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**NUMBER 53**

*TRIARTHURUS EATONI* (TRILOBITA):  
ANATOMY OF ITS  
EXOSKELETAL, SKELETOMUSCULAR, AND DIGESTIVE SYSTEMS

By

JOHN L. CISNE

**1981**

Paleontological Research Institution  
Ithaca, New York, U.S.A. 14850

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May 22, 1981

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*TRIARTHURUS EATONI*\* (TRILOBITA):

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ABSTRACT

The following description of the exoskeletal, skeletomuscular, and digestive systems in the trilobite *Triarthrus eatoni* (Hall) is based on stereoscopic x-radiographic study of over 100 specimens from Beecher's Trilobite Bed in the Upper Ordovician Frankfort Formation near Rome, New York. The head includes one preoral segment bearing paired uniramous antennae, and three postoral segments bearing paired biramous limbs. The relatively large basal segment of postoral limbs, on which both the telopod and exite are inserted, bears a large inward-projecting endite. While all postoral limbs show a high degree of serial homology, postoral head limbs are slightly differentiated from trunk limbs. Basal endites of postoral head limbs were evidently parts of a gnathobasic mandibular mechanism. The abdomen is divided into an anterior pygidial region comprising the five segments that bear the pygidium (their tergum), and a posterior post-pygidial region comprising six to twelve tiny, weakly sclerotized, limb-bearing segments and the telson. The thoracic musculature and endoskeleton conforms to the same basic pattern found in cephalocarid, branchiopod, and phyllocarid crustaceans. Elements of the skeletomusculature show a high degree of serial homology among all postoral segments, and some of these elements are present in not much modified form in the antennal segment. The digestive system includes a J-shaped gut and extensive glands in the head region. The muscular foregut is seemingly developed for suctorial ingestion and trituration of food. A combination of characters — a food groove along the midline between paired postoral limbs, a posteriorly directed mouth cavity, and the conformation of the trunk musculature — indicates that the trilobite had a trunk-limb feeding mechanism of the general type found in primitive, particle-feeding crustaceans.

INTRODUCTION

In this paper I describe the anatomy of the exoskeletal, skeletomuscular, and digestive systems in the trilobite *Triarthrus eatoni* (Hall). This description is based on my studies of X-radiographs of over 100 specimens from Beecher's Trilobite Bed in the Upper Ordovician Frankfort Formation near Rome, New York. I have interpreted the anatomical evidence to ascertain the segmental construction of the body and to reconstruct body mechanisms. I have incorporated new anatomical findings in a review of the trilobite's development and segmental growth.

The papers by Beecher (*e.g.*, 1894a, 1895b, 1896), Raymond (1920), and Størmer (1939, 1951) on these specimens have made *Triarthrus* one of the textbook examples of a trilobite. High resolution stereoscopic X-radiography, a

relatively new technique unavailable to earlier workers, has revealed a wealth of new information on internal as well as external anatomy. Working from many stereopairs of X-radiographs for each specimen, it has been possible to piece together the first moderately detailed picture of trilobite internal anatomy. Economics permit the publication of only a small selection of these pairs. The chosen pairs illustrate only the most important points. As has been discussed elsewhere (Cisne, 1974, 1975; Hessler and Newman, 1975; Manton, 1977) the findings indicate that several changes should be made in earlier ideas on the structure of *Triarthrus*, on the structure of trilobites in general, and perhaps on the relationships of the Trilobita to other arthropod groups.

ACKNOWLEDGEMENTS

This paper is based on my doctoral dissertation in the Department of Geophysical Sciences, University of Chicago (Cisne, 1973 MS). The late R. G. Johnson supervised my

\*Cisne, Molenock, and Rabe (1980) placed *Triarthrus eatoni* (Hall) in synonymy with *Triarthrus becki* Green. The name *Triarthrus eatoni* is retained here because specimens from Beecher's Trilobite Bed have become widely known under that name.

work in cooperation with R. R. Hessler. R. Zangerl supervised my radiographic work, which was carried out in the Department of Geology, Field Museum of Natural History. S. M. Manton, A. R. Palmer, E. S. Richardson, R. Wenzel, and H. B. Whittington reviewed the manuscript. I have had enlightening discussions with many others, and benefited much from the NATO Advanced Study Institute (Martinson, 1975) organized by D. L. Bruton. K. M. Waage, S. J. Gould, N. Eldredge, and E. S. Richardson loaned specimens from, respectively, the Peabody Museum (Yale University), the Museum of Comparative Zoology (Harvard University), the American Museum of Natural History, and the Field Museum of Natural History. I thank these friends and institutions for their help. I thank my wife Robin for typing the manuscript, and P. R. Hoover for editing it. Responsibility for errors is exclusively mine.

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#### ABBREVIATIONS OF REPOSITORY INSTITUTIONS

AMNH	American Museum of Natural History, New York, NY, USA
FMNH	Field Museum of Natural History, Chicago, IL, USA
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA
PRI	Paleontological Research Institution, Ithaca, NY, USA

YPM Peabody Museum, Yale University, New Haven, CT, USA

#### MATERIALS AND METHODS

##### MATERIALS STUDIED

The *Triarthrus* specimens on which this study is based have long been famous for the detail with which they show delicate structures of the ventral appendages. Some of these specimens have been described by Beecher (1893a, 1893b, 1894a, 1894b, 1895a, 1896, 1902) and Raymond (1920). From several tons of bulk material collected between 1892 and 1895, Beecher selected and prepared approximately 700 specimens. From these, he selected about 60 specimens for more elaborate preparation, delicately using fine bits of pencil eraser to remove matrix from the fossils. Previous work on the trilobite's external anatomy has been based almost entirely on these preparations. Save for observations on possible impressions of muscles on the ventral cuticle in some specimens (Beecher, 1902, Raymond, 1920), the presence of preserved internal anatomy has gone unsuspected.

The 171 *Triarthrus* specimens used in this study were selected, for their quality of preservation and for representation of the range in specimen size, from over 600 specimens, all from Beecher's original collection, and now belong to several museums. These specimens include tiny protaspids (larvae) only 0.6-0.7 mm long, meraspids (juveniles), and holaspids (adults) up to 40 mm long. Most specimens are complete except for chipping incurred in the initial stages of preparation; a few are small, broken pieces. Most specimens have been subjected in varying degrees to Beecher's further mechanical preparation. The specimens used are:

AMNH 839/14A-K	YPM 209 - YPM 211	YPM 2780A-H,J-L
FMNH 4738A-C UC	YPM 213 - YPM 223	YPM 27813
MCZ 3506/1a	YPM 226 - YPM 230	YPM 27818
MCZ 3638/1-4	YPM 246	YPM 28131
MCZ 7190/1,2,7,14A-E,15,17-22,24-26	YPM 6695	YPM 28201 - YPM 28269
YPM 201 - YPM 207	YPM 27802A-H	YPM 28270A-H,J-N,P-V

#### METHODS OF STUDY

The specimens and X-radiographic stereopairs of *Triarthrus* were examined with a dissecting microscope. The specimens are especially suited for radiographic study be-

cause the iron that is more abundant in the pyritized fossils than in their matrix makes them less transparent to X-rays than the surrounding shale.

All but the protaspid specimens and a few others were

surveyed from stereopairs made using a Siemens Pantix X-ray apparatus. This medical X-ray machine allowed the production of negatives on Kodak Type M Industrial X-ray film in exposure times from seconds to minutes. Enlarged prints of the negative stereopairs, on high contrast photographic paper, were the actual images from which observations were made.

From this examination, 68 superior specimens were selected and prepared for more intensive study using a Siemens Beryllium Window X-ray apparatus, a "soft" X-ray apparatus with a continuously water-cooled head designed for high resolution radiography. The specimens intensively studied using this machine were:

AMNH 839/14A-C,G	YPM 223	YPM 28217
FMNH 4738B UC	YPM 227 - YPM 230	YPM 28222
MCZ 3638/3,4	YPM 27802A	YPM 28226
MCZ 7190/1,2,14B,14C,15,17,18,21,22,25,26	YPM 27804L	YPM 28250
YPM 201 - YPM 207	YPM 27813	YPM 28253 - YPM 28260
YPM 211	YPM 28131	YPM 28264
YPM 213 - YPM 216	YPM 28205	YPM 28265
YPM 218 - YPM 220	YPM 28206	YPM 28268
YPM 222	YPM 28210	YPM 28269
	YPM 28216	YPM 28270J,M,P-R

Sufficient stereoscopic negative pairs to produce altogether suitable results were made for each specimen. A distance of about 60 cm between the specimens and the X-ray tube head was maintained as the head was shifted approximately 28 cm to either side of the midline and re-directed in making the paired exposures. This procedure produced stereoscopic pairs with a vertical exaggeration of approx.  $\times 3$ . The specimens rested a fraction of a mm from the film emulsion. Single exposures ranged from 30 to 180 minutes, at voltages from 25 to 45 kilovolts, and at currents from 5 to 20 milliamperes. The negatives were made on Kodak Fine-Grain Positive Film, which is well adapted for radiographic use. Using this film allowed a considerable savings in cost and darkroom inconvenience over maximum resolution glass plates at what, for my purposes, has been an insubstantial sacrifice in graininess.

Several 68 mm  $\times$  85 mm paper enlargements of each negative pair were studied using a pocket stereoscope. For each specimen, negative pairs were enlarged to fill the available printing area with an image of the entire specimen or some especially interesting part of it. For my purposes, the use of photographic paper, rather than film, generally was preferable because of the greater contrast attainable. High contrast and its precise control are essential to bring out details of internal anatomy from the very low contrast X-ray negatives.

Some trilobite specimens were sectioned so that they could be examined in other views. Sets of optically transparent, transverse thin-sections were made from YPM 28201-28204. After having stereoscopically x-rayed them in dorsoventral view, six additional specimens (*e.g.*, Pl. 18, fig. 1; YPM 28206, YPM 28250) were cut into 5 mm slices, as indicated:

- YPM 28206 (transverse) (Pl. 18, fig. 2)
- YPM 28208 (sagittal)
- YPM 28210 (transverse)
- YPM 28211 (sagittal)
- YPM 28250 (transverse) (Pl. 18, fig. 2)
- YPM 28266 (transverse)

These slices were then stereoscopically x-rayed, and enlarged prints of these x-radiographic stereopairs were prepared for each of the several serial slices.

For the 68 selected specimens, more than 1000 individual prints comprising over 150 stereopairs were prepared and intensively studied using a pocket stereoscope. These were supplemented by 203 mm  $\times$  254 mm paper enlargements from photographic and radiographic negatives of many specimens. For the 20-odd most interesting specimens, the best stereopairs of X-radiographic negatives were enlarged and printed on 203 mm  $\times$  254 mm sheet film. These were studied on a transmitted-light Wheatstone stereoscope at Field Museum of Natural History. Radiographs were

compared in detail with the specimens themselves to combine information from both, and to identify preparational artifacts. The negatives on which this study is based are deposited with the Department of Geology, Field Museum of Natural History.

Radiography has proved to be a far more effective method for studying the *Triarthrus* specimens than those previously employed [see Stuermer (1970) for a general discussion of pyritized specimens; Størmer (1939) and Stürmer and Bergström (1973) describe radiographs of a few *Triarthrus* specimens from Beecher's Trilobite Bed]. In the course of Beecher's delicate preparation, fine details of those parts exposed for study have inevitably been damaged. The treatment has tended to modify and bias the interpretation of these structures, and in some specimens gives them a peculiar form that is not recognizable in microscopic examination. It is preferable that delicate structures be left in the matrix where they can be studied radiographically in their pristine condition. Using "soft" X-rays, I commonly could identify small setae ( $\geq 10 \mu\text{m}$  in diameter). This illustrates the resolution attainable with the technique and the exquisite quality of the preservation.

Stereoscopy takes on special importance in combination with radiography as a means of visualizing the spatial relationships among the anatomical parts of the three-dimensionally preserved trilobite specimens, otherwise projected into two dimensions in a single negative, and as a means of sorting out these parts from pyritized debris in the vicinity of the trilobites. Stereoscopic exaggeration of the vertical dimension proved particularly useful in studying relationships among closely spaced, overlapping structures. Stereopairs provide a clearer image than does a single radiograph. As is important for enlargements at high magnification, the random distribution of graininess in either radiograph tends to mask the grain in the other. This redundancy also helps to identify technical artifacts.

#### METHODS OF ANATOMICAL INTERPRETATION

The fossilized parts of the trilobite were identified by applying a knowledge of comparative arthropod anatomy. For parts of the exoskeleton, these interpretations are simple and straightforward. However, for the internal anatomy, they are necessarily more involved. Trilobite anatomy is reflected by iron pyrite residues that are observed directly from specimens or indirectly from radiographs. The diagnostic characters of each structure accompany its description. Applying the same principles of comparative arthropod anatomy, Hupé (1953) produced a theoretical reconstruc-

tion of internal anatomy for a generalized trilobite. Not surprisingly, my study confirms most of its basic points.

However, the phylogenetically most interesting points of internal anatomy are details that could not be predicted from basic principles alone. Because some of the trilobite's anatomical parts may have no exact counterpart in living arthropods, and because various unsystematic preservational artifacts are common among specimens, tentatively identified anatomical structures have been tested for recurrence from specimen to specimen and, for serially repeated structures, from segment to segment in the same specimen. Data on recurrence were collected for each tentatively identified structure. Given a subjectively sufficient frequency of recurrence, that structure was accepted as a real and original feature of the trilobite. The problem is most critical for features of "soft" anatomy. Internal anatomical parts reported without special qualification have been identified in at least four, and usually many more, of the 68 intensively studied specimens. Structures accepted on the basis of few specimens were found serially repeated and paired in some of them. At the opposite extreme, parts of the intestine were identified in about two-thirds of the 68 specimens. Structures suggestive of ganglia, the optic nerve, and ovaries have been pointed out in some photographs, but they have otherwise been set aside pending further investigation. It has not been possible to identify unequivocally all seemingly real anatomical features. Recurrence data given with documentation provide some idea of the confidence attached to the respective structures. For convenience, references to individual specimens by catalogue number are given only for structures preserved in ten or fewer specimens. Comparison of recurrence frequencies may give some idea as to the relative preservability of structures.

