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THE MORPHOLOGY AND AFFINITIES OF
TULLIMONSTRUM

RALPH GORDON JOHNSON
AND
EUGENE S. RICHARDSON, JR.

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SCORPIONIDA: THE HOLOTYPE OF MAZONIA
WOODIANA MEEK AND WORTHEN
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Pennsylvanian Invertebrates of the
Mazon Creek Area, Illinois:
The morphology and affinities of *Tullimonstrum*¹

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INTRODUCTION

Two distinct faunal assemblages have been recognized in the Middle Pennsylvanian Francis Creek Shale in the Mazon Creek area of northern Illinois (Johnson and Richardson, 1966), both associated with the well-known Mazon Creek flora. The Braidwood concretion fauna is largely terrestrial in aspect and occurs in the principal plant-bearing localities in Grundy and Will counties. The Essex concretion fauna is dominated by marine forms and is known extensively from but a single locality, on the Will-Kankakee county line, although elements of it occur elsewhere. At Braidwood localities plant fossils outnumber animal fossils by more than a hundred to one. In contrast, plant and animal fossils are about equally represented in the Essex facies. Among the most common of the Essex fossils is *Tullimonstrum gregarium*, a large wormlike form (Richardson, 1966). It appears that *Tullimonstrum* represents an extinct and previously unknown phylum.

Tullimonstrum was first brought to our attention in 1958 by Mr. Francis Tully, of Lockport, Illinois. Since that time, thousands of specimens have been collected by amateur and professional paleontologists. The generic name formalizes the usage of the amateur collectors, who called it the "Tully Monster." The name is appropriate in yet another sense: a Norwegian paleontologist has pointed out that *tull* means "nonsense" in Norwegian.

¹This study has been supported in part by a grant from the National Science Foundation (GB 5772).

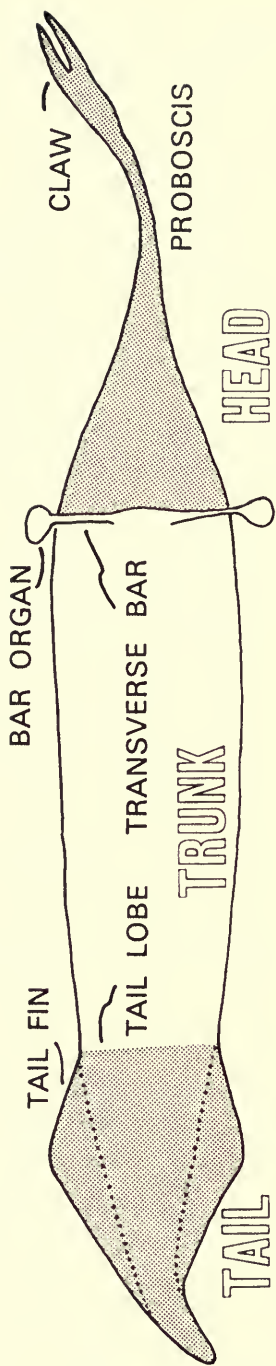


FIG. 63. Principal features of *Tullimonstrum*.

The fossils occur in ironstone concretions in the Francis Creek shale and are found in the spoil heaps of strip mines, principally Pit Eleven of the Peabody Coal Company, two miles south of Braidwood, Illinois. The preservation of fossils in these ironstone concretions has been discussed by Richardson (1956). Most of the best *Tullimonstrum* specimens are from concretions that have split naturally while exposed to weathering on the surface of the spoil heaps. *Tullimonstrum* concretions are difficult to split in the plane of the fossil by a hammer blow. Apparently, the actual fossil is not sufficiently substantial to create a sharp discontinuity, particularly in the slender anterior region.

We have not yet been able to locate the stratum within the Francis Creek Shale in which the *Tullimonstrum* concretions occur, or to determine whether they are indeed confined to a single level. The formation is about 40 feet thick at the mine site, exposed only in a vertical wall that is hazardous to approach. A particular face is exposed for no more than six months before it is removed. Concretions are evident in the shale in the first 6 to 10 feet above the coal and in distinct layers higher in the section. The large number of concretions on the surface of the spoil heaps is the result of a lag concentration due to weathering.

Tullimonstrum concretions are more common in some parts of the pit than in others. The mining operation is such that the shale is dumped in hills opposite the part of the mine face from which it has been stripped. Concretions from a particular geographic part of the mine thereby may remain in association on the spoil heaps though stratigraphic association is disturbed. The local high abundance of *Tullimonstrum* concretions must therefore mean that the fossils were not randomly distributed in the rock. Other fossils occur in similar concentrations. A small hill in the older part of the mine has yielded hundreds of crustacea. Other areas are noted for the occurrence of jellyfish, pectinids, holothurians or other particular elements of the fauna.

The general body shape and principal parts of *Tullimonstrum* are illustrated in Figure 63. The animal was bilaterally symmetrical with a head region, trunk and tail. The head tapers to a long proboscis bearing at its distal end a strange jaw-like apparatus. The head and trunk are delimited by a transverse bar. The trunk is segmented, narrowing posteriorly to the tail. The tail lobe expands laterally into flexible, triangular fins.



FIG. 64. Specimen PE 13867, the head region folded across the body at the transverse bar. Note medial plate of transverse bar. $\times 1.8$.

