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This volume is dedicated to Dr. Rainer Zangerl

New Agnathous Fishes from the Pennsylvanian of Illinois

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Among the several well-preserved but perplexing animals in the Middle Pennsylvanian (early Westphalian D) Essex fauna of northern Illinois (Richardson and Johnson, 1971) are two which appear to be chordates at the agnathan level of organization. Both show elaborate oral and pharyngeal structures without analog among known chordates. Some cranial elements are indicated by darkly stained patches on the plane of the concretions, but, if cartilaginous skeletons were developed, they were uncalcified and less substantial than those of *Mayomyzon*, a lamprey (Bardack and Zangerl, 1971) found in the same fauna. It is quite possible that the two animals described here are larvae with a still unknown adult phase.

The Essex fauna lived on a delta at the end of an embayment in the northeastern corner of Illinois Basin. Fine clastic material, with occasional increments of sand, was brought in by streams that flowed for long distances through a coal swamp; in and adjacent to the streams lived animals of the Braidwood fauna. The vertebrates of both faunas are represented almost entirely by small individuals; the presence of large and presumably mature individuals is indicated by scattered scales and bones of large lungfishes and rhipidistians plus large coprolites and rare teeth and cartilage elements of

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sharks. The delta environment, both subaerially and subaqueously, provided suitable habitat for young animals. The specimens here described occur in Pit Eleven of the Peabody Coal Company in Will and Kankakee counties. Within this pit, one traverses a sequence of ancient environments from shallow marine at the south to a marginal shore zone at the north, and in the band of other pits farther north a subaerial zone. Local concentrations of various members of the fauna indicate that local habitats must have varied in depth, salinity, warmth, vegetational cover, turbidity, and other environmental parameters. The preponderance of small forms among the fishes (as well as the tetrapods, eurypterids, and xiphosures) suggests that this portion of the delta provided a modicum of protection from rapacious adults.

Phylum Chordata

Class Agnatha

Pipiscius, new genus

Diagnosis.—Small agnathous fishes with oral structure comprising 23 collar lamellae and 23 plates surrounding a circular buccal cavity. At least 4 gill clefts. Post-anal dorsal fin.

Derivation of name.—From *pisc*, L. for fish + *pi* as a reduplicated syllable.

Pipiscius zangerli, new species. Figures 1-5.

Diagnosis.—Same as for genus.

Holotype.—Field Museum of Natural History (FMNH) PF 8344 part and counterpart, Pit Eleven, Peabody Coal Co. Collected by Mr. and Mrs. F. A. Wolff.

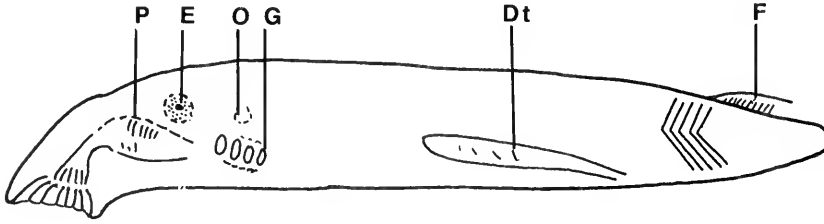

FIG. 1. *Pipiscius zangerli*, n. g., n. sp. Diagrammatic restoration of the whole animal in lateral view, including internal structures. Dt, digestive tract; E, eye; F, fin, G, gill pouches; O, otic capsule; P, pharyngeal chamber.