Ontogenetic development is dealt with only briefly and as necessary in treating certain problems in anatomical reconstruction and interpretation. Overall length (distance between the margins of the head and pygidium along the midline) was measured to the nearest 0.1 mm with a micrometer caliper for specimens showing only dorsoventral deformation. Measurements were then taken by ratio to this length from radiographs for the midline lengths of the cephalon, hypostoma, metastoma, pygidium, and post-pygidial abdomen. The lengths of these structures were then plotted against overall length in the attempt to discern the basic patterns of their relative growth. Because of the geometry of the radiographic equipment and the low relief of the specimens, lengths measured from radiographs are affected insignificantly by parallax. Deformation has of course altered the lengths of specimens and their constituent

structures, but apparently to a proportionately lesser degree than it has affected the respective widths.

#### METHODS OF RECONSTRUCTION

As Beecher (*e.g.*, 1894a, 1896, 1902) noted, the *Triarthrus* specimens have been flattened and deformed in the process of preservation. An understanding of their post-mortem deformation is essential to accurate reconstruction of the living trilobite. But this can be understood only in the larger context of the taphonomy of the fossil assemblage. Beecher (1894a) and Cisne (1973a, 1973b) have already dealt at length with the mode of occurrence, state of preservation, and manner of accumulation and preservation of the assemblage.

The specimens come from a turbidite siltstone bed about 4 cm thick, Beecher's Trilobite Bed. They occur only in the basal 5-10 mm of this bed, and most come from a lamina about 3 mm thick which is centered about 5 mm above the base of the bed. Specimens of all sizes are disposed more or less horizontally in this layer. Most post-larval individuals are oriented in the direction of turbidity flow, but without preferred anteroposterior or dorsoventral orientation. About 99% of the post-larval specimens in the assemblage, including the very small ones, are complete (or evidently were complete prior to breakage in collection and preparation) and preserve the appendages. These specimens represent actual animals, not molts.

The trilobite specimens — their exoskeletons and internal anatomy — are preserved as pseudomorphs in iron pyrite. The microscopic pyrite crystals conform to the contours of the cuticle and other parts of the anatomy. In better preserved specimens, they even conform to tiny setae and muscle fibers. But in less well-preserved specimens, the crystals are agglomerated into framboids that in packed masses less precisely delineate some of the larger structures.

The explanation I propose to account for these and other observations of occurrence and preservation is that post-larval individuals initially lived epifaunally on a soft mud bottom, that they were suspended, transported a short distance, and buried by a turbidity flow, and that they were somehow stunned, perhaps by temperature shock, in the process, so that they were moribund when deposited in sediment rich in already decayed organic matter. There is no apparent evidence of the escape of the buried animals, that might be expressed in "emergency exit" burrows to the surface, nor is there evidence of post-mortem disturbance of trilobite carcasses by burrowing organisms.

Soon after burial, iron sulfides (which were later to

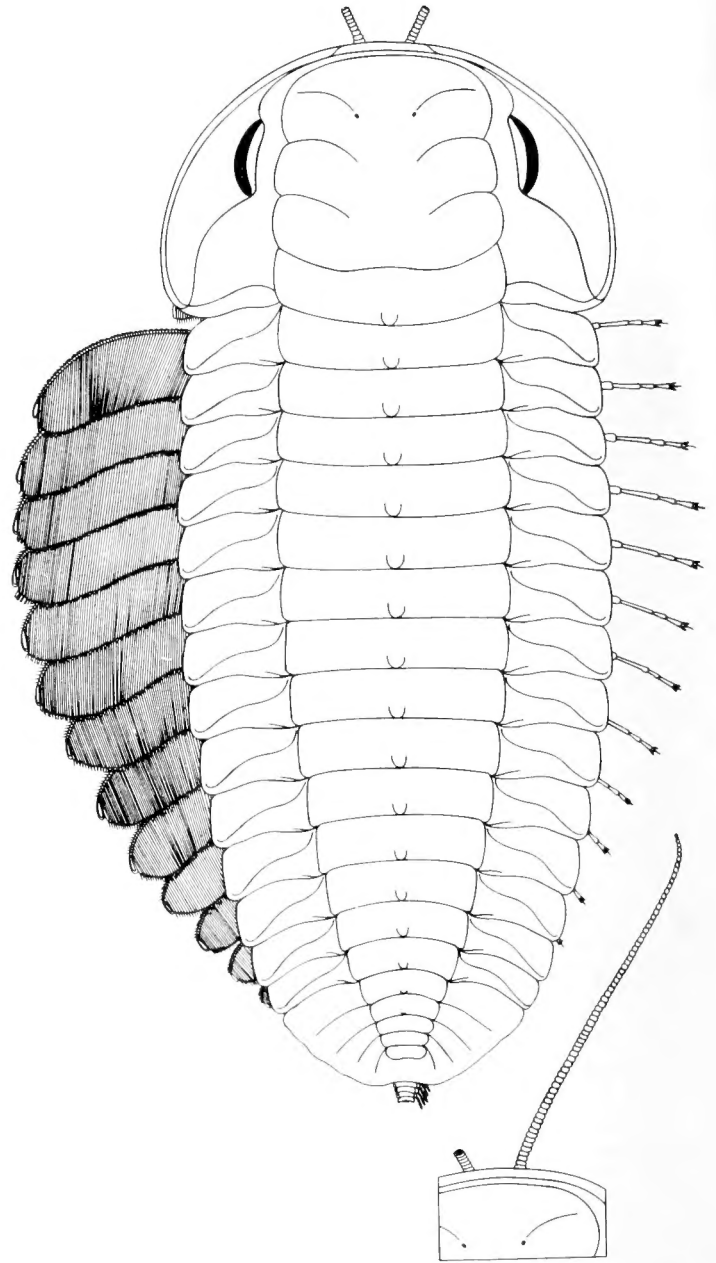
transform to pyrite) were emplaced in body tissues as they decayed. The process of preservation must have been very complex. Judging from the occurrence of internal anatomical structures in fossils, the details of this process varied from specimen to specimen (resulting in the preservation of different structures in different specimens), and from place to place within the same specimen (resulting in the preservation or non-preservation of serially homologous structures from segment to segment).

Concurrent with these early stages of diagenesis, the sediment around the trilobites underwent substantial compaction. As a result, specimens were variously deformed. In all specimens, the body cavity collapsed. The majority, which initially came to rest nearly parallel to bedding, underwent primarily dorsoventral flattening. But other specimens that evidently came to rest more oblique to the bedding underwent both dorsoventral flattening and sidewise shearing. Sedimentary compaction and accompanying anatomical compression generally take place very early, along with the initial stages of diagenesis, in other instances of spectacular preservation (Zangerl, 1969, 1970). The shear strength of a trilobite exoskeleton may have decreased markedly as strengthening material was replaced by iron sulfides. Consequently, the incipient fossil may have had mechanical properties under compression different from those of the unaltered body.

An empirical approach to problems of deformation is thus required, and stereoscopic X-radiography provides an ideal means for study. By careful examination and comparison of a large number of specimens, the attempt has been made to distinguish the consistent anatomical features and relationships of fossil structures that are thought to reflect the anatomy of the living animal, from the variable features that may represent artifacts of preservation and deformation. Working reconstructions were built up as models to explain the constant features of anatomy and, at the same time, to account for the various ways in which observed fossil structures could have been derived through deformation. The disposition of a specimen gives much evidence on how particular structures were deformed. A specimen having all its limbs bent to one side, for example, clearly shows one of the directions in which deforming stress operated (*e.g.*, Pl. 21, fig. 4). After a working reconstruction for a given structure was completed, specimens having the structure preserved in a seemingly little altered state were reexamined for physical evidence of deformation. In this way, the attempt was made to eliminate systematic bias from the final reconstruction.

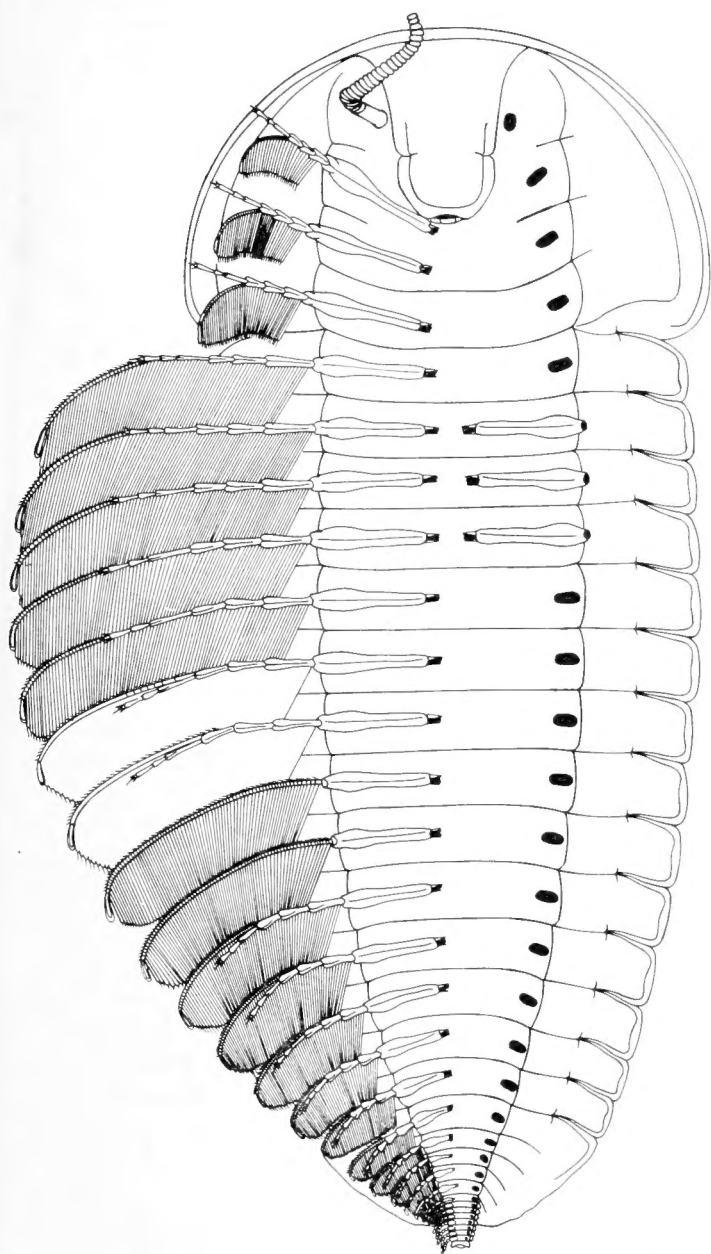
A critical problem in reconstruction of the trilobite exoskeleton and internal anatomy is the extent of compressional deformation, particularly with reference to the body cavity. As illustrated by two specimens (YPM 28206, 28250; Pl. 18, figs. 1, 2), the body cavity has been reduced to a very small space between the dorsal and ventral parts of the cuticle. A small amount of silt, probably introduced during decomposition, and in other specimens including gut contents, fills the preserved body cavity. This material forms the matrix for the preserved internal anatomy. This configuration of the exoskeleton is functionally impossible. The ventral longitudinal muscles must have passed ventral to the intertergal hinge developed at the axial furrows, so that the trilobite could have flexed ventrally (as some specimens are in fact flexed). The body cavity, which as for most small arthropods was probably occupied largely by "empty" hemocoelic space, is thus shown to have collapsed during sediment compaction. Otherwise, deformation is apparent in the asymmetry of both trilobites in cross-section, in the bending of the smaller trilobite around the lateral edge of the larger, and in the conformable curvature of laminar structures in the sediment around the trilobite specimens.

The attempt to approximate the shape of the body cavity used evidence from the morphometric study of development and deformation, from the mutual "fit" of structures, and from the functional considerations noted above. In the thorax, the dorsal outline of the body cavity in cross-section is defined by the shape of the axial rings. Specimens adjudged to be least deformed (having a maximum height/width ratio for the axial rings and having no marked lateral component of compression) were used as models in reconstruction. In specimens not showing lateral distortion, the height (dorsoventral distance between the deepest point of the axial furrow and the crest of the ring along the midline; determined by measuring the travel on a dissecting microscope between focuses at the two points) and width (transverse distance between the deepest points of the axial furrow) of the axial ring was measured on the first ( $T_1$ ), fifth ( $T_5$ ), and fourteenth ( $T_{14}$ ) thoracic tergites. Heights were plotted against widths on logarithmic graph paper. When the lengths of the head tergum, hypostoma and pygidium are plotted logarithmically against overall length of the tergal exoskeleton (Text-fig. 12) the lines all have slopes near one. The structures evidently followed growth patterns similar to those of the entire body. Hence it is reasonable to assume that the shapes of the three thoracic segments likewise did not change with growth, and that the height-to-width ratio was essentially constant for a given axial ring in adults of all sizes. Consequently, it would be



Text-figure 1.—Dorsal view of reconstruction of large (ca. 4 cm. long) adult *Triarthrus eatoni* (Hall) [from Cisne, 1975].

expected that when height was plotted against width on logarithmic graph paper the points would fall along a straight line with a slope near one. When the data for each segment were plotted in this way, it was found that points signifying a maximal ratio did indeed fall closely along a line with a slope of unity, and that points signifying lower ratios fell in no discernible pattern below this line. Barring some systematic error, the seemingly least deformed speci-



Text-figure 2.—Ventral view of reconstruction of large (ca. 4 cm. long) adult *Triarthrus eatoni* (Hall) [from Cisne, 1975].

mens would appear to give reasonably accurate representation of the shape of the thoracic axial rings and thus of the dorsal contour of the body cavity. The overall shape of the tergal exoskeleton in these evidently least deformed specimens is very much the same as in an apparently undeformed specimen of *T. eatoni* (PRI 30016) preserved in vertical position in a calc-turbidite.

