19447; two mandibles and one pterygoid of a single individual, CM 19485; vomerines, CM 19433, 19487, 19488.

**Provisional Diagnosis:** Lungfish of genus *Monongahela*, known chiefly from jaw elements. Jaw elements with cusps strongly flattened along axes of tooth ridges; cusps always united into distinct, separate ridges, with cusps becoming progressively less discrete with age. Pterygoid element with four ridges (a,b,c,d, anterior to posterior, fig. 12), angle ab plus bc usually equaling 90 degrees, angle cd with a mean of 30 degrees, range of 23-40 degrees, the angle decreasing with increasing individual age. Ridges a,b,c are all slightly convex anteriorly, and do not add cusps with increasing size, ridge d almost straight and adding cusps with increasing size. Lower jaw with three ridges (a,b,c anterior-posterior), angle ab with a mean of 48.6 degrees, range 25-65 degrees, median of 45 degrees; angle

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**Fig. 10.** *Monongahela stenodonta*. CM 19413. Right splenial. A. Dorsal view. B. Lateral view. Unit is 1 mm.
be with a mean of 70.2 degrees, range 100-130 degrees, median of 115 degrees. Vomerines with over 10 small cusps and blade-like.

**Geologic Range:** Upper Freeport limestone, Allegheny series (=Westphalian of European section, Desmoinesian of Western North America), Pennsylvanian, through the lower Washington limestone member of the Washington formation, Dunkard group, Wolfcampian (?), Permian (?).

**Discussion:** The jaws of small individuals of this species were very common in DL 2a, and were present in DL 2. One fragmented jaw was found in DL 6. Preservation was generally excellent; very few fragmentary jaws were found. Size variation is between 1 mm. total lower-

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**Fig. 11. Monongahela stenodonta. CM 19450, Type. Right pterygoid. A. Ventral view. B. Lateral view. Unit is 1 mm.**
jaw length and 9 mm. total jaw length. One pterygoid (CM 19455) shows growth and wear indicative of a specimen much older than the others. Most of the remains seem to represent young specimens, possibly young-of-the-year.

The pterygoid plates (fig. 11) show an interesting pattern of growth of the various ridges, which sheds light on changes in feeding during the life of the fish. The three anterior-cusp ridges are extremely sharp-edged in the small specimens with individual cusps quite discrete although not isolated from each other. The number of cusps per tooth-ridge stays constant through growth of the animal until all cusps are obliterated by wear (fig. 13). The fourth cusp row consists of one relatively rounded cusp in the smallest individuals. Cusps are added with growth until the adult condition of the tooth plate is reached. At this point, the posterior ridge is of significant size, may contain up to seven cusps, and addition of cusp ceases. The three anterior ridges of the pterygoid are discrete in the young and meet at an apical cusp contributed by the central ridge. The posterior ridge is subsidiary to the ridge next anterior, originating on the side of that ridge (fig. 11). Growth of the ridges results in early union of the first three ridges at the apex, and considerably later in the incorporation of the fourth ridge.

There is little wear in juvenile Monongahela pterygoids. Slight wear facets are developed only at the tips of the cusps, and extremely sharp edges are maintained in valleys and all sides. There is no indication of shearing of upper against lower jaw and no means of crushing food items. The mode of feeding is almost certainly that of an active predator with teeth designed to pierce and hold prey.

Fig. 12. Occlusal pattern in *Monongahela*. Solid lines represent pterygoid tooth ridges, dashed lines represent splenial tooth ridges. Ridges A, B, C, and D (pterygoid only) labelled from anterior to posterior.
With the achievement of a subadult size, as evidenced by growth of the fourth pterygoid ridge, aspects of wear become evident. Cusps gradually are obliterated by growth, from within and by abrasion, to form unified ridges. Ridges a and c, (see fig. 12 for key) united at the apex, are separated from b by a valley (fig. 13) produced by wear of the mandibular element, and a notch tends to be worn into ridge c by the mandible, generally lateral to the junction of c and d. The subadult shows a plate with one sharp, arcuate mesial ridge, composed of ridge a, the mesial part of c, and ridge d, plus two converging ridges separated from it, ridge b, and the lateral part of ridge c. Upon occasion, a specimen may be found where ridge c is notched mesial to its juncture with ridge d (CM 19455).