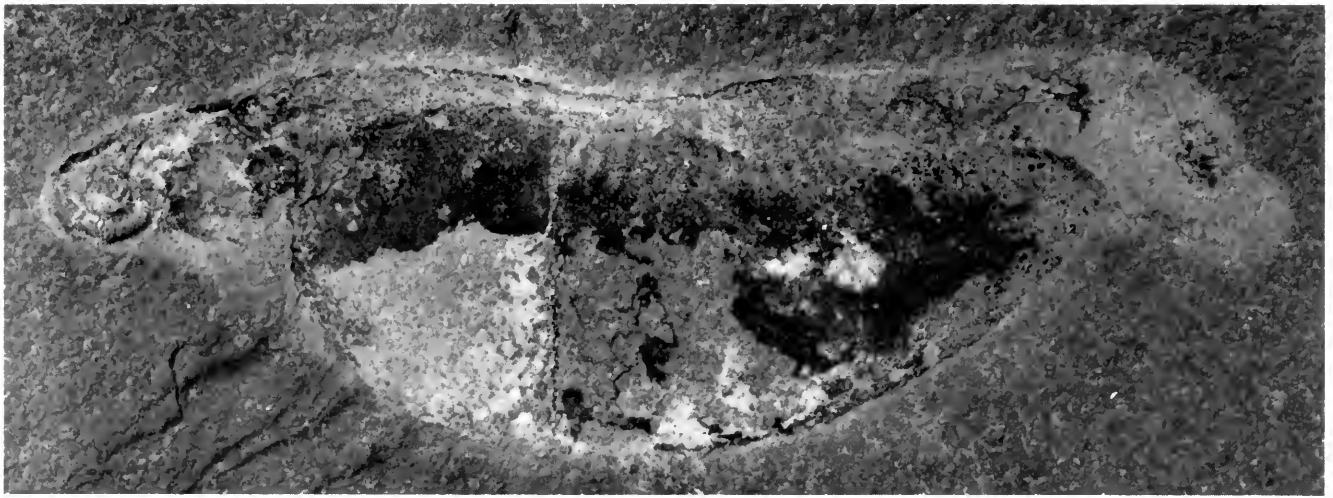

FIG. 2. *Pipiscius zangerli*, n. g., n. sp. Specimen 34 mm. long, anterior to the left. Douglass Collection, no. 604.

Referred specimens.—FMNH: PF 8345, one piece; PF 8346, part and counterpart; PF 7514, part and counterpart. Sobolik Collection, P 33, part and counterpart. Piecko Collection: HTP 153, one piece; HTP 5099, part and counterpart; HTP 5431, one piece. Kimball Collection, part and counterpart. Sherman Collection, 1180, part and counterpart; Douglass Collection 604, part and counterpart.

Geologic horizon and locality.—Pit Eleven, Peabody Coal Co., Will and Kankakee counties, Ill., Francis Creek Shale, Carbondale Formation (Westphalian D).

Derivation of name.—In honor of Dr. Rainer Zangerl.

Description.—This account is based on all 10 known individuals (fig. 1). Specimens range in length from about 4 to 6.5 cm. and body depth varies from 0.7 to 1.4 cm. About half of the specimens, predominantly the shorter individuals, exhibit a plump ventral distension of the body. This ventral expansion may be a remnant of a yolk sac similar in form to that of a late stage of anuran embryonic development (fig. 2). Larger individuals are elongate and possibly circular in cross-section. Most individuals are preserved in lateral aspect, although the head end is often twisted so that the characteristic mouth structure is viewed dorsally or ventrally (fig. 3). Although no distinct hard parts are preserved, certain consistent pigmentation patterns, depressions and ridges, particularly in the mouth region, permit tentative reconstruction of some internal anatomy.

The head as a whole is not topographically distinguished from the body. Anteriorly, between the mouth and the eye, the head appears rather flexible, as suggested by the rotation of the mouth parts in laterally preserved individuals. A notch in the dorsal and ventral margins of the head anterior to the eye, ventrally extended profile of the oral part of the head and some darkly stained areas above the mouth all suggest the presence of an oral hood analogous to that of modern adult lampreys.

The mouth margin and the wall of the mouth cavity were surrounded by a firm substance that has not been preserved but has left a distinct impression (figs. 4, 5). Proximally, the mouth structure comprises a collar in the shape of a thin truncated cone, its wall composed of 23 rectangular lamellae (collar lamellae), with thin radial vanes (collar vanes) projecting into the lumen of the oral cavity at the junctions between lamellae. Distally the collar vanes terminate in a knob-like thickening. The lamellae and vanes on the