PRESERVATION

Tullimonstrum is preserved as an impression, detailed in outline but rarely showing evidence of internal features. There are no hard parts, and such organic substance as remains is evidenced only by the retarded oxidation of the fossil impression relative to the sur-

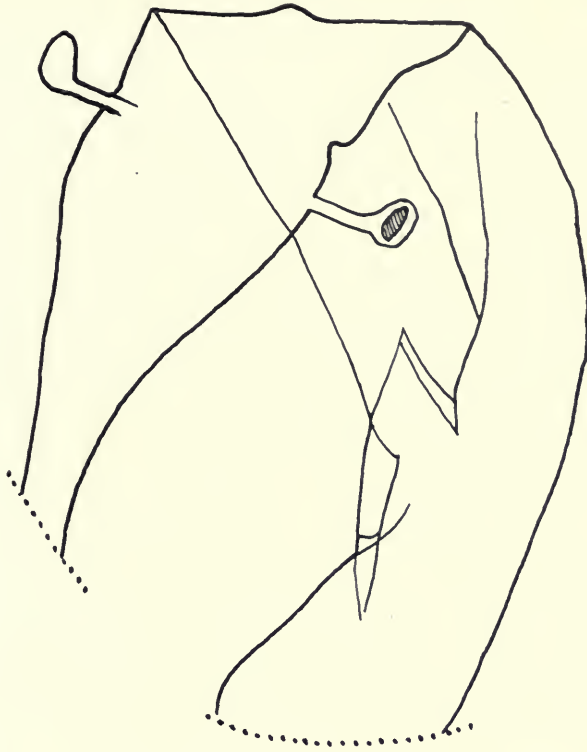


FIG. 65. Sketch of a specimen in the collection of Mr. and Mrs. Ted Piecko, HTP 5212 possibly a folded and flattened empty skin.

rounding matrix. The tooth-like stylets in the jaw remain simply as sharp impressions. Bone, chitin and heavily sclerotized epidermis are preserved in other elements of the fauna, although skeletal calcium carbonate is rare. Associated pelecypods are occasionally coated with a thin carbonate deposit, probably secondary. If *Tullimonstrum* had hard parts they were not composed of bone, chitin or calcium carbonate.

Tullimonstrum is commonly preserved in one plane. Rarely the proboscis or one arm of the transverse bar projects out of the plane of the trunk. The surface of the impression is usually irregular, as if the body of the fossil had been wrinkled or folded before preservation. In specimens having oblique parallel creases or undulations across the trunk, the medial structures are invariably displaced to one side. This circumstance suggests that the oblique markings are produced by twisting of the trunk. Often the proboscis is folded back

across the trunk and in a few specimens the trunk is folded back upon itself. All these features indicate that the animal was soft bodied. Impressions of some sharply folded specimens show no relief and no wrinkling, suggesting that they may have derived from a very thin and delicate empty skin.

It is reasonable to suppose that the relative strength of the impression is related to the density of the original tissue. This is the case in other kinds of fossils where morphology and composition can be inferred from modern analogues (e.g., crustacea, annelids, jellyfish). The jaw apparatus, bar and body margin are the strongest of the impressions. The distinct outlining of the body may be interpreted as due to the stacking of dorsal, ventral and lateral skin under compaction. Not uncommonly, there is a weaker linear impression outside of the trunk, paralleling it and approximating its outline. We offer no explanation of this feature: it may record oscillation of the carcass on the substrate before burial, or an encasing mucous layer.

The sharp outline of the bar demonstrates that it was firm, and composed of relatively dense tissue; it is often the only recognizable structure on badly weathered specimens. The bar organs retain, in part, their three dimensional character (this feature will be discussed in more detail below). The jaws are also preserved in sharp outline and were probably denser in composition than the trunk, a conclusion that is strengthened by the common occurrence of a film of cavity-filling mineral on the jaw.

Serial structures, probably representing internal segmental organs, are seen on a few specimens (Fig. 77). The uncommon occurrence of these structures may be due to the stage of decomposition, particularly in the presence of oxygen (Zangerl and Richardson, 1963, p. 161), attained before burial. In order that such soft-bodied creatures as jellyfish, polychaetes and *Tullimonstrum* be preserved at all, aerobic decomposition must have been minimal. The differences encountered in the state of preservation may relate to trivial differences in the time during which the body of the dead animal was exposed to decay in oxygenated water. Probably the period of exposure was usually long enough for destruction of the softer tissues. Traces of softer, internal tissue were only occasionally preserved. If we had available only a few specimens of *Tullimonstrum*, we would probably have no evidence of the internal structure. It is only by comparing a large number of individuals, in various stages of decomposition, that it has been possible to reconstruct, even tentatively, some features of the internal anatomy.



FIG. 66. A nearly complete specimen of *Tullimonstrum*; PE 8719, X 1, that probably was bitten in the mid-region of the trunk.

Some specimens were mutilated before burial. A few terminate abruptly, a portion of the trunk having been torn away. Several intact but damaged specimens appear to have been bitten (Fig. 66). As the Essex fauna includes a variety of sharks, we may readily interpret these injuries as due to predation. Both the mutilated specimens and abundant coprolites in the associated concretions indicate that feeding activity took place at the locus of deposition.

Nearly all *Tullimonstrum* concretions contain most of an individual. Some concretions have been found to contain only the bar.

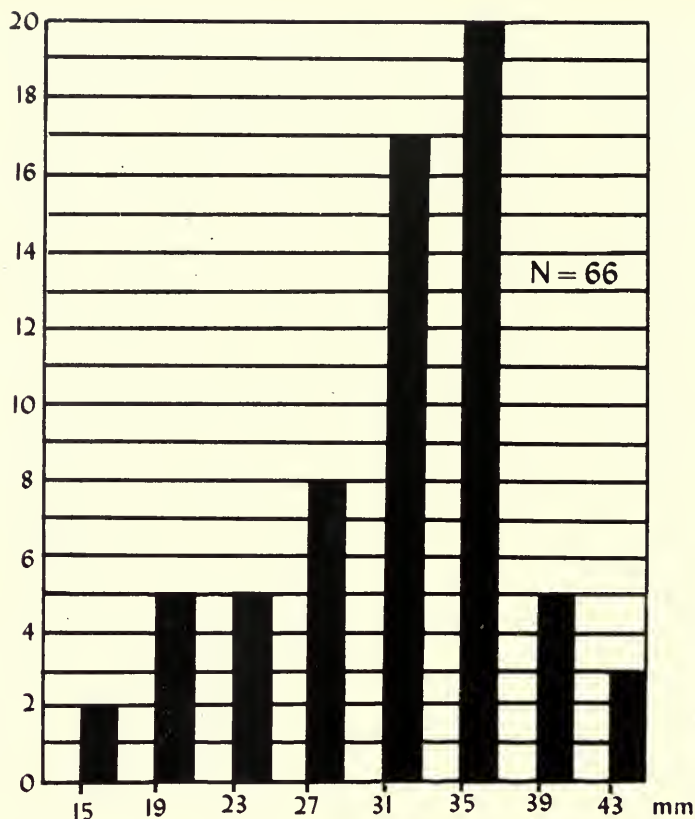


FIG. 67. Size frequency distribution of the width of the bar in mm. in a sample of 66 individuals.