The shape of the ventral cuticle was geometrically reconstructed from observed relationships between the ventral

cuticle and the ventral body musculature and endoskeleton, and observed relationships between the body musculature and the dorsal cuticle. In parts of some especially well-preserved specimens, it was possible to measure the height and width of the thoracic axial ring, the separation of the paired ventral longitudinal muscles, and the lengths of dorsoventral muscles that indirectly link the dorsal and ventral sides of the cuticle. Knowing these dimensions, it was possible to geometrically construct an idealized transverse section through the specimen in its undeformed condition. Having an estimate of the true ratio of height to width for the axial ring, adjustment of the vertical dimensions of the reconstructed transverse section should approximate the anatomical relationships the parts had in life. Details were then added to this reconstruction, in turn based on the "fit" of internal and external structures. For example, the construction of the coxal endites suggests that their dorsal edges could not have been far from the ventral side of the axial region of the body. Consequently, the dorsal outline of the limb segment indicates the shape and convexity of the body cavity defined by that part of the cuticle.

Once working reconstructions of the trilobite had been reasonably refined, badly deformed specimens were re-examined in these frames of reference as conveniently prepared dissections, the only ones available. Obliquely sheared specimens proved to be of particular value in clarifying the anatomical relationships of structures that in life lay one above the other.

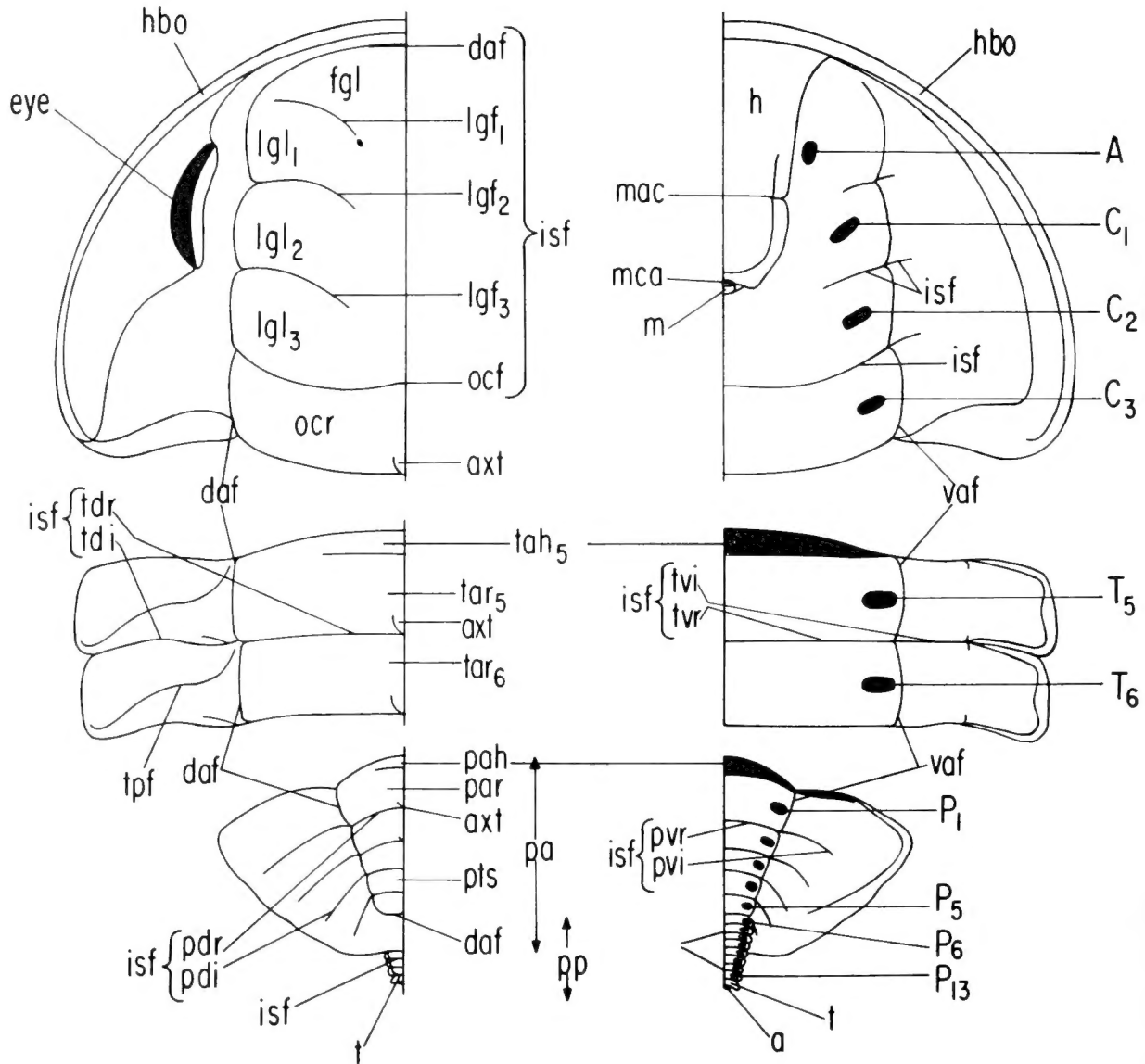
## ADULT ANATOMY

For clarity, most sections on an aspect of the trilobite's anatomy are divided into three subsections. In the first, I describe the reconstructed holaspid (adult trilobite). In the second, I document and discuss the more important points of anatomy. And in the third, I consider problems of terminology and anatomical interpretation.

### EXTERNAL ANATOMY

#### Description

The body proper (body exclusive of the limbs) of the holaspid individual has the shape of an elongate, oval saucer that is convex dorsally. In dorsal view (Pl. 17; Text-fig. 1), the body proper is surrounded laterally by the distal portions of the limbs. In ventral view (Pl. 17; Text-fig. 2), the body proper is concave. Holaspids, distinguished from meraspids (juveniles) in having fourteen thoracic segments, range in overall length from about eight to at least 39 mm



Text-figure 3.—Reference diagram for external features of the body proper of *Triarthrus eatoni* (Hall) showing dorsal (left) and ventral (right) views of the head, the fourth and fifth thoracic segments, and the abdomen. See Appendix for explanations of abbreviations.

(Cisne, 1973a). No clear indications of sexual dimorphism have been found at any developmental stage.

The body is divided longitudinally into a head, thorax, and abdomen. The abdomen is further subdivided into an anterior pygidial portion (*pa*; hereafter see Text-fig. 3 for diagrammatic identification of external parts) and a posterior post-pygidial portion (*pp*). Except for the post-pygidial abdomen, the body is divided into a central axial lobe and paired pleural regions by the dorsal and ventral axial furrows (*daf*, *vaf*, respectively). The post-pygidial abdomen forms the posterior end of the axial lobe.

The body proper, exclusive of the telson (*t*) at the extreme posterior of the abdomen, and that part topologically anterior to the antennal segment, is divided into limb-bearing exoskeletal segments by intersegmental furrows (*isf*), some of which are known by more specific names. The exoskeletal segments and their intersegmental furrows do not necessarily correspond exactly to the true body segments and their boundaries.

The body bears about 31 limb pairs: one preoral pair of uniramous antennae (*A*; only the limb foramina are shown in Text-fig. 3) and a variable number of postoral



pairs of biramous limbs: three in the head ( $C_1 - C_3$ ), fourteen in the thorax ( $T_1 - T_{14}$ ), five in the pygidial abdomen ( $P_1 - P_5$ ), and from six to twelve, commonly eight, in the post-pygidial abdomen ( $P_6 - P_{11-17}$ ). Each limb pair is inserted in the (anteroposterior) middle of its respective exoskeletal segment on the ventral side of the body and on the lateral part of the axial lobe. All along the postoral part of the body, the endites of the paired biramous limbs closely approach one another transversely. The midventral space between their proximal edges forms a food groove (*vt*, Text-fig. 8). The thoracic exites are imbricated: the posterior portion of one laps dorsally over the anterior part of the one just posterior to it.

The head, semioval in dorsoventral outline, has its dorsal axial portion divided into the glabella (*g*) and the occipital ring (*ocr*) by the occipital furrow (*ocf*), an intersegmental furrow. Three pairs of intersegmental furrows, the lateral glabellar furrows (*lgf<sub>1</sub> - lgf<sub>3</sub>*), divide the glabella into a frontal lobe (*fgl*) and three pairs of lateral glabellar lobes (*lgl<sub>1</sub> - lgl<sub>3</sub>*). The occipital ring (*ocr*) bears an axial tubercle (*axt*) medially. The pleural region, surrounding the glabella anteriorly and laterally, has the border (*hbo*) marked off by furrows dorsally and ventrally.

On the ventral side of the head, the anterior portion of the axial lobe bears the hypostoma (*h*), and on the lateral edges of that structure is a pair of indentations, the maculae (*mac*). Dorsal to the posterior margin of the hypostoma is the metastoma (*m*). Between the hypostoma and the metastoma lies the opening of the mouth cavity (*mca*; a "preoral cavity").

The fourteen exoskeletal segments comprising the thorax ( $T_1 - T_{14}$ ; this notation is applied both to segments and their respective limbs), are demarcated circumferentially by intersegmental furrows (*isf*), which are divided into the dorsal and ventral ring furrows (*tdr* and *tvr*, respectively) and the dorsal and ventral interpleural furrows (*tdi* and *tvi*, respectively). For the "free" portion of each segmental pleural lobe, these furrows are, in effect, the same. The dorsal axial portion of each exoskeletal segment is divided indistinctly into an anterior articulating half ring (*tah*) and a posterior axial ring (*tar*). Only the axial ring is normally exposed exteriorly; the articulating half ring projects beneath the axial ring anterior to it (see Text-figs. 7, 10). Each axial ring bears an axial tubercle (*axt*) medially. The pleural portion of each segment is marked obliquely by a pleural furrow (*tpf*). The "free" portion of each segmental pleural lobe — the distal part separated from anteroposteriorly adjacent pleural lobes by a double exoskeletal wall — extends inward past the bend of the

pleura but not to the level of the axial furrows (see Text-fig. 8).

The abdomen is semioval in dorsoventral outline. The dorsal axial portion of the pygidium is divided into four axial rings (*par*) and a terminal axial segment (*pts*) by the dorsal ring furrows (*pdr*), sections of intersegmental furrows. The ventral axial region of the pygidium is likewise marked by ventral ring furrows (*pvr*). As for a thoracic exoskeletal segment, the dorsal site of the pygidial axial region bears an articulating half ring (*pah*); and the most anterior one to three dorsal axial rings may bear faint suggestions of axial tubercles (*axt*) medially.

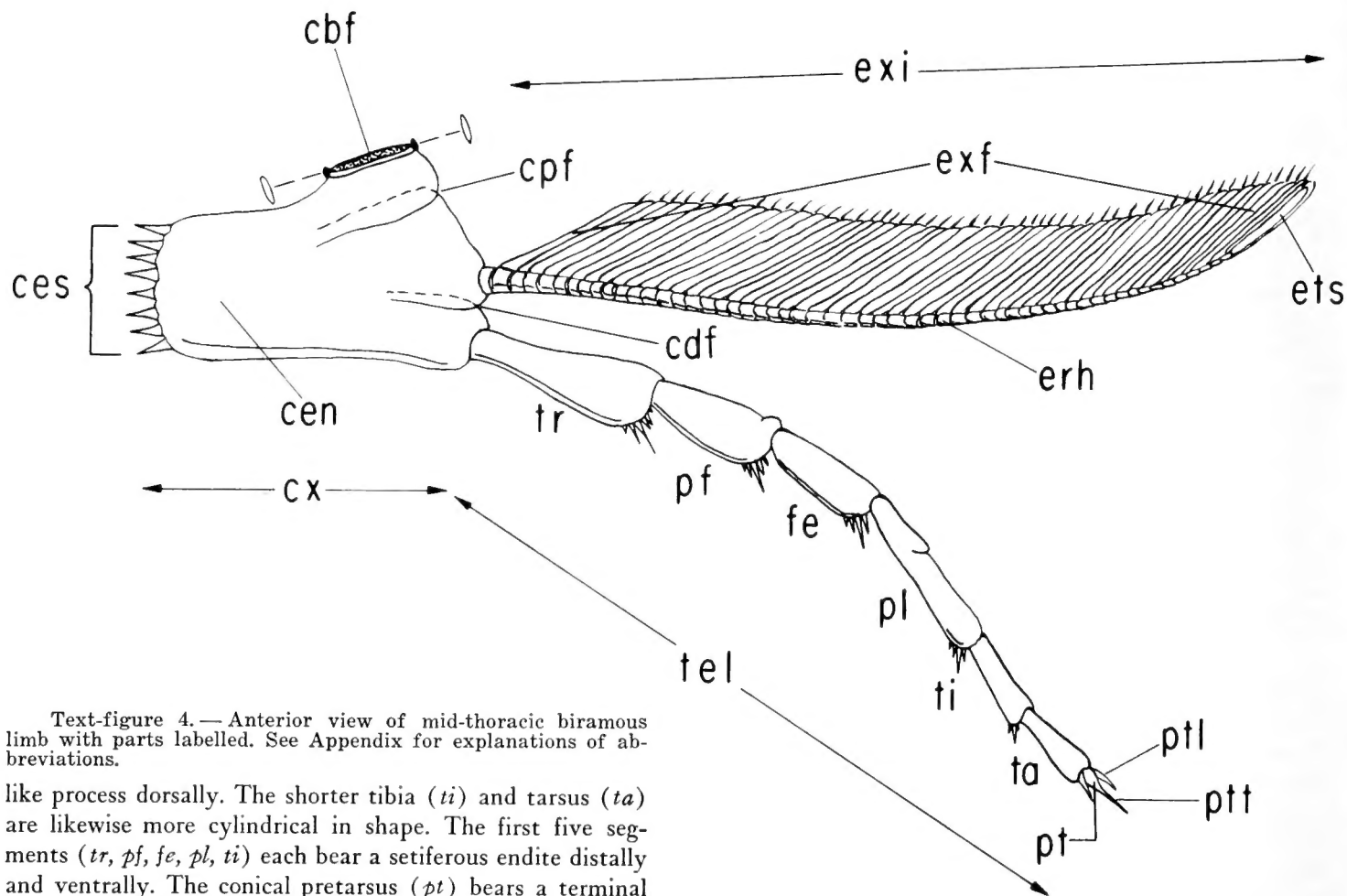
The post-pygidial abdomen (*pp*) is overhung dorsally by the posterior part of the pygidial pleural region. The very small telson (*t*), demarcated from the terminal limb-bearing segment by an intersegmental furrow (*isf*), apparently lacks furcal rami. It bears the anus (*a*).