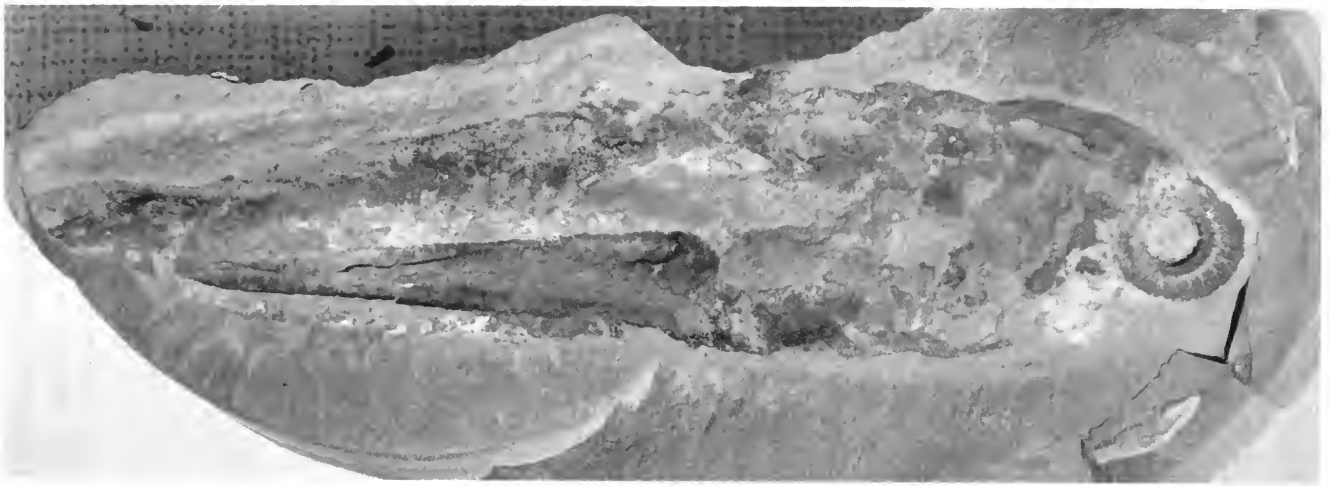

FIG. 3. *Pipiscius zangerli*, n. g., n. sp. Holotype, FMNH PF 8344, 56 mm. long, anterior to the right.

FIG. 4. *Pipiscius zangerli*, n. g., n. sp. Impression of inner surface of mouth, as viewed from within the animal, anterior to upper left. FMNH PF 8344, holotype, ×12.5

anterior aspect of the collar are somewhat longer and wider than those on the posterior. A deep pit (collar pit) is excavated into the junction of each pair of collar lamellae, on the outer surface, opposite each vane; these pits are very pronounced in the anterior aspect and become faint or absent toward the posterior aspect. An irregular system of polygonal ridges on the outer surface of the lamellae suggests that either the substance was cracked by volume loss during decay or the lamellae were compound.

Distally, the collar articulates at about a right angle to a more elongated and distally expanded set of 23 plates, forming a circle that is gently inflected to embrace the margin of the mouth. Distally, the diameter of the circle is about twice the proximal diameter of the collar. The circle plates, like the structures of the collar, are larger in the anterior aspect. A plate lies opposite each collar vane. Each plate is roughly triangular in outline, thickened just beyond its junction with the collar, then thinning and narrowing distally. The thickened regions of neighboring circle plates abut against each other and probably could pivot on this abutment. Each plate also bears on its midline a radial vane (circle plate vane) projecting into

FIG. 5. *Pipiscius zangerli*, n. g., n. sp. Impression of outer surface of mouth, as viewed from outside the animal, anterior toward left. FMNH PF 8344, holotype, ×12.5

the lumen of the oral cavity. The vane terminates in a thickening adjacent to that of the corresponding collar vane. A triangular area with its broad base at the distal end of the mouth lies between each pair of circle plates. It, too, has a central vane on the buccal surface.

This complex mouth structure must have been operated by a set of muscles. The collar formed a fixed diameter, with little or no potential for expansion or contraction; however, a set of circumferential collar muscles might have provided for a limited amount of expansion. Most of the movement of the mouth structure was confined to the circle of plates. Muscles running between the terminal knob-like thickenings of the collar vanes and plate vanes could draw the plates inward. Circumferential muscles between adjacent circle plates assisted in constricting the distal opening of the mouth. Restoration of an open position could have been achieved by muscles or ligaments extending between the collar pits and the thickenings of the circle plates.

Behind the mouth, several specimens exhibit an impression of a slender tube followed by an expanded cavity with a series of ridges

and grooves. We interpret this as a pharyngeal tube and pharyngeal pouch surrounded by muscles and capable of pumping nutritive material into the animal. Coupled with the mouth structure, it provided a strong feeding mechanism capable of ingesting detritus or small invertebrates.

A pair of eyes represented by discs of pigmented material with a small, clear central area doubtlessly occupied in life by a lens, lies above the pharyngeal pouch. Behind the eyes a slightly anteroposteriorly expanded bulbous structure may represent the otic capsule. Beginning behind the pharyngeal pouch and extending below and behind the otic capsule lies a series of at least four dorsoventrally expanded clefts (clear, unpigmented areas). Each is surrounded by darkly stained areas which are most emphatically marked ventrally. In some specimens these pouches are small and closely packed, while in others they occupy a broader area. These clefts and surrounding tissues are probably the gill pouches. We are somewhat puzzled by the limited number of such respiratory structures in an agnathan. Possibly the entire set is not well preserved or more may be added ontogenetically. The latter alternative is unlikely, however, as living *Petromyzon* show all gill pouches by embryonic stage 15 (Piavis, 1971)—at about 0.5 cm. body length.