Rarely more than one individual fossil occurs in a single concretion. A jellyfish, a polychaete annelid and an insect have been found associated in this way with specimens of *Tullimonstrum*, and thus manifestly were buried in temporal and spatial association.

Many of the concretions contain pyrite, variously related to the enclosed fossil. Sometimes the pyrite occurs as single crystals or as a dust scattered over the surface of the impression. In one specimen, the bar and bar organs are pyritized in such a way as to reveal the form of the bar and its attachment to the trunk (Figs. 73-75). In many instances the pyrite is not localized directly upon the fossil but occurs in irregular bodies throughout the concretion; in others it forms an imperfect halo around the fossil impression. We do not fully understand the relation between the pyrite and the fossil. The ob-

served variations are probably related to conditions during decomposition of the organic matter incorporated in the concretion.

At present there is no adequate theory to account for the formation of concretions. It is clear that it is partly controlled by the fossil, as the outline of the concretion commonly follows the broad outline of the fossil (e.g., Fig. 66). The preservation, in concretions, of such delicate structures as the tentacles of jellyfish would seem to require that the protective geochemical regime was established very soon after burial. The concretions were certainly formed very rapidly, before complete destruction of the fossil and even before complete compaction of the shale; the reduction of the body of a *Tullimonstrum* to a mere film was probably accomplished as much by biological degradation as by load.

GENERAL FORM AND SIZE

Thirteen measurements were taken on 116 selected specimens. It was not possible to measure more than a few of the 13 characters on any particular individual. The data are summarized in Table 1.

TABLE 1.—Average and range of 13 measurements (in mm.) taken on *Tullimonstrum gregarium* Richardson, 1966.

	Number of specimens	Average	Range
Total Length.....	1	—	91
Bar to Tip of Proboscis.....	13	78	34-103
Length of Jaw Apparatus.....	16	18	5-26
Width of Proboscis at Base of Jaws....	16	3	1-4
Bar to Base of Proboscis.....	66	17	6-34
Length of Trunk.....	32	74	20-154
Bar to Tip of Tail.....	14	97	29-159
Length of Tail.....	33	44	9-65
Width of Bar.....	65	32	16-45
Width of Trunk at Bar.....	79	34	12-40
Maximum Width of Trunk.....	40	25	11-42
Posterior Width of Trunk.....	51	18	6-31
Maximum Width of Tail.....	50	35	9-50

There is no evidence of polymorphism; the size frequency distribution of bar width exhibits a single mode, as shown in Figure 67.

Complete specimens of *Tullimonstrum* are very rare. In order to estimate the range of total length from fragmentary material, the relations between the width of the bar, length of trunk and length of tail were investigated. A least square line of best fit was calculated for the regression of each measure on the others. An example is shown in Figure 68. The regression coefficients were then used to

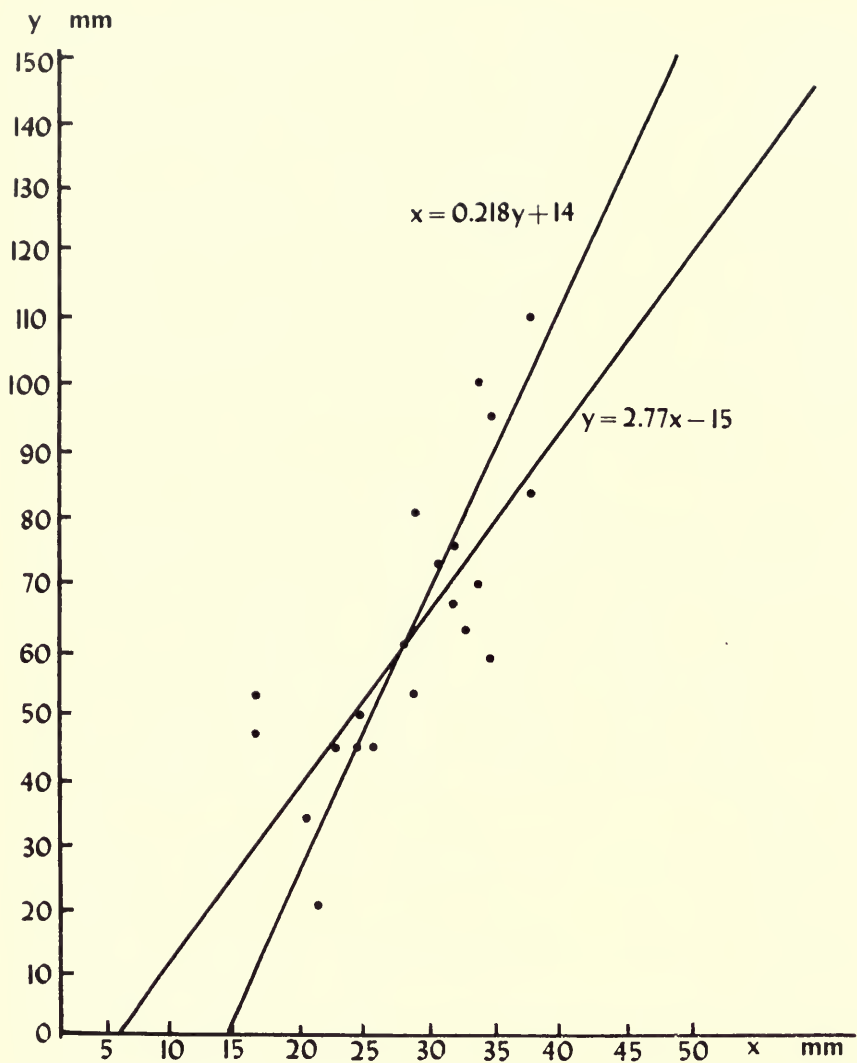


FIG. 68. Regression of width of bar (X) on length of trunk (Y) and *vice versa*.

estimate the restored total length of the largest and smallest specimens known at this time. The largest specimen is represented by a complete trunk, 154 mm. in length, in the collection of Mr. James Konecny. We estimate that this specimen represents an individual 342 mm. in length. The smallest specimen (Field Museum PE 10503) is a complete trunk 20 mm. in length. This corresponds to an individual 80 mm. long.