The antenna (Text-figs. 1, 2), inserted lateral to the hypostoma (*h*) and ventral to the first lateral glabellar lobe (*lgl<sub>1</sub>*), is comprised of a short, cylindrical peduncle and a long shaft that is divided into up to about 100 annuli.

The postoral biramous limbs (Text-figs. 1, 2, 4, 5) all have the same basic structure. The typical limb (a mid-thoracic ( $T_5$ ) limb [Text-fig. 4]) is composed of a large, blade-like coxa (*cx*) that bears two rami: a feather-like exite (*exi*) inserted medially, and a telopod (*tel*) inserted distally (Here the term "coxa" is used loosely; as discussed below, it is not necessarily a single podomere.). The coxa has a narrow, thickened lip immediately around the coxa-body foramen (*cbf*), a proximal furrow (*cpf*) partially surrounding that opening ventral to it, a distal furrow (*cdf*) between the insertions of the two rami, and a thickened ventral keel. The adaxial part of the coxa forms a long endite (*cen*) that bears about eight large enditic setae (*ces*).

The exite (*exi*) is composed of a thin, annulated shaft (*erh*) that terminates distally in a spatulate segment (*ets*). The annuli, up to over 100, each bear one or more posteriorly and outwardly directed filaments (*exf*), each of which in turn terminates distally in a seta. The filaments together lie in a plane inclined slightly to the posterior. Along the anterior edge of the shaft (*erh*) is a row of small setae, at least one of which is inserted between successive annuli.

The telopod is composed of seven limb segments: trochanter (*tr*), prefemur (*pf*), femur (*fe*), patella (*pl*), tibia (*ti*), tarsus (*ta*), and pretarsus (*pt*), following the terminology of Størmer (1939). The first three segments (*tr*, *pf*, *fe*) are similar in shape. Each segment is compressed anteroposteriorly and has a ventral keel. The elongate patella (*pl*) is more cylindrical in shape and bears a low, rounded knob-



Text-figure 4.—Anterior view of mid-thoracic biramous limb with parts labelled. See Appendix for explanations of abbreviations.

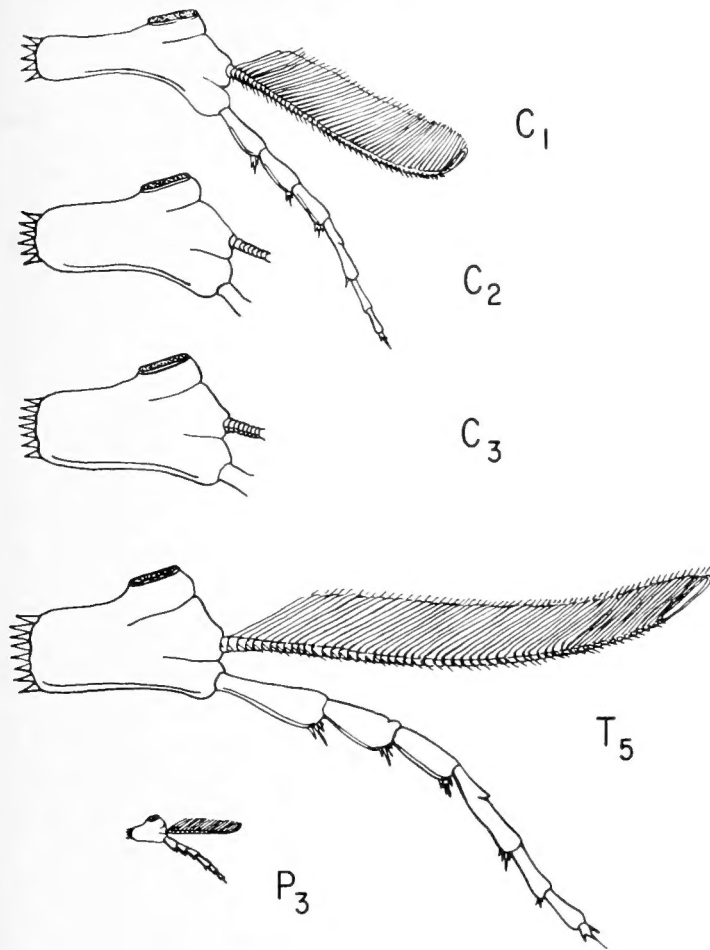
like process dorsally. The shorter tibia (*ti*) and tarsus (*ta*) are likewise more cylindrical in shape. The first five segments (*tr*, *pf*, *fe*, *pl*, *ti*) each bear a setiferous endite distally and ventrally. The conical pretarsus (*pt*) bears a terminal seta (*ptt*). Lateral to the pretarsus (*pt*) are a pair of lateral setae (*ptl*) that arise anteriorly and posteriorly from the vicinity of the arthrodial membrane across the tarsus-pretarsus joint. The pretarsus and the two lateral setae thus give the tip of the limb the appearance of a tripartite claw.

The biramous limbs are graded in size and shape from segment to exoskeletal segment along the body (Text-fig. 5). As compared with a mid-thoracic limb, (*T<sub>5</sub>*), the coxal endites of the head limbs (*C<sub>1</sub>* - *C<sub>3</sub>*) are reduced progressively in dorsoventral depth but not in transverse length, from posterior to anterior pairs. Along the same gradient, the exites and telopod of the head limbs become more and more ventrally directed with respect to their articulations to the coxae. Coxal enditic setae on the first and second (*C<sub>1</sub>*, *C<sub>2</sub>*) limbs have been reconstructed by analogy with the thoracic coxa. Along the trunk, limbs posterior to the middle of the thorax become progressively reduced in size (e.g., *P<sub>3</sub>*, Text-fig. 5). As a result of poor preservation, it is not known whether post-pygidial limbs bore exites.

#### Documentation

Many of the finer external details are illustrated by MCZ 7190/18 (Pl. 18, fig. 3; Text-figs. 13, 14). Features of special interest are the three pairs of cephalic limbs (*C<sub>1</sub>* - *C<sub>3</sub>*, Text-fig. 13), coxal enditic setae (*ces*) on the head and thoracic limbs (*C<sub>2</sub>*?, *C<sub>3</sub>* - *T<sub>5</sub>*, Text-fig. 13), and possible (and very questionable) paired ganglia (*gan*?, Text-fig. 14; possibly belonging to the antennal segment) and circum-esophageal commissure (*ecm*?, Text-fig. 14) surrounding the esophagus (*e*).

This specimen provides an example of how much fossil trilobite bodies may be deformed, of the greater deformation of the ventral parts of the exoskeleton than of the sclerotized dorsal shell, and of the common oblique displacement of the limbs with respect to the body proper. In Text-fig. 13, the entire set of limbs has been shifted toward the upper left corner of the diagram with respect to the dorsal exoskeleton.



Text-figure 5.—Anterior views of the first, second, and third postoral head limbs ( $C_1$ - $C_3$ ) (only the basal portions of the second and third limbs are shown), the fifth thoracic limb ( $T_5$ ), and the third abdominal limb ( $P_3$ ). From Cisne (1975).

In Text-fig. 14, the ventral axial furrow (*vaf*) and ventral ring furrows (*tvr*), shown as solid lines, have been shifted obliquely with respect to the dorsal axial furrow (*daf*) and dorsal ring furrows (*tdr*), shown as dashed lines. The anatomical relationships of the living animal are seen in much modified form in the fossil. Segmental structures, the limbs in particular, have been shifted so that, with reference to the dorsal exoskeleton, they are associated with segments to which they did not belong in life. In line with the overall sidewise deformation of the specimen, limbs on the right side of the body in Text-fig. 13 have been moved anteriorly and to the left toward the midline so that, with respect to the dorsal exoskeleton, the  $T_1$  limb lies across the posterior margin of the head and might appear to belong to the segment of the occipital ring. Limbs on the right side in the figure have, further consistent with the overall pattern of

deformation, fallen anteriorly so that the anterior faces of their coxae rest more or less against the ventral body wall. Limbs on the left in the figure have correspondingly been moved to the left. However, as further indicated by the lack of anteroposterior displacement between the dorsal and ventral ring furrows (*tdr*, *tvr*) on this side, the thoracic limbs ( $T_1$  -  $T_4$ ) have been crushed almost exactly dorsoventrally. Segmental structures on the left side have kept their true dorsoventral relationships in the fossil whereas structures on the right side have been shifted by almost an entire segment length between the dorsal and ventral sides of the body.

On both sides of the body, the biramous head limbs ( $C_1$  -  $C_3$ ) have fallen anteriorly just as thoracic limbs ( $T_1$  -  $T_4$ ) on the right side have fallen anteriorly. This is a common configuration for these limbs in fossils, and a likely reason why it should be so common is that this set of limbs tended to fall forward into the cavity of the glabella as the body collapsed during compaction of the sediment.

The three pairs of postoral head limbs are shown more nearly in their natural, upright position in YPM 27813 (Pl. 18, fig. 4; Text-fig. 15). The metastoma (*m*) is also well shown. External details in this specimen have been somewhat eroded by Beecher's preparation.

The post-pygidial abdomen is especially well illustrated in YPM 28131 (Pl. 23, fig. 1) and MCZ 7190/15 (Pl. 19, figs. 1, 2). Specimen YPM 28131 represents an extreme in the development of the post-pygidial abdomen. The tagma protrudes far beyond the posterior margin of the pygidium.

The structure of the basal portion of the limb is well illustrated in MCZ 7190/18 (Pl. 18, fig. 3; Text-fig. 13), YPM 27813 (Pl. 18, fig. 4; Text-fig. 15), MCZ 7190/1 (Pl. 22, fig. 1; Text-fig. 25), and in MCZ 7190/15 (Pl. 19, figs. 1, 3; Text-fig. 16). Among the more than 1000 fossil limbs examined, the basal portion is often well-preserved and simply deformed, but many times has been strangely deformed, in many ways, around the edges of the axial region of the dorsal exoskeleton. Specimen MCZ 7190/15 shows a notable case of deformation of the telopod (Pl. 19, figs. 1, 3; Text-fig. 16): its midsection is squeezed through the small space separating the "free" portions of two thoracic pleura ( $T_{10}$ ,  $T_{11}$ ). Telepodal enditic setae are illustrated in YPM 28264 (Pl. 20, figs. 3, 4; Text-figs. 19, 20). The tips of the telopods are well shown in YPM 228 (Pl. 17; Text-fig. 21).

Specimens that include the head confirm that it bears three pairs of biramous limbs. Though this condition is diagrammed only for YPM 27813 (Pl. 18, fig. 4; Text-fig. 15), YPM 28257 (Pl. 22, fig. 2; Text-fig. 26), and MCZ

7190/18 (Pl. 18, fig. 3; Text-fig. 13), it is also demonstrated in YPM 201 (Pl. 22, fig. 4), YPM 204 (Pl. 21, fig. 4), YPM 228 (Pl. 17; Pl. 21, fig. 3), YPM 27802A (Pl. 21, fig. 1), YPM 28259 (Pl. 19, fig. 4), MCZ 7190/14B (Pl. 20, figs. 1, 2), MCZ 7190/15 (Pl. 19, fig. 1), and MCZ 7190/22 (Pl. 22, fig. 3).

#### Discussion

The single most important finding on external anatomy is that there are three pairs of biramous head limbs, not four as counted by Beecher (1895a, 1896) and as subsequently believed by Raymond (1920) and Størmer (1944, 1951). Such a difference in findings is not as surprising as it may seem. Beecher's original count was based on an interpretation of fossil anatomy that can be seen to be quite logical given the specimens he studied and the means he had for preparing and studying them. His error seems to have arisen from the inadequate methods of specimen examination he had available. Beecher quite clearly saw the potential biases of his interpretations. He (1895a) explicitly set them forth: deformation of the fossils themselves, difficulties of preparing specimens and dangers of biasing fossil anatomy, technical difficulties of examining specimens to sort out preservational, deformational, and preparational artifacts, and practical difficulties of correlating segmental structures between the dorsal and ventral surfaces of the body when only one surface could be mechanically prepared for study. From the evidence available to him, Beecher could not have known that his specimens were as deformed as this radiographic study shows, and that the limbs were more highly deformed than the stronger tergal exoskeleton.

In making his reconstruction, Beecher (1895a, 1896) assumed that the forms of structures most commonly seen among the specimens at his disposal should represent more or less those in the living animal. The flaw in his interpretation is that the biramous limbs of the head and the first one or two thoracic segments ( $T_1$ ,  $T_2$ ) more often than not have fallen forward, more or less into the cavity produced by collapse of the crop, so that they rest with their anterior faces against the body. This condition is disproportionately common among larger specimens, which Beecher preferentially selected for preparation and study. These overturned limbs, having the broad posterior surfaces of their coxae exposed to view in preparations of the ventral side, appear to be limbs of a different type from thoracic limbs. Because they commonly remained more or less upright, thoracic limbs have been flattened dorsoventrally. Having fallen forward, the more anterior limbs lie across segmental boundaries in

the exoskeleton and may appear to have been inserted across those boundaries as Beecher (1895a, 1896) and Raymond (1920) thought — a very peculiar conformation. In most of Beecher's preparations, the first thoracic limb ( $T_1$ ), having the same gross form as the three head limbs ( $C_1 - C_3$ ), appears to be a fourth head limb. This interpretation, however, does not hold up when the specimens are re-examined radiographically, as has already been shown for representative specimens. The specimen on which Beecher (1895a) particularly based his reconstruction (YPM 220, Pl. 23, fig. 2) is most unusually deformed. The entire set of limbs has been sheared anteriorly with respect to the dorsal exoskeleton during compaction of the sediment so that much of the first and second thoracic limbs ( $T_1$ ,  $T_2$ ) lies in the head region. Consistent with the overall pattern of deformation, the trunk limbs have been rotated anteriorly about their articulations to the body proper.

Once the idea that *Triarthrus* has four pairs of postoral head limbs becomes fixed in one's mind, it becomes easy to find all or part of a fourth pair of head limbs when re-examining Beecher's specimens under a dissecting microscope. But when checked radiographically, what has been identified as that pair of limbs is revealed to be either not a pair of head limbs or not a part of a limb at all.