Several other deeply pigmented areas, especially in the head region, are indicative of developing cartilaginous or other head structures. None shows a sufficiently consistent pattern in several specimens to enable us to assign it to a specific structure. Some of these pigmented areas, especially around the eyes and below the gill pouches, suggest that thick, rigid structures would be formed.

No distinct features of the anterior part of the digestive cavity are indicated by pigmentation patterns as in *Mayomyzon.* Two specimens (FMNH: PF 8344 and PF 8345), however, display an elongate tubular swelling which is rounded at its anterior end about midway along the length of the body and tapers toward the rear margin of the body cavity. This expanded area is filled with fine-grained mineral material somewhat different from that of the rest of the concretion and characterized by several irregular vertical grooves and folds. It probably represents the digestive tube; the folds and grooves suggest muscular folds of the tube wall. It is probably not a coelom filling because it is surrounded by large, clearer spaces and lies well below a darkly pigmented region which should be expaxial musculature.

Myomeric segmentation is evident at the rear end of the body. The segments are especially distinct across the posterior end of the body cavity, where more than 20 may be counted. While dorsal and ventral ends are indistinct, the myomeres appear in the form of a posteriorly opened V with a shorter upper than lower arm. There are neither paired fins nor a distinct caudal fin. There is a short dorsal fin at the posterior end of the body, supported by at least 10 slender rays.

Gilpichthys, new genus

Diagnosis.—Elongate agnathan fishes with tubular, muscular buccopharynx bearing teeth; at least six gill clefts; no fins.

Derivation of name.—For Orville L. Gilpin, Chief Preparator, Department of Geology, Field Museum of Natural History; and *ichthys*, G., fish.

Gilpichthys greenei, new species. Figures 6-11.

Diagnosis.—Same as for genus.

Holotype.—FMNH PE 18703, part and counterpart, Pit Eleven of Peabody Coal Company, Will or Kankakee County, Illinois.

Referred specimens.—FMNH: PE 23464, part and counterpart; PE 18703, part and counterpart; PF 8349, part and counterpart; PF 8347, part and counterpart; Douglass Collection, unnumbered, part and counterpart; Piecko Collection, HTP 4700, part and counterpart; Wolff Collection 164, one piece; Rockwell Collection 5211, part and counterpart.

Geologic horizon and locality.—Pit Eleven of Peabody Coal Company, Will and Kankakee counties, Illinois; Francis Creek Shale, Carbondale Formation (Westphalian D).

Derivation of name.—For Mr. Frank A. Greene, Jr., of Coal City, Illinois.

Gilpichthys is an elongate, slender animal ranging in length from about 4 to 14 cm. and in depth from about 5 to 13 mm., measured in the area of the gills (fig. 6). We have examined more than 100 specimens. Before well-preserved specimens became available, the buccopharyngeal structure was taken to be a radula, with the consequence that *Gilpichthys* was called a mollusc. It has appeared in the literature as "nudibranch gastropod" (Johnson and Richardson, 1966, table 1 and p. 628), "sea slug" (Richardson, 1966), "nudibranch" (Johnson and Richardson, 1970, p. 56), and "an elongated,

banana-shaped soft-bodied animal . . . with a molluscan radula" (Richardson and Johnson, 1971, p. 1,229).

It appears that the body was somewhat deeper than wide, i.e., somewhat compressed laterally, as nearly all specimens lie on a lateral surface. The body is inflected ventrally anterior to the gills on most specimens. Others simply show the body in the form of a gentle curve, concave ventrally. We are not certain as to the functional significance of this shape, but do not believe that it represents a post-mortem deformation. There are no external projections from the body. *Gilpichthys* lacks both paired and unpaired fins.

Differential staining of the matrix demonstrates the presence of a coelom (fig. 7). This lies between an anterior head end, which is somewhat more than one-quarter of the total length of the animal, and a tail area slightly less than one-fifth of the body length. Within the coelom, several specimens show the digestive tract as an irregularly zigzagging tube filled with compressed, finely comminuted material. Across the body in the area of the coelom, many specimens show a dozen to 20 myomeric segments. Additional segments no doubt were present. Although dorsal and ventral ends of the myomeres cannot be clearly seen, it appears that each myomere includes a long ventroposteriorly directed section and a shorter (less than one-third as long) dorsoposteriorly sloping section. In addition to the digestive tract, several specimens show a broad, elongate, darkly stained area at the anterior end of the coelom. By analogy with *Mayomyzon*, this is believed to be the liver (fig. 8). It is concave anteriorly, and in this concavity lies another dark region