In general size and body proportions, *Tullimonstrum* resembles the larger bathypelagic nemerteans of the present. These attain a maximum length of several hundred millimeters, with a broad and flat body. If *Tullimonstrum* was circular in cross-section, the largest specimen known would have had a diameter of 35 mm. However, a subcircular cross-section seems more likely. If *Tullimonstrum* had, in life, the body proportions of one of the larger modern bathypelagic nemerteans, it would have had a body thickness of 5 to 15 mm., with a flattened cross-section (Fig. 80c).

MORPHOLOGY

THE HEAD REGION

The head region consists of that part of the body anterior to the bar and including the proboscis. Our division of the head from the trunk is arbitrary: the bar provides a convenient and conspicuous reference. Segments are poorly developed anterior to the bar. The segmental organs occasionally seen in the trunk are not found in the head region. On the other hand, if the bar organs were sensory, as we believe they were, their location along the posterior border of the head is very unusual among invertebrates. The dilemma serves to emphasize the important point that the head region is not well differentiated in the animal.

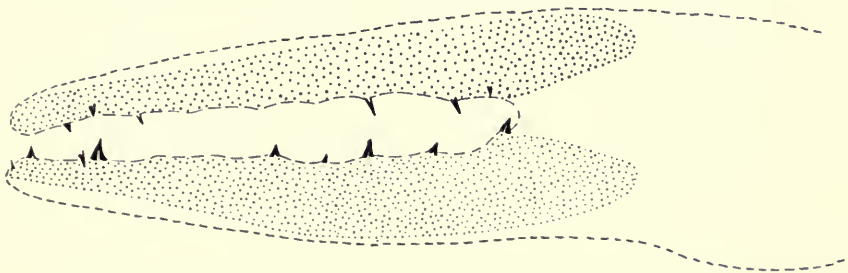


FIG. 69. The jaw of a *Tullimonstrum*, with numerous stylets. The dashed outline represents the margin of the jaw; the stippled area represents pyrite, perhaps localized here by replacement of firm tissue.



FIG. 70. A partial specimen of *Tullimonstrum*, PE 10628, $\times 1$, with the proboscis bent back upon the head. It is the jaw of this specimen that is drawn in Figure 5.

Commonly, the proboscis is not preserved or recovered. In a sample of 511 specimens, the entire proboscis was present in only 14 individuals, although part of it was observed in over half of the specimens. The proboscis constitutes nearly one-third of the total length of the animal.

The anterior end of the proboscis may be considered as two regions; the jaws and their base (Fig. 69). Thirty-three specimens exhibiting these features were studied in detail. The jaws range from 5.5 to 16.5 mm. in length and from 3.5 to 6 mm. in maximum width, including the gape. The base of the jaws varies from 1.5 to 9.5 mm. in length and 3 to 6.5 mm. in width. There is no evidence of a corre-



FIG. 71. Specimen in the collection of Mr. and Mrs. Ted Piecko showing gut and trunk and head segmentation. HTP 727, $\times 1.7$.



FIG. 72a. The anterior region of a specimen in the collection of Mr. James Turnbull.

lation between the length of the jaws and the size of the jaw base. The jaw apparatus may be set at a sharp angle to the stalk of the proboscis.

The jaws bear minute stylets along their inner margins (Fig. 69). The stylets are preserved only as sharp impressions or pyrite replacements; the original material is always absent. They have a broad base and concave sides, and taper to a needle-like point. They are usually about 0.5 mm. in length but range up to 2.4 mm. They



FIG. 72b. The anterior region of a specimen in the collection of Mr. Jay Wollin (W90) showing a very distinct anterior crescent. $\times 1$.

are spaced at regular intervals of 0.8 to 2.4 mm. along the jaws without any apparent order in size. We have observed as many as eight stylets in a single ramus. In some cases, the stylets of one ramus alternate with those of the other, while in other specimens they are directly opposed. The stylets are often scattered about the jaw region as if they had become dislodged upon the death of the animal.

The impressions of the jaws are unusually sharp and clear. Frequently the jaw area is covered with kaolin that was probably introduced into an unfilled space during diagenesis. This feature implies

that the jaw apparatus consisted of denser or more durable tissues than the remainder of the creature. In several instances, the jaws are partially replaced by pyrite (Fig. 69). In one specimen the bases of the stylets are joined by a thin ribbon of pyrite.

The jaw apparatus of *Tullimonstrum*, mounted in the midline of the animal, is unique among invertebrates. The minute, sharp stylets suggest that the jaws served a grasping rather than a masticatory function. The jaw base provides space for a muscle mass to operate the jaws. Although most jaws are very slightly agape, the rami of a few specimens are rather widely spread.

The stalk of the proboscis is usually preserved in outline only. In a few specimens there is a faint medial structure, visible more as a color difference than in relief, running the length of the proboscis from the jaw to about the medial plate of the transverse bar. This structure is interpreted as the lumen of the proboscis; it had not been observed at the time the species was first described.

There is no evidence to suggest that the proboscis was eversible or contractile. No portion of the proboscis has ever been observed within the trunk region except when the proboscis has been folded around the outside of the body and back upon the trunk. In such cases, the outline of the proboscis across the trunk is sharp. If any part of the proboscis could have been withdrawn into the body, the sheathing walls should have been discerned within the trunk. Further, there is no evidence of an internal structure to receive it. No specimens have been seen in which the proboscis is unusually short relative to the rest of the body, although one specimen was found to have an unusually long proboscis. It is possible, but unlikely, that the proboscis was contractile or eversible in life but on death was always extended to its full length. Modern marine animals possessing probosces (e.g., nemertean, echiuroids, polychaetes) usually withdraw them at death.