The head limbs, as segmental organs, are of great importance to interpretations of head segmentation. Through this connection, the number of head limb pairs is immediately involved with the interpretation of other segmentally related aspects of external anatomy, especially the intersegmental furrows. All along the body, the limbs are inserted between intersegmental furrows, not across them as thought by Beecher (1895a, 1896) and Raymond (1920). The first, second and third pairs of postoral head limbs ( $C_1 - C_3$ ) are respectively inserted beneath the second and third lateral glabellar lobes ( $lgl_2$ ,  $lgl_3$ ) and the occipital ring (*ocr*). The antennae (*A*) are inserted beneath the first lateral glabellar lobe ( $lgl_1$ ). There has been some confusion on this point. Beecher (*e.g.*, 1896) and Raymond (1920) based their interpretations of the first lateral glabellar furrow ( $lgl_1$ ) on a few specimens. This furrow is fainter than the other lateral glabellar furrows and is variably developed among the several hundred specimens in the total sample. In some specimens (*e.g.*, YPM 28257), only the distal portion and the pit at the extreme proximal end of the furrow are expressed, and the middle section is not recognizably developed. Beecher and Raymond depicted this condition in their reconstructions, and interpreted the two portions of the same furrow rather as two distinct lateral glabellar furrows. This interpretation does not hold for most specimens. Most com-

monly, only the midsection of the first lateral glabellar furrow but not its ends are impressed (*e.g.*, YPM 28253). In some specimens (*e.g.*, YPM 228) almost the entire furrow is faintly impressed, and the proximal pits are absent. Regardless of what parts of the first lateral glabellar furrow are visibly expressed, they all fall along the same arcuate path and so appear to belong to a single furrow. The first lateral glabellar lobe as here recognized is thus a single lobe, not two as thought by Beecher and Raymond.

The post-pygidial abdomen is another unexpected structure. Though the posterior part of it had been described by Walcott (1918) and Raymond (1920) as a post-segmental "anal plate," it was entirely unexpected that such a series of limb-bearing segments should be present posterior to the terminal axial segment (*pts*) of the pygidium. So far as can be determined, the post-pygidial abdomen is a constant feature of body organization. It has been identified in specimens of all sizes from larger meraspid to very large holaspid. It grew in length with increasing overall body length (Text-fig. 12; Table 1, Equation 5), though it is variable in size and segmental composition (this may be in part an artifact of preservation and difficulties in measurement). It thus seems unlikely that the post-pygidial abdomen represents an asexual bud or deciduous reproductive structure like the epitoke in polychaetes. However, it has not been identified in all specimens. These apparent absences can reasonably be explained as the consequence of poor preservation. To be identifiable, the tiny post-pygidial abdomen must be preserved in some detail.

In the attempt to reconcile the post-pygidial abdomen with accepted notions of pygidial segmentation in trilobites, it might be supposed that the group of segments was in life attached to the terminal axial portion of the pygidium and that, during post-mortem compression, the post-pygidial abdomen came to be squeezed out and telescoped posteriorly. At least three arguments against this interpretation may be made. First, the posterior axial portion of the pygidium would be far too small to accommodate so many small, limb-bearing segments. The pygidial axial rings (*par*) and terminal axial segments (*pts*) each correspond to individual limb pairs. The posterior edge of the pygidium is reflected ventrally into a doublure, indicating that at least the more posterior segments of the post-pygidial abdomen could not have been fused with the ventral edge of the pygidium. It is unreasonable to believe that so long a post-pygidial abdomen as that seen in YPM 28131 (Pl. 23, fig. 1) could have been compressed in the fashion of an accordion into the much smaller volume immediately posterior to the terminal axial segment. There would simply not be enough space to

accommodate the many pairs of post-pygidial limbs. Second, there is no evidence that the post-pygidial abdomen has been blown out and detached from the pygidial abdomen. As well illustrated in MCZ 7190/15 (Pl. 19, figs. 1, 2), the pygidial and post-pygidial parts of the abdomen are contiguous. And third, the pygidium itself is anatomically accommodated to protrusion of the post-pygidial abdomen beyond its posterior margin. As a continuation of the trend of the elevated dorsal axial region, the posterior border of the pygidium is arched so as to provide a passageway for the post-pygidial abdomen.

Rather than coining a name for this body tagma other than "post-pygidium," which would be a misnomer, it seems preferable for the sake of simplicity in nomenclature to call the pygidial and post-pygidial regions together the "abdomen." At least for *Triarthrus*, it is clear that the pygidial region is not what its name suggests. It is not a tagma comprised of segments fused to the post-segmental region, the post-segmental region or telson being the "pygidium" as the term is applied to annelids. In comparisons between trilobites and other arthropods, I prefer to adopt the simpler, more standardized term "abdomen," and to restrict the term "pygidium," which has been applied to a variety of non-homologous parts in several different kinds of arthropods, to the abdominal tergum in trilobites, as done by Harrington (1959). For the same reason, I use the simple term "head" rather than "cephalic region." It is also preferable to use the term "head tergum" in place of "cephalon" in referring to the tergal exoskeleton of the head, for the term "cephalon" already has a meaning entrenched in the literature on arthropods as the primitive head region.

The longitudinal ridges that Beecher (1902) found along the ventral axial portion of the thoracic exoskeleton, which he interpreted as apodemes, are instead impressions of the viscera. This is true for those specimens that I could identify by number from the publication (Beecher, 1902: YPM 205, pl. 5, fig. 2; YPM 219, pl. 4; YPM 220, pl. 3; see Pl. 23, fig. 2 here). The ridges exposed on the surfaces of specimens are probably in part not original features but rather artifacts of preservation, and hence do not give an entirely fair representation of the pristine fossil condition of those structures. In YPM 219 and YPM 220, Beecher evidently cut into the intestine. But owing to preparation effects, it is unclear if the longitudinal ridges may in part be flexures imposed on the ventral cuticle by the intestine during compression of the trilobite carcasses. In YPM 205, Beecher may have exposed preserved parts of the dorsal longitudinal muscles as well as parts of the intestine. Some of the ridges he figured in this specimen are clearly scratch

marks from preparation. Overall, the destruction wrought on this specimen makes the structures difficult to determine. Judging from the difference in appearance of the thoracic region between Beecher's (1902, pl. 5, fig. 2) illustration and the existing specimen, it may have been prepared further.

My reconstruction of the biramous postoral limbs (Text-figs. 4, 5) agrees in essence with the reconstruction of Beecher (1893b, 1894a, 1894b, 1895a, 1896) and Raymond (1920) as regards the structure of the exite and telopod. Further, it agrees with improvements suggested by Størmer (1939) on the structure of the exite. It differs chiefly from these earlier reconstructions as regards the structure of the basal part of the limb. Beecher and Raymond recognized that the head and trunk coxae bore long endites. Though not realizing it at the time, they described the typical blake-like, rectangular outline of the trunk coxae in anteroposterior view in describing what they took to be the fourth biramous head limb. They described the other trunk coxae as finger-like, a shape their usual dorsoventrally-flattened condition produces. Beecher's and Raymond's reconstructions of the bases of the trunk limb show the coxa in just this deformed condition.

Størmer's (1939) interpretation of the base of the limb in *Triarthrus* appears to be inaccurate on several points, and he properly qualified his interpretation by stating (p. 204) that he had not studied the specimens in detail and was forced to rely primarily on the works of Beecher and Raymond. He (1939) proposed in his reconstruction that the coxa lacked a long endite and that the exite was inserted near the attachment of the limb to the body. Størmer's (1939, pp. 202-209) argument rests primarily on a drawing (text-fig. 22d, p. 206) which purports to show the basal portion of a limb complete with a precoxa and with an exite inserted on it. This drawing, as he states, is based not on the specimen but on Beecher's (1902, pl. 4) published photograph of it. The negatives for Beecher's and Raymond's published photographs, which I helped curate in Peabody Museum, were all taken at high magnification and with lighting designed to bring out only certain anatomical parts in the field of view. Features which Beecher was not specifically illustrating may not be well-represented. I compared Størmer's (1939, text-fig. 22d) drawing, Beecher's (1902, pl. 4) published photograph, stereoscopic radiographs of the specimen, and the specimen (YPM 219) itself as examined under a dissecting microscope. The supposed limb in Størmer's drawing proved to be a preparation mark in the matrix that was highlighted in Beecher's photograph.

The coxa would seem to be most reasonably interpreted as a single leg segment in the sense that it forms a single,

continuous exoskeletal structure. However, it is quite another question whether it represents a single podomere or a collection of incipiently differentiated podomeres, like the crustacean protopod, or a collection of fused podomeres, formerly separate, like the crustacean sympod. This question cannot be answered in the absence of detailed knowledge of the intrinsic limb musculature. The term "coxa" as applied to the basal segment of the limb is used with this reservation.

There is no articulation dividing this basal limb segment into precoxa and coxa, and there is otherwise no evidence that demands recognition of a precoxal segment. Among trilobites, the presence of a possible coxa-precoxa division has been clearly demonstrated only in a few limbs of specimens of *Ceraurus pleurexanthemus* (Størmer, 1939). Størmer's interpretation of the precoxa in this species has been strongly criticized (*e.g.*, Calman, 1939; Garstang, 1940; Snodgrass, 1952). In *Triarthrus*, the coxal proximal furrow (*cpf*), which could perhaps be taken for the line of division between the coxa and precoxa, is an area of attachment for some extrinsic limb muscles (*e.g.*, the dorsomedial extrinsic limb muscle, *dmm*, Text-fig. 8). The precoxa, and the question of whether it is a characteristic podomere in arthropod limbs, has a long and involved history in studies of comparative anatomy. Sometimes, as in stomatopod crustaceans, it is clearly recognizable. But in the great majority of cases in which it has been identified, the interpretation of its presence rests on the presence of a furrow across the coxa. An independent musculature, the critical diagnostic feature, is almost always much reduced. In *Triarthrus*, there is no compelling evidence either in the external anatomy of the limb or in the fragmentarily preserved limb musculature for recognizing a distinct precoxal segment.

The exite, inserted medially on the coxa and not on that part of the coxa dorsal to the coxal proximal furrow, is evidently not a pre-epipodite as thought by Størmer (1939). The simple and general term "exite" seems preferable as a designation for this structure, and it has already been used in this connection by Manton (1964) and Bergström (1969).

Størmer's (1939) interpretation of the structure of the exite itself represents a considerable improvement over reconstructions of the ramus by Beecher and Raymond. His (1939) observations on the shaft (*erh*), terminal segment (*ets*), and filaments (*exf*) are here confirmed. The improvements he suggested have been incorporated in my Text-figures 4 and 5. However, it is still not completely clear whether the flattening of the "gill blades," as Størmer (1939) called them, is entirely an original feature or an arti-

fact of deformation. In this paper, the term "exitic filament" is preferred over Størmer's functionally suggestive term. Though Størmer (1939) clearly demonstrated the blade-like structure of the filaments in *Geraurus*, it is not clear how closely this structure resembles the exitic filaments in *Triarthrus*. Some limbs, originally more or less cylindrical in shape, have been pressed flat (e.g., MCZ 7190/18, Pl. 18, fig. 3; Text-fig. 13). It is possible that the commonly blade-like appearance of the filaments in *Triarthrus* has been secondarily enhanced through post-mortem deformation. The filaments in medium-sized specimens are cylindrical (Hartman and Cisne, *in preparation*). Until the internal structure of these filaments is resolved, it will not be clear whether they are setae or actual gill blades as on the opisthosomal limbs of *Limulus*.

My reconstruction of the telopod (Text-figs. 4, 5) agrees with previous interpretations as regards the number of segments (in the sense of independently articulated exoskeletal pieces) comprising it. There has, however, been disagreement among previous workers as to which of these represent true podomeres. Beecher (1894a, 1894b, 1896) and Raymond (1920) considered the telopod to consist of six segments, regarding what is here termed the pretarsus (*pt*) as simply a seta. Størmer (1939), to the contrary, regarded this part of the limb as a true segment, and thus counted seven segments in the telopod. This may be reasonable, as radiographs have revealed the pretarsus as larger and less seta-like than Beecher and Raymond had thought. Størmer's terminology for the parts of the telopod, which is that traditionally applied to arachnid legs, is herein adopted. However, it must be pointed out that, with the very incomplete knowledge of the intrinsic limb musculature, there is no means of reliably determining whether all of these segments are true podomeres or if any are fused or secondarily divided, or in fact if the pretarsus is independently muscled, and is a true podomere rather than a seta.

## EXOSKELETON

### Sclerites and Sclerotization

Only certain parts of the cuticle were sclerotized, that is, thickened and reinforced with sclerotin and mineral matter. In the pyritized *Triarthrus* specimens, the original nature of the sclerites is expressed primarily in their thickness, and secondarily in their lesser degree of deformation as compared with less sclerotized parts of the cuticle.

The tergal exoskeleton is divided into a head tergum ("cephalon"), fourteen thoracic tergites usually called simply "thoracic segments," and the pygidium. The strongly

sclerotized sternal structures are the hypostoma and the metastoma. A rostrum, a small sclerite between the head tergum and hypostoma found in many trilobites, has not been identified. To differing degrees, tergal structures extend around the edges of the dorsal surface into their ventral continuations, their doublures.

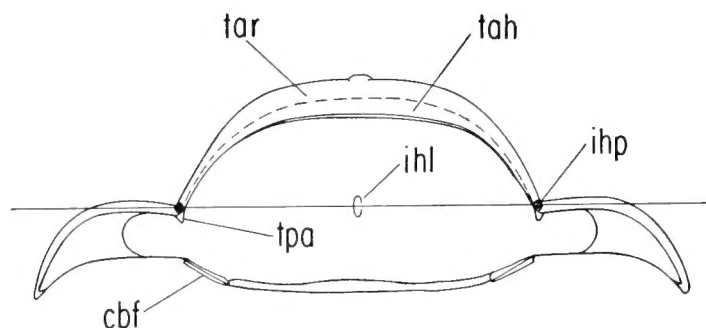
### Tergites and Intertergal Articulation

Trilobites characteristically had two-point hinge joints between successive tergites that permitted dorsoventral flexure of the body, as in enrollment, but that did not permit much sidewise flexure (see in particular, Bergström, 1973). In *Triarthrus*, intertergal hinge structures are not elaborately developed (Text-fig. 6; see also Text-figs. 3, 7 for identification of parts). As indicated by the ventral tapering out of the articulating half ring, the intertergal hinge line (*ihl*, Text-fig. 6) passed transversely between tergites at the level of the dorsal axial furrow. A strong boss has not been found associated with the inferred intertergal hinge point (*ihp*), nor have groove hinge structures been found along the inferred course of the hinge line across the pleural region of the tergite.