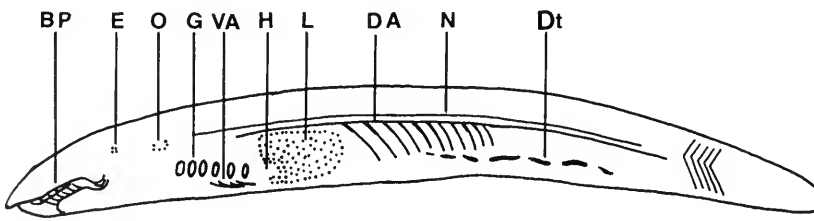

FIG. 6. *Gilpichthys greenei*, n. g., n. sp. Diagrammatic restoration of whole animal in lateral view, including internal structures. BP, buccopharynx; DA, dorsal aorta; Dt, digestive tract; E, eye; G, gill pouches; H, heart; L, liver; N, notochord; O, otic capsule; VA, ventral aorta.

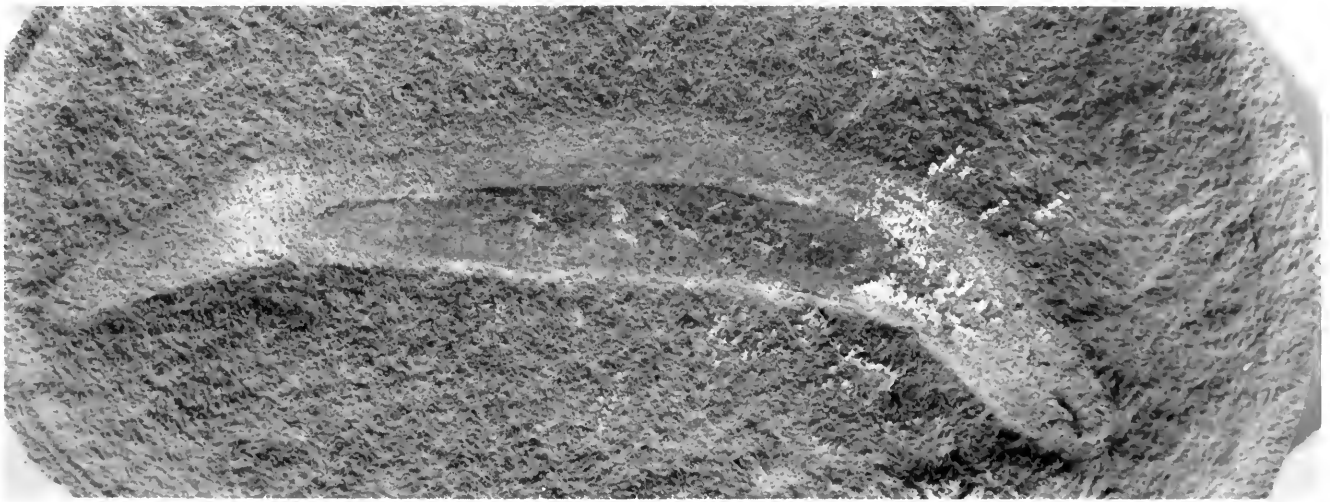

FIG. 7. *Gilpichthys greenei*, n. g., n. sp. Specimen 7 cm. long, anterior to the right. Rockwell Collection, no. 5211.

slightly separated from the liver; this is presumably the heart. Emerging from the ventroanterior end of the heart, a short, dark linear stain appears. A similar darkly stained linear structure runs along the dorsal margin of the coelom. These structures, the darkest-stained features of the animal, are ventral and dorsal blood vessels, respectively. From the dorsal aorta several dark stain patterns, evenly spaced, extend ventrally across the upper part of the coelom. These are segmental blood vessels, one parallelling each myomeric segment. Anterior to the heart one sees four to six (the exact count is uncertain) clear areas surrounded by dark stains. These presumably represent gill pouches and gill pouch openings.

The notochord (fig. 9) is represented by an impression of the notochordal sheath, glabrous but transversely striated in irregular wrinkles; the sheath is 0.7 mm. wide. It is flanked dorsally by a similar structure, 0.4 mm. wide, more prominently wrinkled and with well-defined margins; this is the covering of the dorsal nerve cord. A second sheath, similarly wrinkled and also with well-defined margins, flanks the notochord ventrally and embraces the dorsal blood vessels; this sheath is also 0.4 mm. wide. Within the notochord there are numerous small bodies of a brownish mineral, weakly effervescent in dilute hydrochloric acid, soft and waxy to the pressure of a needle. It is not possible to remove a mineral body for analysis without undue damage to the notochordal structure, so we simply call attention to its similarity to the phosphatic material of bones and ganoid scales in associated concretions. These bodies are probably centers of mineral deposition marking an early stage of chondrification of the notochord. There is no evidence of development of neural or haemal arches. Heavy wrinkles in the firm margins of the neural and haemal sheaths are irregularly spaced at about five to the millimeter. As preserved, the notochordal sheath appears to originate in the vicinity of the otic capsule. It is not visible beyond the anal region, but must have continued caudally in life, as its position is indicated by a line of slender, longitudinally oriented phosphatic rods about 0.2 mm. long. The tripartite sheathing of the neural canal, notochord, and dorsal blood vessels is similar to that of a lamprey as shown by Devillers (1954).