The change in ridge shape and relationship occurs when the jaw is relatively large. Therefore it is postulated that the change occurs at a subadult stage. The change results in a style of feeding better adapted to cutting and chopping. Both animal and vegetable material could be obtained and chewed with this mechanism.

The vomerine teeth attributed to this species (fig. 14) are rarely

![Fig. 13. *Monongahela stenondonta*. CM 19455. Right pterygoid. Ventral view. Unit is 1 mm.](image-url)
Fig. 14. Monongahela stenodonta. CM 19433. Left vomerine. A. Posterior view. B. Ventral view. Unit is .5 mm.

found, as they are tiny. They are blade-like, slightly convex anteriorly, and grow by addition of successively larger cusps laterally. Newer vomerine cusps are slightly serrated along their mesial edges. The older cusps show wear only on the mesial sides of their tips. As the vomerine teeth are not opposed by any known toothed elements, it is inferred that wear was produced by the action of tooth against prey, which suggests prey with a resistant external layer. The ostracods found in the same deposits would be within the size-range of prey for most of the Monongahela specimens represented.

The mandibular, or splenial, elements of Monongahela (fig. 10) do not differ noticeably from those of the Permian genus Gnathorhiza (Berman, 1968, fig. 2), except in size. The smallest specimen found, CM 19460, shows that: the anterior ridge a includes the apical cusp, ridge b (see Fig. 12 for key) originates from the cusp next posterior to the apex, and ridge c includes only the remainder of the cusps on a
line from the apical cusp. The separation between ridges is lost very early.

The range of angles found between ridges of the mandible is much greater than those of the relatively unvarying pterygoid. Bilateral variation is strong in CM 19485. The degree of latitude in lower jaw angles virtually prohibits accurate shearing action of the upper against the lower jaw and reinforces the belief that the feeding was accomplished by chopping and piercing. In the young, cusps served to hold, pierce, and cut prey, while older individuals lost the need for cusps, either as a result of change in the predator-prey size relationship or a change in diet.

The presence of single-bladed splenial elements in populations of Permian *Gnathorhiza* has been noted by Berman (1968). Single-bladed splenial elements comprise 19.5 percent of the total number of *Monongahela* lower jaws, and comprise a minimum of 16.1 percent of individuals sampled in this study. The size-range of single-bladed splenials is great. CM 19464 (fig. 14) is the largest splenial of any sort found.

These peculiar elements differ from normal *Monongahela* splenials in few ways. Most important, the transverse and posterior tooth blades are not present. The anterior blade is proportionally equal, in length, to the same element of a normal splenial. Shearing wear along the posteromesial half of the blade is evident (fig. 15) in all but the smallest specimens, as Berman (1968, fig. 2D) has illustrated for *Gnathorhiza*. No other acute differences are known and no palates that match this lower jaw have been found. Several specimens give some insight into a developmental peculiarity of high frequency and surprisingly great duration. CM 19461, a very small single-bladed splenial, displays one cusp oriented at an angle equivalent to the transverse blade, and one cusp oriented at an angle equivalent to the posterior blade. These two cusps are quite small, and are at the posterior end of the large anterior blade. CM 19464 bears one exceedingly small, rounded cusp on its posterolateral edge. CM 19463 bears a slight posterolateral ridge. CM 19444 and CM 19476 each display two rudimentary cusps of the transverse ridge, and CM 19481 displays a rudimentary transverse ridge.

The single-bladed splenial is evidently produced through a reduction in the number of teeth in the posterior two ridges coupled with a lack of growth or exceedingly limited growth of the teeth that were present.
Fig. 15. Monongahela stenodonta. CM 19464. Right splenial, single bladed. Lingual view. Unit is 1 mm.
The anterior ridge is normal in shape, size, and position, but the splenial lacks a prominent "heel" to stop jaw travel by contact with the "heel" of the upper jaw. An abnormal, though functional, shearing action can thus take place between the anterior ridges of upper and lower jaws.

No palate has been found that would correspond to a single-bladed splenial in form or function, either in the Duquesne limestone or in the Permian Leuders formation (Berman, 1968). Berman has inferred that this type of splenial is simply an aberrant lower jaw. When a specific change in dentition of this magnitude, reflecting a relatively major change in jaw function and almost certainly in diet, can be demonstrated in high proportion over a considerable span of time and space, it is obviously an important biologic and ecologic factor. As the single-bladed splenial seems to arise through a developmental abnormality, it seems unwise to grant it separate taxonomic status at present.