The head region usually appears unsegmented even in specimens in which the trunk segmentation is distinct. However, several specimens are known in which this region shows traces of two or three segments (Fig. 71). In two instances, head segmentation is represented by small transverse tears or markings along the edge of the head.

Various impressions may occur at the base of the proboscis. Most commonly this region contains one or several circular or crescentic impressions on the midline, extending forward into the basal part of the proboscis. In a few instances these impressions are subcircular



FIG. 73. The transverse bar and bar organs of the pyritized specimen, PE 11211, during the acid treatment. The proboscis and jaw were not adequately pyritized for preservation in this form. $\times 1.1$.

ridges and valleys (Fig. 72a) suggesting strong wrinkles in the basal portion of the proboscis. Invariably, the most posterior of these impressions is the largest and strongest. A large crescent-shaped impression, just anterior to the bar, is the most common feature of this part of the head (Figs. 72b and 80b). In a sample of 511 individuals this structure was observed on 51 specimens. A similar crescent, to be mentioned later, may occur behind the bar.

A medial gut-like structure is visible in trunks of some specimens; in others, the putative lumen of the proboscis extends back to the bar. In one remarkable specimen, these medial structures are continuous, expanding in the vicinity of the bar to a pronounced impression that occupies one-third of the width of the head (Fig. 71). It is conceivable that the expanded portion represents a pharynx or stomach. The

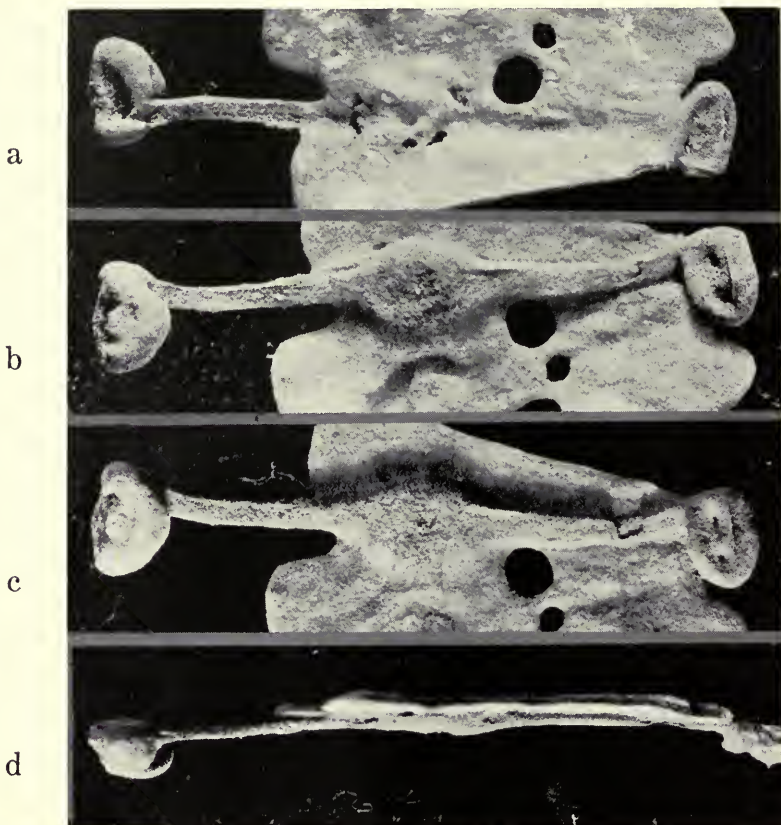


FIG. 74. The pyritized bar and bar organs freed from the matrix (PE 11211): a, upper surface; b, lower surface; c, lower surface, lighted from below to emphasize relief differently; d, cross-section. $\times 2.4$.

anterior and posterior crescents may be relics of the muscular walls of the pharynx or suspensory mesenteries (Fig. 80a). The rarity of the preservation of head segments may be due to the presence of a pharynx which masks other head detail. There would also be less of a tendency for head segments to separate in decomposition in the presence of such a structure (compare trunk and head segments in Fig. 71).

THE BAR AND BAR ORGANS

The most remarkable and constant feature of *Tullimonstrum* is the transverse bar in the anterior region. The bar is preserved in 321 specimens in a sample of 337 anterior trunks. It consists of a

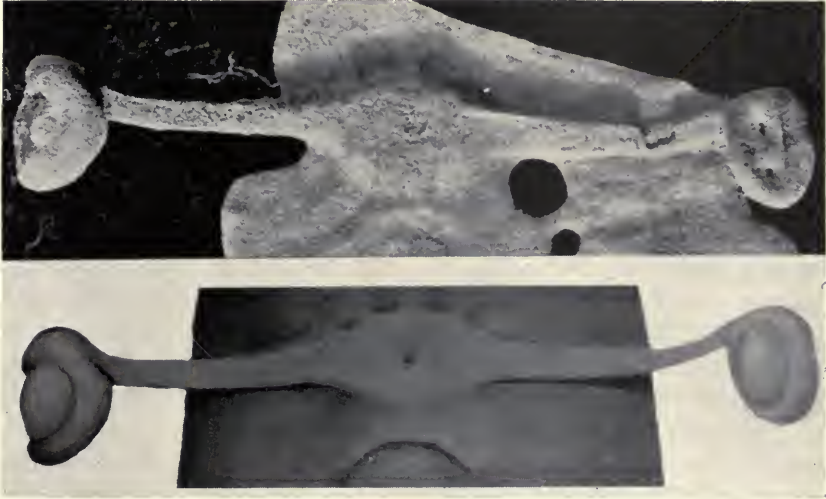


FIG. 75. The pyritized bar and bar organs: a. actual specimen; b. reconstruction.

medial plate and a thin, straight or variably angulated rod (Fig. 80), terminating in small ovoid bodies external to the trunk impression (Figs. 71 and 72). The bar impression is quite strong and often the only recognizable feature of badly weathered specimens. The bar, together with the terminal organs, ranges from 15 to 46 mm. in width.