Several structures are preserved in the head region. There is a pair of eyes which are represented by the pigmented retina and a central clear region which in life was occupied by a lens. The eyes are between 0.15 and 0.2 mm. in diameter, with lenses 0.03 mm. in all specimens, regardless of body size. They lie about midway between

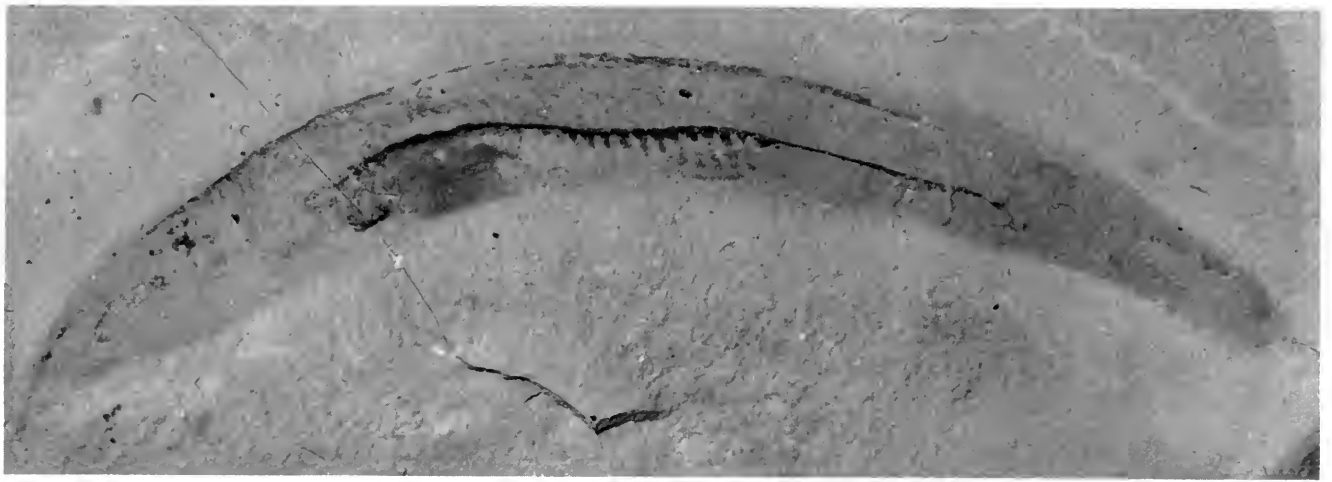

FIG. 8. *Gilpichthys greenei,* n. g., n. sp. Specimen 8 cm. long, anterior to the left. Wolff Collection, no. 164.

FIG. 9. *Gilpichthys greenei*, n. g., n. sp. Dorsal region of trunk, showing neural (Ne), notochordal (No) and haemal (H) sheaths. FMNH PE 23464, ×15.

the gills and the front of the head, behind the buccopharyngeal chamber. Behind and above the eyes, many specimens show a pair of ovoid dark stains which represent otic capsules. We have observed several stains in the head region in the form of plates or bars. A pair of bars runs across the otic capsules from back to front. Another mass characterized by vertical linear striations across its surface appears at the anterior end of the head. A cup-shaped structure (? an olfactory capsule) lies anterior to and above the eyes. The outlines of these masses are not distinct and consistent from specimen to specimen, so they cannot be compared with confidence to known features of the head skeleton of agnathans. They probably indicate that cartilaginous (?) structures of the cranium were being formed in these areas.

The most striking feature of *Gilpichthys* appears in its mouth and pharyngeal region. The buccopharyngeal chamber, 0.5 to 1 cm. long, comprises an elongate lumen surrounded by a series of muscular segments. The buccopharynx parallels the body, but is bent sharply ventrad at the anterior end. There does not appear to be direct contact with the exterior of the animal. Possibly some kind of hood or lip-like structure surrounded the mouth opening, by analogy with lampreys or hagfish, as is suggested by the projection of a part of the head outline anterior to and below the mouth.