Conclusions

*Monongahela* is clearly related to the Permian *Gnathorhiza* (fig. 16), differing chiefly in the interrelationships of the pterygoid tooth rows. Derivation of the *Gnathorhiza* palate may have been accomplished by a mesial shift in the point of origin of the most posterior tooth row, plus a spreading of the space between rows. Detailed treatment of this problem will appear in a later paper on some lower Dunkard *Monongahela*.

The *Monogahela-Gnathorhiza* group shows definite similarities to the very young *Sagenodus* described above. The blade-like anterior tooth row, and the tendency towards a blade-like second row in *Sagenodus* is quite reminiscent of *Monongahela*. The presence of only one more tooth row in *Sagenodus* jaws than in *Monongahela* jaws of the same size is an important addition to the similarities. At present, however, there are obvious barriers to a clear relationship between *Sagenodus* and *Monongahela*. Similarities exist only at the earliest ontogenetic stages of *Sagenodus*. As *Sagenodus* grows, it adds cusps and tooth rows, until at the adult condition it reveals basically different chewing motions, dietary adaptations, and ontogenetic patterns from *Monongahela*. Body form and skull bones are also quite different. Nevertheless, it is possible to conceive of an ancestral condition of *Sagenodus* from which both *Monongahela* and *Sagenodus* might be derived.

Contrary to the assertions of Berman (1968), there is a striking
Figs. 16-17. Fig. 16 Gnathorhiza dikeloda. FMNH UF 45. Right pterygoin. Ventral view, Unit is 1 mm. Fig. 17. Protopterus annectans. Right pterygoid. Ventral view. Unit is 1 mm.

similarity between the Gnathorhiza-Monongahela group and the recent lepidosirenians in cranial morphology (Olson, 1951), in habit (Romer
and Olson, 1954; Sterba, 1963), and in tooth-plate structure, development, and function. Two differences are conspicuous.

The palate of Protopterus (fig. 17) has but three tooth blades, contrasted with four in Paleozoic forms. Further, the proportionally longest tooth blade is the most posterior rather than the most anterior blade. It has been shown, however, that the most posterior pterygoid tooth row of Monongahela is very short in small individuals and that it is late in developing. Further, suppression of splenial tooth rows is not unusual in M. stenodonta and Gnathorhiza, and is not an improbable mechanism by which the Protopterus pattern may have been derived. It may be pointed out that two small palates of M. stenodonta (CM 19420 and 19421) apparently lack a posterior-tooth row. Differences in proportional length of tooth rows between the Paleozoic and the Recent are to be expected.

The pterygoid bone of Protopterus is a vertically expanded element with little flattening under the tooth rows. The pterygoid bones of the Paleozoic genera are thin, flattened horizontal plates, somewhat extended under the tooth rows. The Recent fish appear to have strengthened the bony support for the palate considerably, a difference that is not anticipated in the Pennsylvanian fossils.

The diet of the Recent forms varies between small vertebrates and shelled invertebrates like snails and small bivalves (Sterba, 1963, p. 846). The tooth-blades, admirably suited to such a diet, are themselves substantially identical in form to those of the Paleozoic genera, and widely divergent from the crushing dentition of the ceratodont line and Epiceratodus.

Summary

The non-actinopterygian portion of the Duquesne limestone fish fauna consists of an acanthodian (microphagous?), two xenacanthid sharks (large and small predator), a hybodont shark (crushing-invertebrate feeder), a large dipnoan (scavenger-predator-herbivore) and a small dipnoan (crustacean feeder-predator). The actinopterygian portion of the fauna contains small, abundant secondary and tertiary consumers only.

Monongahela is a dipnoan approximating the ancestors of Gnathorhiza, and closely approximating the ancestor of the modern Lepidosirenidae. Although an ancestor for Monongahela is not known, the young stages of Sagenodus seem to be morphologically close to the necessary conditions.
References Cited

Agassiz, L.

Berman, D. S.

Bevrich, E.

Case, E. C.

Darrah, W. C.

Eastman, C. R.

Fritsch, A., von

Gluckman, L. G.

Hotton, N.

Johnson, M. E.

Kent, B. H.

Moran, W. E.

Newberry, J. S.

Olson, E. C.

Raymond, P. E.

Romer, A. S.

Romer, A. S., and E. C. Olson

Schweinfurth, S. P.
Sterba, G.

Stevenson, J. J.

Stromer, E.

Westoll, T. S.

White, J. C.

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