Much of our interpretation of the bar structure is based upon a pyritized specimen in which the bar and terminal organs are preserved in three dimensions (Figs. 73, 74 and 75), along with some parts of the dorsal and ventral body walls. In this specimen (FMNH PE 11211), the medial plate is a subcircular feature 9.5 mm. in length and 6.0 mm. in width. One surface of the plate, assumed to be ventral, is irregular, with a shallow fan-shaped impression opening out posteriorly (Fig. 74b). The other surface is concealed behind the dorsal body wall (Fig. 74a). The medial plate projects into the same plane as the ventral body wall (Fig. 74c). The rod is straight and nearly rectangular in cross-section, and, as preserved, hollow. The terminal organs are flattened ovoid structures, partially hollow, 5.5 and 6.5 mm. in length. The bar and bar organs project beyond the pyritized trunk (Figs. 74c, 75 and 80c). The pyritized portion of the trunk is two layered, the pyrite having replaced the dorsal and ventral body walls, but not the internal tissues. This interpretation is supported by the fact that the pyritized trunk is 0.6 mm. thick medially and 1.1 mm. thick at the border. As the bar lies distally outside of the

plane of the trunk, it must have been external to the body wall, with the point of attachment at the medial plate (Fig. 75). This plate was probably in part internal.

The medial plate is a featureless swelling on most impression specimens. In some, it appears as two or three adjacent beads on the bar. The bar is usually straight but in a few specimens it is bent backward or forward. In several specimens a straight bar lies obliquely across the trunk. In folded and mutilated specimens, the bar is commonly undistorted. A few remarkable concretions contain only a well-preserved bar and bar organs without a trace of the body (Fig. 76). These circumstances suggest that the bar was a rigid structure, denser and more durable than other body tissues. No original skeletal material, however, has been preserved.

The terminal bar organs are hollow in the pyritized specimen, the matrix material having been removed by the acid used to free the specimen. The greatest part of the organ lies below (or above) the bar and behind it (Fig. 74). The proximal wall of the bar organ is



FIG. 76. Complete concretion containing only a well-preserved bar and bar organs. Wollin Collection, W57 \times 2.

thinner than the distal in the specimen. In the usual specimen, the proximal half of the bar organ is black (Fig. 76). Dr. Edward Olsen has analyzed the black material and found that the color is likely due to a very small amount of an unidentified organic substance. The black material is often distributed in three dimensions as a flattened cup, opening outward. A material very similar in gross appearance is consistently associated with the orbits of fish in these concretions.

✓Our colleagues have suggested that the bar and bar organs might have functioned as stabilizers or otocysts. From a hydrodynamic standpoint, these structures would not seem to be very effective as stabilizing organs. It is also difficult to understand why otocysts would be situated in paired organs projecting outside of the trunk. Sensitive otocysts in other invertebrates are located in the lateral body wall or on the midline. ✓It seems more likely to us that the bar organs are eyes. The hollow ball of the pyritized specimen, and the cup shape in the usual compression fossil strongly suggest a common form of invertebrate eye. The black substance may be derived from the retinal pigment. Overall, *Tullimonstrum* appears to be an active, pelagic animal; it seems probable that such a creature would possess well-developed eyes.

TRUNK

Immediately behind the bar, there is often a strong crescentic impression similar to the one commonly found at the base of the proboscis. The posterior crescent was observed in 123 specimens in a sample of 337 individuals in which the anterior trunk region was preserved. We have no explanation of this feature. In a few specimens, the posterior crescent appears to be the first and strongest impression of a series of medial organs. In other instances, the crescent seems to be associated with the bar region and gut. As suggested earlier, the anterior and posterior crescents may represent the muscular walls of the pharynx, or the attachment of mesenteries. Trunk segmentation was observed in 65 specimens in a sample of 431. In most cases, only a few segments are discernible. The number of segments in complete specimens of the trunk varies from 10 to possibly 16. There does not appear to be any relationship between the number of segments and the size of the individual. One specimen with a trunk length of 33 mm. had 12 segments. Another 57 mm. long had ten. Thirteen trunk segments were observed in a trunk 77 mm. long. The segments can be traced across the entire width of the trunk. In specimens in which a medial gut-like structure is preserved, the segments are faint but clearly visible in the midline. In some instances, the



FIG. 77a. Specimens showing medial trunk organs. $\times 2$. Piecko Collection, HTP 759.



FIG. 77b. $\times 1.75$. PE 10621.

segments appear to have separated laterally during decomposition (e.g., Fig. 71).

In a few cases, there are round impressions on the midline, one such impression within each segment (Fig. 77). These might repre-



FIG. 78. Specimen PE 10616 showing medial impression interpreted as a trace of the gut. $\times 0.9$.

sent nephridia, gonads, ganglia, annulations of the gut or several such structures. Whatever they may be, they are evidence that the transverse lines across the trunk are not superficial, and that the animal was truly segmented. The presence of internal organs in many specimens and the level of organization indicated by segmentation, suggest that *Tullimonstrum* was a coelomate animal.

Several specimens display a straight medial structure throughout the trunk region. Sometimes this structure can be seen to continue into the head and tail (Figs. 71 and 78). If this is the gut, the animal must have had a straight intestine with the anal opening probably at the tip of the tail lobe.

TAIL

The posterior fourth of the body bears lateral fins; this is the tail region (Fig. 63). The body tapers to a blunt point projecting beyond the fins (Fig. 79c). Eight to twelve body segments are found in the region. The tail is spatulate to nearly circular (Fig. 79a,b). The fins appear to have been thin and flexible, as they are commonly wrinkled. In some instances, the fin is thrown into several strong folds normal to the body. In other cases, the wrinkling is very fine and obliquely oriented (Fig. 79a). The wrinkles and folds have never

been seen to continue into the segmented body lobe, except in damaged specimens whose bodies have been distorted.

As we suggested earlier, the gut probably extended through the length of the body to an anus borne at the blunt posterior tip. Although several specimens do show the medial gut-like structure in the tail region, it has not been traced into the terminal lobe. There is no physical evidence of the anal opening, nor would we expect to find one, as it is inconspicuous in most invertebrates.