The buccopharyngeal structure itself comprises a series of about 20 segments which decrease in thickness posteriorly (fig. 10). Each is made up of four block-like masses, presumably formed of muscular tissue. There is no indication of hard structure, either bone, cartilage, or keratin. The rigidity and tumescence of these units suggests that they were dense and muscular, and were wrapped in thick but elastic connective tissue. Their block-like, massive appearance is similar to that of the myomeres, and presumably their shape was preserved because these animals were buried rapidly under anaerobic conditions.

The dorsal muscular blocks, the largest and most massive in each segment, cover the dorsal and dorsolateral surface of the buccopharyngeal lumen. Short projections of tissue extend into the lumen from the dorsolateral surfaces of the upper block, and support a single, elongate, slender, fang-like tooth that projects medially and posteriorly (fig. 11). These teeth, large anteriorly, diminish in size posteriorly, and may be present only on the anterior two-thirds of the buccopharyngeal chamber. They were presumably formed of a

FIG. 10. *Gilpichthys greenei,* n. g., n. sp. Scanning electron micrograph of buccopharynx, showing muscle blocks. Anterior to the right. FMNH PE 18703, × 30.

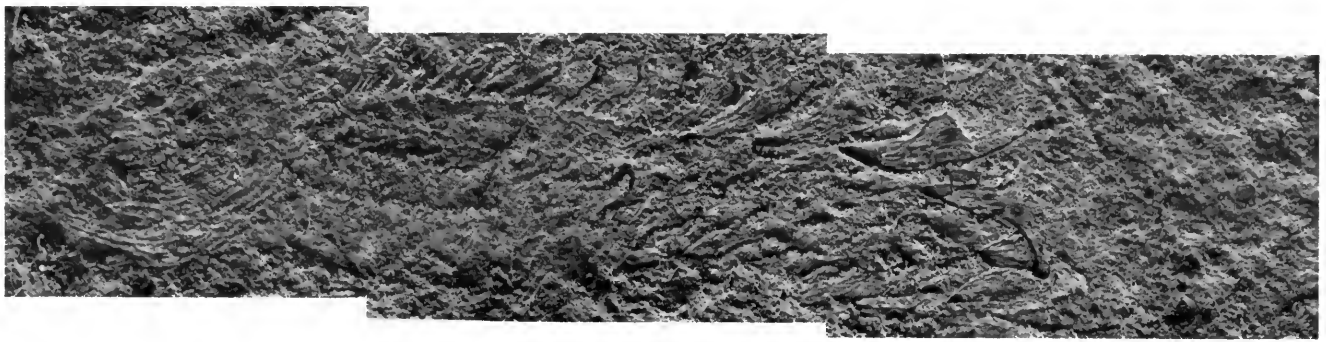

FIG. 11. *Gilpichthys greenei*, n. g., n. sp. Scanning electron micrograph of buccopharynx, showing teeth. Anterior to the right. FMNH PF 8347, × 33.

keratin-like material, and are slightly striated longitudinally. Each lateral wall segment of the buccopharynx is formed by an anteriorly slanted muscle block. Near the ventral end of these lateral blocks a single tooth, shorter than the upper tooth, points medially and posteriorly. The ventral rim of the buccopharynx is completed by another muscle block perhaps a quarter or a fifth the size of the dorsal block. At the anterior end of the mouth cavity there appears to be a single mediodorsal block with a single large tooth which projects posteriorly.

In addition to the muscle blocks which surround the lumen of the buccopharynx, other muscles involved in the function of this organ are preserved. A series of elongated swellings and shallow valleys extends dorsoposteriorly from the dorsal muscle blocks. It is not clear whether these attached dorsally to muscles of the body wall or to cranial cartilages. Thinner bands run ventroposteriorly from the ventral muscle blocks.

A series of semi-circular ridges and valleys, superimposed and giving the appearance of the layers of an onion bulb in cross-section, is connected to the back end of the buccopharynx, surrounding a circular clear area which leads into a dorsoposteriorly directed tube-like structure. Presumably all of these parts are components of the digestive system.

The shape of *Gilpichthys* and its lack of fins suggests that it was not an active predator. Food material probably ranged from living benthos (e.g., annelids, which are common in the fauna) to detrital material that could be procured by simple wriggling movements of the body coupled with ingestion through the specialized buccopharynx. Insofar as intestinal content can be recognized in a few specimens, it appears to include spore exines and crustacean fragments. Presumably the buccopharynx functioned by peristaltic movement. Thus, food could be moved along the buccopharyngeal canal by means of sequential circumferential contraction of the muscular blocks surrounding the canal, coupled with vertical elongation and compression of the canal effected by those muscle masses which attach to the dorsal and ventral blocks. It is possible that the anteromedial muscle block of the buccopharynx with its tooth, and perhaps also the large teeth on the first entire set of muscle blocks, could be everted to assist in picking up food materials. Such eversion of lingual dentition occurs, for example, in hagfishes (Marinelli and Strenger, 1956) when the mouth is opened. It is not clear why teeth should be present along most of the buccopharynx.