Two interior views of the right halves of three articulated thoracic segments ( $T_4 - T_6$ ; Text-fig. 11) show the overlap between the articulating half ring (*tah*) of one tergite and the axial ring (*tar*) of the tergite anterior to it, and show the intertergal membrane (*itm*) inferred to have connected adjacent tergites. The tergites are in this way telescoped.

As indicated by specimens preserved in flexed position, *Triarthrus* could flex the body ventrally to enroll the posterior part of the body loosely and bring the abdomen up beneath the anterior part of the thorax. It could flex the body dorsally through at least 20 degrees of arc, but could not flex the body sidewise to any appreciable extent. The very small lateral flexure in some specimens is probably the result of post-mortem deformation. All of this would be expected from the characteristic structure of trilobite intertergal hinge joints.

In Text-figure 7, the approximate maximum ventral (A) and dorsal (B) flexures across the three thoracic segments are reconstructed on a strictly anatomical basis. The maximum ventral flexure should be roughly delimited by the point at which the anterior margin of an articulating half ring lies beneath the posterior margin of the axial ring anterior to it (Text-fig. 7, A), though it may have been possible to flex the joint more, to expose the intertergal membrane between the two tergites. The maximum flexure

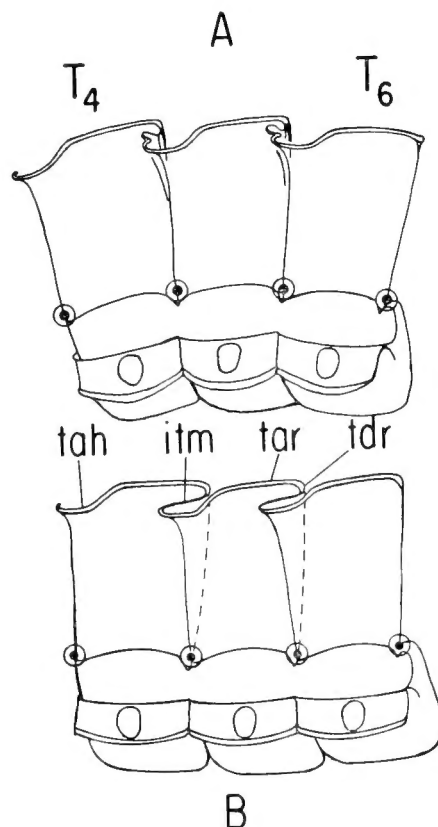


Text-figure 6.—Anterior view of the fifth thoracic exoskeletal segment ( $T_5$ ) showing in particular the intertergal hinge points ( $ihp$ ) and the intertergal hinge line ( $ihl$ ).

would thus appear to have been 10 to 15 degrees ventrally across each joint. Given fifteen intertergal joints, this amount of angular displacement across each joint would have been just sufficient to permit the loose enrollment observed in some specimens. On dorsal flexure (Text-fig. 7, B), the anterior face of one axial ring should have come into contact with the posterior edge of the axial ring just anterior to it after a rotation of only three to five degrees across the joint. At this point, the joint should have locked. Hence it would appear that the body could have been flexed dorsally through no more than a few tens of degrees of arc, or not much more than has been observed in specimens.

#### Joints and Articulations of the Limbs

To make a rough judgment from its variety of positions among specimens, the antenna was movable about its articulation to the body. From observations of the variety of configurations of the shaft, Beecher (1894a) and Raymond (1920) suggested that it had considerable flexibility in life. Indeed the antenna had extrinsic muscles and, at least through the proximal third of its shaft, intrinsic muscles that could have effected both kinds of movement in life (see "Skeletomusculature"). All postoral limbs have basically the same type of articulation to the body. The coxa-body articulation was probably loose, as in the prosomal legs of *Limulus* (Manton, 1964, suggested this possibility). While no exoskeletal joint structures suggest a one- or two-point hinge at the articulation, the limbs evidently had a preferred axis of swing oriented more or less horizontally and transverse to the body, as appropriate to a back and forth promotor-remotor swing. But the limbs could probably have been put through a greater variety of movements. Though there is no good evidence on how loose the articulation may have been, the absence of structures suggesting a definitive hinge suggests that movements of the limb were probably



Text-figure 7.—Interior views of the right halves of the fourth through sixth exoskeletal segments ( $T_4$ - $T_6$ ) showing their conformation in approximate maximum ventral flexure (A) and approximate maximum dorsal flexure (B). The trilobite could flex its thorax to a greater extent ventrally than dorsally.

governed by a complex musculature, only the general features of which are known.

The trunk limbs, as illustrated by the fifth thoracic limb ( $T_5$ , Text-figs. 4, 5), and the head limbs ( $C_1$  -  $C_3$ , Text-fig. 5), have a preferred axis of swing of the coxa extending across the coxa-body foramen ( $cbf$ ) in the plane roughly defined by the coxal endite and projecting upward at an angle of about 20 degrees to the horizontal for the trunk limbs and at a lower angle for head limbs. For trunk limbs, the axis of swing is transverse to the body. However, for head limbs, the axis anteriorly ( $C_3$  -  $C_1$ ) becomes more oblique to the body, as the exoskeletal segments bend around the mouth region. The primary mode of movement of the coxa about its articulation to the body would appear to have been a back and forth swing. The only direct evidence bearing on movement about the coxa-body articulation comes from post-mortem deformation of specimens. When limbs have fallen over, they have rotated more or less about the transverse hinge inferred for the coxa-body articulation (e.g.,



MCZ 7190/18, Pl. 18, fig. 3; Text-fig. 13; YPM 27813, Pl. 18, fig. 4; Text-fig. 15). The joint, as a zone of weakness in the cuticle, should have yielded more readily to deforming stress than other parts of the cuticle. The dorsal and ventral extrinsic limb muscle arrangement facilitated the inferred simple back and forth swing (see Text-fig. 8; "Skeleto-musculature"). Dorsal extrinsic muscles (*dam*, *dpm*; Text-fig. 8) and ventral extrinsic muscles (*vam*, *vpm*; Text-fig. 8) were situated symmetrically anterior and posterior to the limb. In this orientation, they could easily have acted to move the limb back and forth about an axis of swing transverse to another swing axis that ran transversely across the plane defined by the coxal endite.

As a consequence of the difference in the orientation of their articulations with respect to the body, the head and trunk coxae operated differently. Because the dorsoventral cant of the hinge was slight (e.g., the hinge line was subhorizontal), and because the approximate hinge line was transverse to the body axis, the transverse separation of paired trunk endites should not have varied much through the course of the stroke. But because the orientation of the approximate hinge line for head limbs was oblique to the body, the transverse separation of head endites should have varied through the stroke. The head coxae, the first pair ( $C_1$ ) in particular, should have moved back and apart on the backstroke and forward and together on the forestroke.

The exite shaft (*erh*), which consistently follows a posteriorly-curved course and maintains a nearly constant relationship to the coxa, would seem to have been stiff and rigidly articulated to the coxa. Likewise, the exitic filaments (*exf*) maintain their posteriorly and outwardly directed courses from specimen to specimen, and also appear to have been stiff.

Judging from the positions of limbs in specimens, angular displacements across the telopodal joints from the coxa-trochanter joint at least to the patella-tibia joint distally appear to have been primarily dorsoventral with respect to the coxa. The hinge lines were thus oriented approximately anteroposteriorly, as indicated for the coxa-trochanter joints (Text-fig. 5). Only very small displacements were noticed across more distal joints. No well developed hinge structures were identified in conjunction with the joints. It is possible that the limb had no well-developed and rigidly circumscribed one-point or two-point hinges, and that displacements of the segments were governed by a correspondingly complex musculature. The one joint notably unlike the rest is the femur-patella joint: the distal segment is inserted very high dorsally on the other segment. This configuration may mean that the hinge joint (or hinge

area) was situated at the top of the limb so that the patella could have had only flexor (but not extensor) muscles. Extension could have been effected instead by internal hydrostatic pressure.

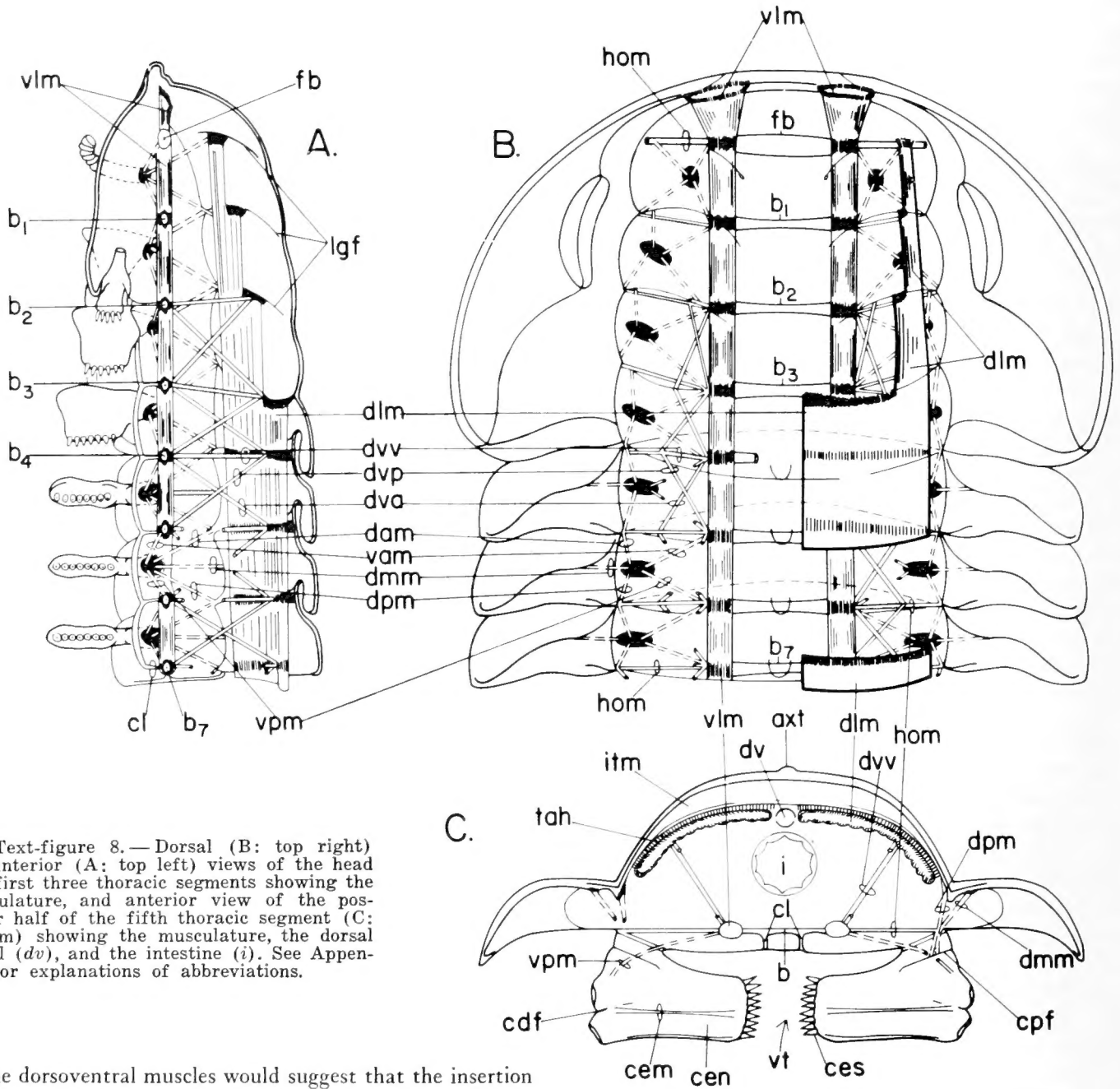
#### SKELETOMUSCULATURE

This description of the skeleto-musculature is necessarily incomplete and generalized insofar as many details of structure are concerned. The reconstructions are no doubt much simplified pictures of the actual trilobite. Smaller muscles are less frequently preserved than larger ones. Many smaller muscles were probably not preserved in a condition in which they could be repeatedly recognized. Some larger muscles whose presence was expected (notably muscles governing the hypostoma) were not identified. Preservation is consistently good enough to reveal the larger body muscles and the fibers that comprise them. Though it is sufficient to reveal extrinsic limb muscles in many specimens, preservation is not good enough to reveal functionally important details on the origins and insertions of their constituent fibers. Consequently, extrinsic limb muscles cannot be clearly identified as promoters or remoters.

#### Description

The skeletal muscles can be divided into five sets: (1) longitudinal body muscles, (2) dorsoventral body muscles, (3) horizontal body muscles, (4) extrinsic limb muscles, and (5) intrinsic limb muscles. An additional component of the skeleto-muscular system is an endoskeleton of inter-segmental bars, probably tendinous, associated with the ventral parts of the musculature. Reconstructions of the skeleto-musculature are given in Text-figures 8 and 9. Additional muscles associated with the gut are described in connection with the description of the digestive system.