RECONSTRUCTION

Our speculation concerning the appearance and gross anatomy of the living animal are schematically shown in Figure 80. There is strong evidence for our reconstruction of the body outline, jaw apparatus, bar and bar organs, segmentation and the tail fins. The lumen of the proboscis and the straight gut are based upon only a few specimens. The details of the anterior gut and our identification of the anterior and posterior crescents as diaphragms are pure conjecture based on what we think we see in the singular specimen shown in Figure 71, and in a few other specimens.

Although the integument is not preserved, it is possible to deduce some of its characteristics by reference to the preservation of other animals in the concretions. The chitinous exoskeleton of insects and crustacea is often well preserved. Occasionally, the surface features of the cutinized epidermis of polychaetes persist as impressions. The outline of polychaetes is often sharper than the outline of *Tullimonstrum*. No features of the epidermis of *Tullimonstrum* have been recognized except those arising from folding or twisting of the body. The *Tullimonstrum* impression most closely resembles that of the jellyfish that occur in the associated concretions. The preservation of *Tullimonstrum* suggests that the integument was thin and not heavily cutinized. The absence of an internal skeleton and the apparent ease of folding, twisting and wrinkling of the trunk indicate a flaccid, soft-bodied delicate-skinned animal.

The scant evidence at hand suggests that *Tullimonstrum* had a straight intestine with a terminal anus. The mouth was probably located at the tip of the proboscis. It is conceivable, on the other hand, that one of the crescents represents the mouth, a quite different organization. If the medial structure in the head region of the specimen shown in Figure 71, however, represents a gullet or pharynx, the mouth must have been anterior to the first crescent.



FIG. 79a. The tail region: a well-preserved specimen, PE 7051. $\times 1.4$.

The interpretation of the bar organs as eyes presents several difficulties. The evidence suggests that most of the bar was external to the trunk. We have no way of determining whether the bar was ventral or dorsal. If the animal was pelagic, the eyes might be carried ventrally as in our reconstruction. If it was benthic, the eyes may have been dorsal.

All the evidence suggests that the bar was a fairly rigid structure. The few specimens of bars bent backward or forward may mean that it could be flexed in life. It is frequently found oblique to the body axis. In the specimen shown in Figure 71, it can be seen lying across a segmental boundary. It is barely conceivable that it could be pivoted with or about the median plate in life. If our interpretation of

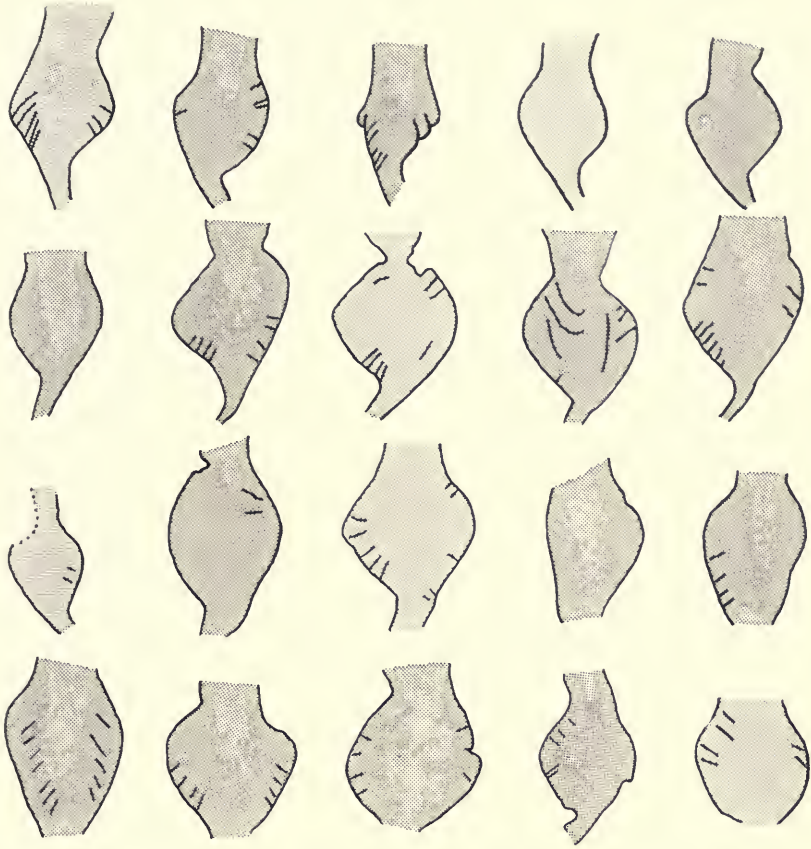


FIG. 79b. Variations in the preserved shape of the tail.

the pyritized specimen is correct, the connection to the trunk through the medial plate could accommodate muscle or ligaments. Such an arrangement would be inefficient, but the force required to pull back one arm of the bar would be small. No other animal is known to have eyes mounted on a fairly rigid bar that could be swung back and forth by muscles located near the fulcrum and point of attachment. This interpretation seems absurd—but the bar itself is a unique and grotesque structure.

There is firm evidence that the body was truly segmented. The width of the segmental boundaries varies as though the segments separated from each other during decomposition. The segmental impressions weaken in the medial region. The medial plate of the bar and the trunk organs occur at the mid-point within segments.