Possibly they aided in restricting escape of ingested living material or, in conjunction with muscular contractions, helped to comminute and move food material. Finally, the bulbous structure at the posterior end of the buccopharynx probably assisted in forcing food farther along the digestive tract.

Discussion:—To what group of animals may these new fossils be assigned? If we list the principal characteristics of chordates and of Vertebrata in particular (table 1), *Pipiscius* and *Gilpichthys* require assignment to the vertebrates.

TABLE 1. Chordate and vertebrate characteristics of *Pipiscius* and *Gilpichthys*.

Characteristic	*Pipiscius*	*Gilpichthys*
1. Notochord	—	+
2. Gill slits	+	+
3. Dorsal hollow nerve cord	—	+
4. Angular metamerism	+	+
5. Coelom	+	+
6. Fins	+	—
7. Post-anal caudal region	+	+
8. Otic structure	+	+
9. Otic capsule	+	+
10. Digestive tract	+	+
11. Pigmented blood	+	+

+: character observed; —: character not observed.

Characteristics 1 to 3 are considered definitive of the phylum Chordata. *Gilpichthys* possesses all three. The seeming absence of a notochord and dorsal hollow nerve cord in *Pipiscius* is probably due to non-preservation rather than to absence in this animal. The notochord, let alone the dorsal hollow nerve cord, is not to be expected in fossils, and appears in only three or four of the more than 100 specimens of *Gilpichthys*. We conclude that both *Pipiscius* and *Gilpichthys* are members of the phylum Chordata. Furthermore, we see no features that would suggest assignment to protochordates *sensu lato*.

Among the vertebrates, the taxonomic affinity of *Pipiscius* and *Gilpichthys* seems to lie among the fishes, and most likely with the agnathans. This suggestion is based on body shape, lack of jaws, apparently simple metameric pattern (like that of anaspids) and presence of a fin (in *Pipiscius*). The lack of cartilaginous or ossified structure even in individuals 10 cm. in length distinguishes these

fishes from other agnathans. Furthermore, no known agnathan exhibits the unique oral structures of *Pipiscius* and *Gilpichthys*.

The discovery of soft-bodied agnathans is not surprising in view of the unusual, diverse, unskeletonized animals seen in the Essex fauna. This fauna has already yielded the first fossil lamprey (Bardack and Zangerl, 1971). It is most likely that agnathans of the Paleozoic included not only the typical hardbodied types but also one or more groups that experimented with limited hard tissues or developed such structures at a late ontogenetic stage. A survey of osteostracans, anaspids, and heterostracans shows a variety of mouth shapes and mouth positions. Yet we really know nothing of the soft structures that surrounded these mouths and the pharyngeal regions. The new genera represent additional evidence of agnathan ventures with mechanisms for ingestion.

We are in a quandary as to whether these forms represent larval or adult organisms. The absence of a mineralized skeletal structure and the remnant of a yolk sac in *Pipiscius* may be evidence for a larval condition. There are no unequivocally adult characteristics. The incipient chondrification of the notochord in *Gilpichthys*, strikingly shown in a specimen 9.5 cm. long (FMNH, PE 23464), probably indicates that our specimens are juveniles. On that specimen, the buccal structure is not preserved, though the two eyes are present and are no larger than the eyes of the smallest specimens (0.4 mm. in diameter, 0.6 per cent of the body length). Such remarkably small eyes don't seem in keeping with a juvenile animal, and would be small even for an adult. Perhaps, though no evidence can be adduced, *Gilpichthys* was functionally blind and a denizen of the infauna.

To what degree are *Pipiscius* and *Gilpichthys* related? Overall similarities of these organisms are shown in the descriptions and in Table 1. The principal differences lie in the short, circular mouth of *Pipiscius* in contrast to the elongate, tubular mouth of *Gilpichthys*, and the presence of a fin in the former and not in the latter. While belonging to the same class, they are not close kin.

Both of these animals are known only from the deltaic Francis Creek Shale. *Pipiscius* occurs only in Pit Eleven in Will and Kankakee counties, Illinois. *Gilpichthys*, the more common form, has also been collected about 150 miles (about 250 km.) to the west in Fulton County, in sediments of the same delta.

ACKNOWLEDGEMENTS

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