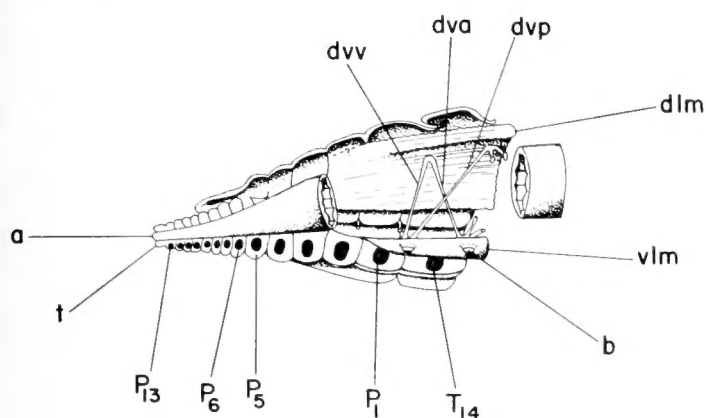
The paired dorsal longitudinal muscles (*dlm*) form a sheet along the axial region on the underside of the dorsal exoskeleton. The lateral part of the dorsal longitudinal muscle extends far forward to the region of the first lateral glabellar furrow, and tapers anteriorly. The muscle probably takes origin gradually. The extreme lateral slips of the muscle originate at the first lateral glabellar furrow (*lgf<sub>1</sub>*), progressively more medial slips originate at the second and third lateral glabellar furrows (*lgf<sub>2</sub>*, *lgf<sub>3</sub>*) and the most medial slips — in all, about half of the muscle — originate at the occipital furrow (*ocf*). Along the trunk, the dorsal longitudinal muscle is almost certainly inserted on each articulating half ring (*tah*, *pah*; see Hessler, 1962). The origins



Text-figure 8.—Dorsal (B: top right) and interior (A: top left) views of the head and first three thoracic segments showing the musculature, and anterior view of the posterior half of the fifth thoracic segment (C: bottom) showing the musculature, the dorsal vessel (*dv*), and the intestine (*i*). See Appendix for explanations of abbreviations.

of the dorsoventral muscles would suggest that the insertion of the dorsal longitudinal muscle was along the antero-posterior middle of the articulating half ring. The tonofibrils which presumably connected the muscle to the exoskeleton have evidently not been fossilized. No antecosta is developed on the articulating half ring. It is not unlikely that the trilobite's dorsal longitudinal muscle was attached over a relatively broad area, perhaps loosely, to the underside of the articulating half ring. The ultimate insertions of the muscle in the abdomen are not known.

The ventral longitudinal muscles (*vlm*) are a pair of muscle bundles, each about one-tenth the width of the axial region, that run in parallel along the axial region of the body just dorsal to the sternal cuticle. The ventral longitudinal muscle takes origin in the vicinity of the head border (*hbo*) anterior to the lateral part of the frontal glabellar lobe (*fgl*); the exact area of origin is uncertain. The muscle is inserted on the distal parts of each of the



Text-figure 9.—Interior view of the left half of the abdomen and last thoracic segment showing the musculature and the intestine (*i*). The limbs and their extrinsic musculature have been omitted. See Appendix for explanations of abbreviations.

succession of endoskeletal bars (*fb*,  $b_1$ - $b_{17}$ ) along the head and thorax. The ultimate insertions of the ventral longitudinal muscle in the abdomen are poorly known. The bulk of the muscle may have been inserted at the pygidial ventral ring furrow (*pvr*) separating the first and second abdominal segments of the pygidium ( $P_1$ ,  $P_2$ ).

The endoskeletal bars (*fb*,  $b_1$ - $b_n$ ), probably tendons, as in more primitive crustaceans, are elongate rods, more or less oval in cross-section, that extend about half the distance transversely across the axial region just dorsal to the ventral cuticle. The most anterior, or frontal bar (*fb*), is larger than the rest (post-frontal bars,  $b_1$ - $b_n$ ) and lies between the first pair of lateral glabellar furrows (*lgf*<sub>1</sub>). Post-frontal bars of the head ( $b_1$ - $b_3$ ) lie respectively between the pairs of second and third lateral glabellar furrows (*lgf*<sub>2</sub>, *lgf*<sub>3</sub>) and more or less across the occipital furrow (*ocf*). The bar between the head and the first thoracic segment ( $b_4$ ) and bars between successive thoracic segments ( $b_5$ - $b_{17}$ ) lie directly beneath their respective articulating half rings (*tah*). An additional bar ( $b_{18}$ ) may have been present between the last thoracic segment ( $T_{14}$ ) and the pygidium, beneath the pygidial articulating half ring (*pah*). It is not known whether the succession of bars continued posteriorly into the abdomen. Post-frontal bars, and perhaps the frontal bar as well, were presumably connected to the ventral cuticle: in at least one specimen, paired connecting structures, probably ligaments, (*cl*) have been identified.

The dorsal and ventral longitudinal muscles (*dlm*, *vlm*) are linked by three kinds of dorsoventral muscles: ventrally descending dorsoventral muscles (*dvv*), anteriorly descending dorsoventral muscles (*dva*), and posteriorly descending dorsoventral muscles (*dvp*). These occur in segmentally re-

peated units. Together, the anteriorly, posteriorly, and ventrally descending dorsoventral muscles from a box truss in each segment (Text-fig. 8). In the thorax, the dorsoventral muscles take origin on the anteroposterior midsection of the articulating half ring (*tah*) in a small area about half the distance between the crest of the axial region and the dorsal axial furrows (*daf*); and the muscles extend inwardly and ventrally to insert on the distal ends of endoskeletal bars. The ventrally descending muscle (*dvv*) extends between segments, but the anteriorly and posteriorly descending muscles (*dva*, *dvp*) extend across segments. It is not known which muscle is exterior as they cross in the midsection of a segment. The segmental units of the dorsoventral muscles are apparently repeated in the two most posterior segments of the head ( $C_2$ ,  $C_3$ ) as a continuation of the thoracic series. Anterior to the articulating half ring (*tah*) of the first thoracic segment ( $T_1$ ), the dorsoventral muscles take origin beneath the occipital furrow (*ocf*) and the third lateral glabellar furrow (*lgf*<sub>3</sub>) in the vicinity of the insertion of thoracic dorsoventral muscles. Dorsoventral muscles have not been recognized anterior to the  $C_2$  segment. Unless substantially rearranged, their presence would seem unlikely, as the crop extends across the expected paths of dorsoventral muscles between the middle sections of the first and second lateral glabellar furrows (*lgf*<sub>1</sub>, *lgf*<sub>2</sub>) and the distal ends of the corresponding endoskeletal bars (*fb*,  $b_1$ ,  $b_2$ ) (see Text-figs. 10, 11). It is not known whether dorsoventral muscles were present in the abdomen.

The extrinsic limb muscles are known, but not at all well, for thoracic segments, for postoral head segments, and for the antennal segment. Only the larger muscle masses are described and figured in this paper. The basic pattern of extrinsic limb muscles is serially repeated in all these segments.

The extrinsic limb muscles of a thoracic segment fall into sets by area of origin: dorsal extrinsic limb muscles (*dam*, *dmm*, *dpm*) which take origin on the tergal exoskeleton, and ventral extrinsic limb muscles (*vam*, *vpm*) which take origin on the distal ends of endoskeletal bars. In the thorax, the dorsoanterior extrinsic limb muscle (*dam*) and the dorsoposterior extrinsic limb muscle take origin on a ventrally directed projection from the extreme posterolateral edge of the axial ring, the thoracic posterior apodeme (*tpa*, Text-fig. 10). The dorsoanterior muscle (*dam*) and the dorsoposterior muscle (*dpm*) extend respectively posteriorly and anteriorly in descending ventrally through the coxa-body foramen (*cbf*) to insert on the inside of the coxa (*cx*). The bulk of the dorsoanterior muscle (*dam*) probably inserted on the anterior face of the coxa and at least in part along the coxal proximal furrow

(*cpf*). The bulk of the dorsoposterior muscle (*dpm*) probably inserted on the posterior face of the coxa and at least in part along the coxal proximal furrow (*cpf*). The dorso-medial extrinsic limb muscle (*dmm*) takes origin beneath the pleural furrow (*tpf*) and descends straight ventrally through the coxa-body foramen (*cbf*) to insert on the inside of the coxa, probably along its distal edge dorsal to the insertion of the exite and at least in part along the coxal proximal furrow (*cpf*). The two ventral extrinsic limb muscles, the ventroanterior extrinsic limb muscle (*vam*) and the ventroposterior extrinsic limb muscle (*vpm*) extend respectively posteriorly and anteriorly in projecting ventrally and outward through the coxa-body foramen to insert on the inside of the coxa (*cx*). Each muscle could have inserted on one or both sides of the coxa. But as suggested by the directions of the muscles as they enter the coxa, it seems likely that the areas of insertion were located in the dorsal part of that limb segment. Some extrinsic limb muscles, for most of which the area of origin cannot be explicitly identified, extend well into the coxa past the coxal proximal furrow (*cpf*).

The extrinsic limb musculature of the postoral head limbs ( $C_1$ - $C_3$ ) conforms to the same pattern as that of the thoracic limbs, but a dorso-medial extrinsic limb muscle (*dmm*) may not have been present. Like a thoracic axial ring (*tar*), the occipital ring (*ocr*) bears a small, ventrally directed projection which, like the thoracic posterior apodeme to which it apparently corresponds, is probably the apodeme for the dorsoanterior extrinsic limb muscle (*dam*) of the first thoracic segment ( $T_1$ ) and the dorsoposterior extrinsic limb muscle (*dpm*) for the occipital segment ( $C_3$ ). The fragmentally-preserved dorsal extrinsic limb muscles for the postoral head limbs have been reconstructed largely by analogy with the extrinsic limb musculature of thoracic segments. They probably take origin beneath the distal portions of the head furrows bounding their respective segments (*lgf<sub>2</sub>*, *lgf<sub>3</sub>*, *ocf*). The dorso-medial extrinsic limb muscle (*dmm*) has not been identified in association with these limbs. As the head apparently lacks analogues of the thoracic pleural furrows (*tpf*), I doubt that this muscle was developed in other than much modified form, if at all. The ventral extrinsic limb muscles are developed similarly for postoral cephalic segments and thoracic segments.

The antenna (*A*) has both dorsal (*dam*, *dpm*) and ventral (*vam*, *vpm*) extrinsic limb muscles. The dorsoanterior (*dam*) and dorsoposterior (*dpm*) extrinsic limb muscles, which are known only fragmentarily, probably take origin respectively beneath the extreme distal portions of

the first and second lateral glabellar furrows (*lgf<sub>1</sub>*, *lgf<sub>2</sub>*). They respectively extend posteriorly and anteriorly as they descend ventrally into the antennary peduncle, where they presumably are inserted. The ventroposterior extrinsic limb muscle (*vpm*) originates at the end of the first post-frontal endoskeletal bar (*b<sub>1</sub>*) and extends anteriorly in descending ventrally into the antennary peduncle, where it presumably inserts. The ventroanterior extrinsic limb muscle (*vam*) originates at the end of the frontal endoskeletal bar (*fb*) and extends posteriorly as it descends ventrally to its presumed insertion inside the peduncle.

Intrinsic muscles of the postoral limbs, or rather bits and pieces of them, have been found throughout the coxa and telopod; but only two could repeatedly be identified in specimens. The coxal enditic muscle (*cem*) extends horizontally across the middle of the coxa from the area of the coxal distal furrow (*cdf*) towards the adaxial edge of the coxal endite (*cen*). A muscle (*ilm*) running from the distal part of the patella (*pl*) across the femur (*fe*) has also been repeatedly identified. Additional evidence is so fragmentary that further interpretation of the musculature pattern is impossible.

The antenna bears intrinsic muscle fibers that have been identified repeatedly through at least the proximal third of the shaft and that probably extended more distally. It has not been possible to work out the overall pattern of these fibers.

#### Documentation

The fossilized muscles, characteristically delicate and subtle structures in radiographs, have been identified by comparison with the musculature of modern arthropods based on similarities in the gross form and structure, and on anatomical relationships of the preserved parts and assemblages of parts, as noted below. In studying and restudying radiographs, particular muscles were identified on the basis of their recurrence in relation to parts of the exoskeleton and other parts of the skeletomusculature. To identify smaller muscles, in particular, it was necessary that the entire muscle be preserved and that it be associated with some larger section of the skeletomusculature and(or) exoskeleton that was also preserved in considerable detail. Many smaller muscles otherwise well preserved, but not in an anatomical context in which they could be identified, have been discounted.

The dorsal longitudinal muscles (*dln*) appear as a thin sheet, or part of a sheet, of tiny pyritized fibers running in parallel along the underside of the axial region of the

dorsal exoskeleton in the trunk (*e.g.*, YPM 207, Pl. 23, fig. 3) and along the side of the glabella in the head (*e.g.*, YPM 28264, Pl. 20, fig. 3; Text-fig. 19.) In gross form, texture, and relationship to the dorsal exoskeleton, these preserved structures have very much the appearance of the dorsal longitudinal muscles of more primitive entomostracan crustaceans, particularly cephalocarids and notostracan branchiopods. These muscles are likewise developed as a sheet of fibers running in parallel down the trunk (Hessler, 1964).

Parts of the dorsal longitudinal muscle have commonly been observed, having been identified in 39 of the 68 specimens intensively studied with "soft" radiography. The muscle, in a mediocre state of preservation, is indicated in YPM 27813 (Pl. 18, fig. 4; Text-fig. 15, *dln*). Specimen MCZ 7190/14B (Pl. 20, figs. 1, 2; Text-fig. 18) shows the many parallel fibers comprising the muscle (*dln*) in various positions across the expanse of the axial region from the midsection of the trunk anterior to the occipital furrow (*ocf*) on the head. The more medial fibers drop out anteriorly past that furrow (*ocf*), and only a few of the more lateral fibers extend anteriorly beyond it. The lateral parts of the dorsal longitudinal muscle (*dln*) and their extension from the thorax along the sides of the glabella are more clearly shown in YPM 28264 (Pl. 20, figs. 3, 4; Text-figs. 19, 20) and YPM 204 (Pl. 21, fig. 4; Text-fig. 24).

The ventral longitudinal muscles (*vlm*) appear as a pair of bundles comprised of thin pyrite fibers that run in parallel along the axial region of the body for all or part of the distance between the anterior part of the head and the anterior part of the abdomen. The particular basis for the identification of these fossil structures is the similarity they bear to the ventral longitudinal muscles in cephalocarid, branchiopod, and phyllocarid crustaceans in the form and arrangement of the bundles and the insertions of the muscle on endoskeletal bars in the head and thorax. These endoskeletal bars bear the insertions of dorsoventral muscles and ventral extrinsic limb muscles.