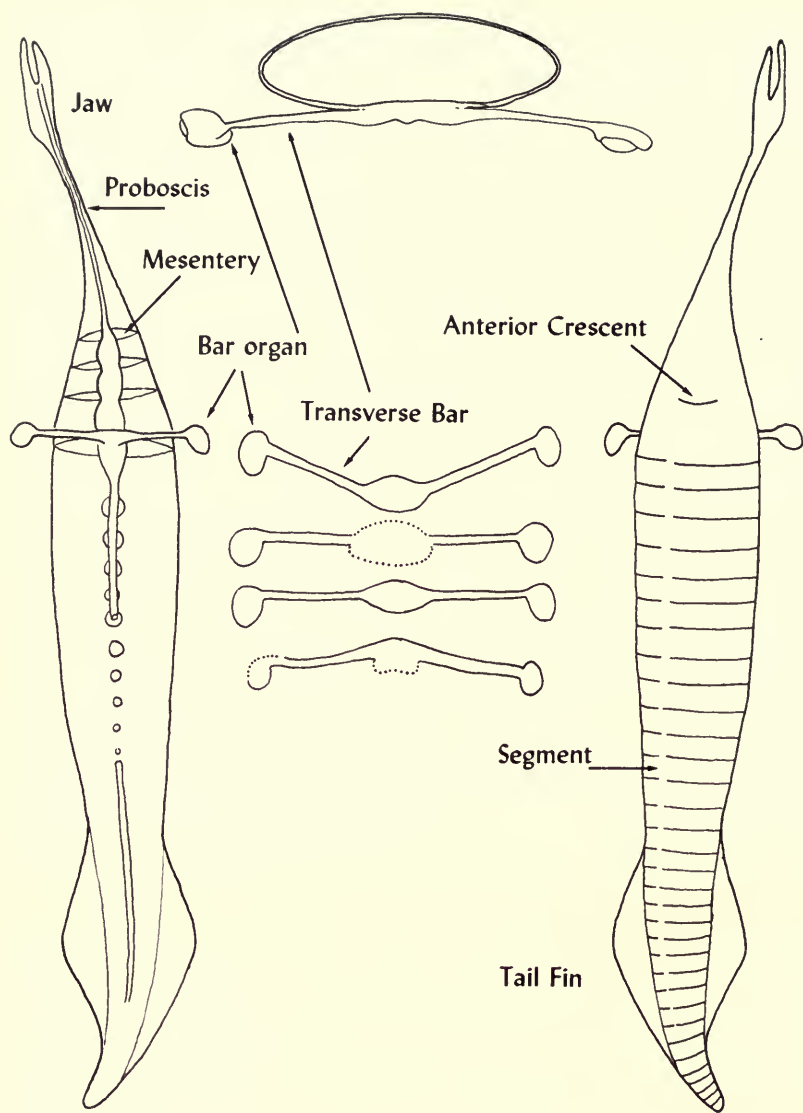


FIG. 80. Reconstructions of *Tullimonstrum*: a. (left) hypothetical internal anatomy; b. (right) external features; c. (center, top) cross-sections in bar region; d. (center) variations in bar flexure.

The segments of the body lobe in the tail region do not impinge upon the fin. It is unlikely that color marking alone would have all of these features. Furthermore, the matrix lying between segments that have pulled apart has the characteristic rough fracture of the matrix outside the limit of the impression.

In summary, our reconstruction of *Tullimonstrum* suggests that it had the following fundamental characteristics:

1. bilateral symmetry
2. homonomous segmentation of body and internal organs; head not distinctly differentiated from the trunk
3. straight intestine, posterior anus
4. irretractable proboscis bearing a jaw armed with stylets.

PALEOECOLOGY

Tullimonstrum was probably a marine organism. It is associated with polychaetes, jellyfish, holothurians, varied crustacea and marine molluscs. There are also terrestrial and possibly freshwater forms present in this association, but these are represented by only a few individuals for each species, and may be assumed to have drifted to this burial site. We have interpreted the environment as shallow marine waters close to extensive swamp forests (Johnson and Richardson, 1966).

Tullimonstrum has the general body form of a pelagic animal. As it was soft-bodied, without an internal skeleton, it was probably a weak swimmer. We suppose it was a carnivore. The stylets of the proboscis do not seem capable of functioning in mastication and were probably used in catching and holding prey. We have never recognized food remnants in the gut region although the gut content is clearly recognizable in many associated species. The gut of detrital feeders is often found to contain sediment, for example.

It seems unlikely that *Tullimonstrum* was a common element of the inshore fauna. If it were, we would expect to find it at more localities. It is possible that *Tullimonstrum* was introduced into the area when a tongue of surface, offshore water was blown inshore. Today, animals characteristic of open offshore waters are occasionally found close to shore in great numbers following a period of strong onshore winds. However, unusual conditions of burial and preservation have given us a glimpse, in this near-shore deposit, of a fauna not normally preservable whatever its habitat.

ZOOLOGICAL AFFINITIES

There is no compelling reason to assign *Tullimonstrum* to any of the known phyla. It could be imagined as an aberrant member of one of several phyla but the critical evidence is not available.

Though the soft body is admirably preserved, the characters that are significant in differentiating the present-day, soft-bodied phyla are not accessible to us. Lacking such information, it would be pointless to assign it to one of these phyla, and even less justifiable to erect a new phylum to accommodate it. It would not be possible to contrast such a phylum with others in terms of such fundamental features as the mode of development of the coelomic cavities. The features of the proboscis and the transverse bar are unique and therefore not useful in assigning *Tullimonstrum* to any known phylum.

In spite of the severe limitations of the materials, we cannot resist the temptation to speculate on the general affinities of *Tullimonstrum*. Its secondary features suggest a systematic position among the lower protostomes at a grade comparable to that of the sipunculoids or echiuroids. It would appear to be of a higher level of organization than the nemertines, although there are superficial resemblances to that group. The degree of segmentation and the differentiation of the body into distinct regions are less than that seen in typical annelids and arthropods. None of the characteristics of known mollusca are evident in *Tullimonstrum*. There is not even a superficial resemblance to echinoderms, chaetognaths, hemichordates or chordates.

Several phyla are represented today by a small number of species (priapulids, phoronids, sipunculids, echiuroids). It is not unreasonable to suppose that these are relics of more extensive radiations in the past. *Tullimonstrum* may also represent a relic in the Middle Pennsylvanian of a more ancient group. Considering the diversity of modern soft-bodied animals, there must be many groups that once flourished and vanished without leaving evidence of their existence. Perhaps the real importance of *Tullimonstrum* is as a reminder that our conception of the diversity of the organic world is based upon a small sample consisting almost entirely of animals with preservable hard parts.

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