In radiographs, the parallel bundles of the ventral longitudinal muscles have a gross similarity to the intestine, which, owing to its shape and to the enhancement of contrasts in prints, has the appearance not of a flattened tube or ribbon but of two parallel streaks that correspond to its lateral edges. In most cases, these muscles and the intestine can be distinguished, though in a few cases, poor preservation or preparational damage makes this impossible. The ventral longitudinal muscles can be identified through their association with endoskeletal bars, dorsoventral muscles, and extrinsic limb muscles, because such a section of the ventral musculature has a gross form and set of anatomical

relationships that is different from the intestine, which is often connected to the crop or anus. Actually, as a peculiarity of preservation, the ventral longitudinal muscle and the intestine are very seldom found well preserved together in the same segments of the body. Specimen YPM 28259 (Pl. 19, fig. 4; Text-fig. 17) is exceptional in showing the ventral longitudinal muscles (*vlm*), and anterior endoskeletal bars (*b<sub>2</sub>-b<sub>4</sub>*), and pieces of smaller body muscles (*hom* or *dvv*) preserved together with the crop (*s*) and intestine (*i*) in the anterior part of the body.

The ventral longitudinal muscles have been identified in ten of 68 intensively studied specimens: YPM 204, YPM 228, YPM 27802A, YPM 28222, YPM 28254, YPM 28257, YPM 28259, YPM 28264; MCZ 7190/2, MCZ 7190/26. The ventral longitudinal muscles (*vlm*) extend along the body from the posterior part of the head to the apparent insertions in the anterior part of the pygidial abdomen in YPM 27802A (Pl. 21, fig. 1; Text-fig. 21) and YPM 28222 (Pl. 21, fig. 2; Text-fig. 22). In both specimens, the muscles (*vlm*) are associated with post-frontal endoskeletal bars (*b*) and dorsoventral muscles (*dva*, *dvp*, *dvv*). In both specimens, the extreme posterior parts of the muscle curve laterally toward the boundary between the first and second abdominal segments (*P<sub>1</sub>*, *P<sub>2</sub>*), where the ventral longitudinal muscle was probably, at least in part, inserted on the ventral exoskeleton. The anterior parts of the ventral longitudinal muscles, which are often difficult to discern because of the anatomical complexity of the front part of the head, are well shown in YPM 228 (Pl. 17; Pl. 21, fig. 3; Text-fig. 23, *vlm*). There they are associated with the frontal bar (*fb*) and postfrontal bars (*b<sub>1</sub>-b<sub>3</sub>*). The extensions of the muscles anterior to the frontal bar (*fb*) toward their probable areas of origin near the head border (*hbo*) are also shown.

The endoskeletal bars, narrow pyrite rods that run transverse to the body cavity, have been identified through association with the ventral longitudinal muscles, dorsoventral muscles, and ventral extrinsic limb muscles, and from their positions with respect to the exoskeleton. Larger bars, when well-preserved, have a more streamlined shape than comparably sized pieces of muscle; and they lack the fibrous texture associated with well-preserved muscle tissue. In their relative size and relationships to the ventral musculature, the bars bear a striking resemblance to tendinous endoskeletal bars in the trunk and posterior part of the head in cephalocarid, branchiopod, and phyllocarid crustaceans.

The frontal bar has been identified in 24 of the 68 intensively studied specimens, and post-frontal bars have been found in 20 specimens. As compared with the number of frontal bars identified, the number of post-frontal bars iden-

tified is lower by a factor of about five than the number expected given the ratio of about 20 to one post-frontal to frontal bars in the actual animal and an equal probability of preservation of each bar independent of all others. In part, the disproportion in numbers is probably due to preferential preservation of the larger and presumably more durable frontal bar. However, differential difficulty in recognition is probably also involved. The frontal bar, relatively large and lying across the anatomically uncluttered center of the frontal glabellar lobe (*fgl*), is an obvious and easily recognized structure. Post-frontal bars, on the other hand, lie parallel to folds and furrows in the cuticle both dorsal and ventral to them. They can be obscured by these other features, especially if the bars are not well-preserved. In practice, it is difficult, and usually impossible, to reliably identify bars of the trunk against the background of the overlapping axial rings (*tar*) and articulating half rings (*tah*) that lie immediately dorsal to them when the anatomical relationships of the living animal have been maintained in a specimen. Consequently, the clearest examples of these particular post-frontal bars come from specimens in which the ventral exoskeleton has been moved anteriorly or posteriorly relative to the dorsal exoskeleton, in post-mortem deformation, such that the bars no longer rest in the region of the tergal overlap.

The frontal bar (*fb*) is related to the ventral longitudinal muscle (*vlm*) and horizontal muscle (*hom*) as indicated in specimens YPM 228 (Pl. 17; Pl. 21, fig. 3; Text-fig. 23, *vlm*), YPM 28257 (Pl. 22, fig. 2; Text-fig. 26), and MCZ 7190/14B (Pl. 20, figs. 1, 2; Text-fig. 18, *hom*).

The post-frontal bars (*b*) are serially repeated in association with the ventral longitudinal muscle (*vlm*) in YPM 228 (Pl. 21, fig. 3; Text-fig. 23, *b<sub>1</sub>-b<sub>3</sub>*), YPM 27802A (Pl. 21, fig. 1; Text-fig. 21, *b<sub>1</sub>-b<sub>4</sub>*, *b*), YPM 28222 (Pl. 21, fig. 2; Text-fig. 22, *b*, *b<sub>11</sub>*, *b<sub>13</sub>*), YPM 28259 (Pl. 19, fig. 4; Text-fig. 17, *b<sub>1</sub>-b<sub>4</sub>*), and YPM 28264 (Pl. 20, figs. 3, 4; Text-figs. 19, 20, *b*). These bars (*b*) are associated with the dorsoventral muscle (*dva*, *dvp*, *dvv*), horizontal muscles (*hom*), and ventral extrinsic limb muscles (*vam*, *vpm*) as indicated in YPM 27802A (Pl. 21, fig. 1; Text-fig. 21, *dvv + dva* or *dvv + dvp*), YPM 28222 (Pl. 21, fig. 2; Text-fig. 22, *dva*, *dvp*, *dvv*), YPM 28257, Pl. 22, fig. 2; Text-fig. 26, *vam*), YPM 28259 (Pl. 19, fig. 4; Text-fig. 17, *hom* or *dvv*), YPM 28264 (Pl. 20, figs. 3, 4; Text-figs. 19, 20, *hom*, *vpm*), and MCZ 7190/14B (Pl. 20, figs. 1, 2; Text-fig. 18, *vpm*). The paired connecting ligaments (*cl*) that lie between the bars and the ventral exoskeleton, have been clearly seen in only one bar (*b<sub>3</sub>*) in a single specimen, YPM 228 (Pl. 17; Pl. 21, fig. 3; Text-fig. 23). This one bar's

peculiar shape, compared with others, may be the result of its having fallen anteriorly, as the anterior thoracic limbs have during post-mortem deformation of the specimen. If this is true, the connecting ligaments (*cl*) as indicated should face posteriorly, as they in fact do.

The dorsoventral muscles appear as pyritized rods contiguous with preserved parts of the ventral longitudinal musculature and (or) the axial portion of the dorsal exoskeleton near its segmental boundaries; these identifications are based upon anatomical relationships and association within characteristic serially repeated units. In these features, the preserved parts bear a marked similarity to the thoracic dorsoventral muscle of cephalocarid crustaceans and a more general similarity to thoracic dorsoventral muscles in notostracan, anostracan, conchostracan, and phyllocarid crustaceans (see Hessler, 1964). Similar configurations of dorsoventral muscles are found in myriapods as well, though not in conjunction with an endoskeleton of the type found in those crustaceans (see Manton, 1965, 1973b).

The dorsoventral muscles have been identified in the indicated areas in five specimens — YPM 204 (head), YPM 27802A (thorax), YPM 28222 (thorax), YPM 28254 (head and thorax), and YPM 28270P (thorax) — and have been questionably identified (as one possibility among others) in YPM 201, YPM 28259, and YPM 28270M. Specimen YPM 204 (Pl. 21, fig. 4; Text-fig. 24) shows the dorsoventral muscles (*dva*, *dvp*, *dvv*) in the second and third postoral head segments (*C<sub>2</sub>*, *C<sub>3</sub>*) in conjunction with the ventral longitudinal muscle (*vlm*). For the *C<sub>2</sub>* segment, the anteriorly descending (*dva*), posteriorly descending (*dvp*), and ventrally descending (*dvv*) dorsoventral muscles originate beneath the dorsal intersegmental furrows bounding that segment (*lgf<sub>3</sub>*, *ocf*). Likewise, the posteriorly descending dorsoventral muscle (*dvp*) for the *C<sub>3</sub>* segment appears to take origin beneath the occipital furrow (*ocf*). The anteriorly descending dorsoventral muscle (*dva*) for that segment appears to be directed toward an origin on the articulating half ring of the first thoracic segment (*tah<sub>1</sub>*). Sidewise deformation has exposed the dorsoventral muscles in a convenient view in this specimen, and the dorsal exoskeleton itself has been sheared to a lesser extent so that the entire set of limbs has been sheared to the side with respect to the dorsal exoskeleton. This is particularly important, because YPM 204 is one of three specimens on which Beecher (1896) particularly based his famous reconstruction (Beecher, unpublished notes on file at Peabody Museum, Yale University, New Haven, CT). Radiographs reveal deformation that visual inspection cannot detect. Beecher was evidently not aware that the specimen was so

severely deformed, and this is probably the prime reason why his reconstruction (Beecher, 1896) shows the unnatural lateral displacement of the thoracic limbs.

One segmental unit of the dorsoventral muscles (*dva*, *dvp*, *dvv*) and parts of other units are shown in conjunction with the ventral longitudinal muscles (*vlm*) and endoskeletal bars (*b*) along the thorax in YPM 28222 (Pl. 21, fig. 2; Text-fig. 22). Specimen YPM 27802A (Pl. 21, fig. 1; Text-fig. 21) affords an unusual view of two dorsoventral muscles (*dvv* + *dva* or *dvv* + *dvp*) owing to anterior or posterior displacement of one of the bars in the posterior part of the thorax (*b*, either *b*<sub>12</sub> or *b*<sub>13</sub>; the direction of morphological deformation is not clear). Had it not been for this displacement one of the two pairs of muscles should have been dorsoventrally crushed and the bar probably would have been rendered indistinguishable against the background of overlapping tergites, so that the entire assemblage of parts probably could not have been recognized. The two pairs of dorsoventral muscles extend posteriorly and anteriorly from articulating half rings (*tah*) to the endoskeletal bars.

The horizontal muscles (*hom*) appear as pyritized rods running transversely from the ends of endoskeletal bars to areas of segmental boundaries along the ventral axial furrow. In relative size and anatomical relationships, the serially repeated fossil structures are very similar to horizontal muscles in cephalocarid, branchiopod, and phyllo-carid crustaceans, hence their identification as such.

The horizontal muscle has been identified in only four specimens: YPM 211, YPM 28264, MCZ 7190/14B and MCZ 7190/26. Except in relation to the frontal bar, this muscle (*hom*) cannot be reliably distinguished from the ventrally descending dorsoventral muscle (*dvv*) in the deformed specimens, in the absence of its critical diagnostic feature, its relationship to the ventral exoskeleton. As might be expected, this combination of features is rarely preserved or observed. In the majority of observations of possible horizontal muscles, the critical relationship to the exoskeleton cannot be discerned clearly (*e.g.*, YPM 28259; Pl. 19, fig. 4; Text-fig. 17, *hom* or *dvv*; extending transverse to the body as they do, it is unlikely that they are extrinsic limb muscles). Consequently the muscle cannot be reliably identified as one or the other of the two types. In relation to endoskeletal bars in the trunk, the horizontal muscles lie parallel to the edges of overlapping axial rings and articulating half rings. Because they are difficult to discern against that background, horizontal muscles are most clearly seen in specimens that have been deformed into an unnatural anatomical position.

The horizontal muscles (*hom*) are best shown in YPM 28264 (Pl. 20, figs. 3, 4; Text-figs. 19, 20), this owing to unusual and particularly deceptive post-mortem deformation. It would appear from the radiograph of the entire specimen (Pl. 20, fig. 3) that limbs in the anterior part of the thorax had been moved anteriorly with respect to the dorsal exoskeleton by something less than half a segment length. However, as can be seen by extending the ventral interpleural furrow of the fourth thoracic segment (*tvi*<sub>4</sub>), the limbs, and the entire ventral cuticle with them, have been moved anteriorly by more than an entire segment length. In this part of the thorax, deformation has resulted in a displacement of the entire ventral part of the body with respect to the dorsal part such that the ventral part of the fourth thoracic segment lies ventral to the dorsal part of the third thoracic segment. Yet in the more posterior part of the thorax, at the level of the eighth thoracic segment, the respective limb has been moved anteriorly by only about half a segment length, as indicated by the connection remaining between that limb and the dorsal cuticle by way of the dorsoposterior extrinsic limb muscle (*dpm*). There may be a tear in the ventral integument somewhere between the fourth and eighth thoracic segments, perhaps across the spatial (but not anatomical) gap in the series of horizontal muscles along the thorax.

On the right side of the body of YPM 28264 is a series of five horizontal muscles (*hom*) — three anteriorly and two posteriorly, the two groups being separated by the aforementioned gap — connected to their respective endoskeletal bars (*b*). The most anterior muscle appears to meet the ventral exoskeleton near the proximal end of the ventral interpleural furrow (*tvi*), that is, at its junction with the ventral axial furrow (*vaf*; not clearly shown). Because of the shearing displacement of the ventral cuticle with respect to the dorsal cuticle, it is clear that each transversely directed muscle in this series was connected distally to the ventral cuticle and, incidentally, that the endoskeletal bars on which they take origin were also connected distally to the ventral cuticle. Were the muscles (*hom*) connected to the dorsal cuticle at their distal ends, they would extend obliquely across segmental boundaries in passing to their attachments on the endoskeletal bars.

The horizontal muscle (*hom*) associated with the frontal bar (*fb*) is shown in MCZ 7190/14B (Pl. 20, figs. 1, 2; Text-fig. 18). The insertion of the muscle on the cuticle is not clearly seen in this case. But, in view of the large extent of the stomach beneath the dorsal cuticle in this part of the head (see Text-fig. 11), it is unlikely that this particular muscle was inserted on the dorsal cuticle (in

which case it would instead be a ventrally descending dorso-ventral muscle [*dvv*]).

The extrinsic limb muscles appear as tiny strands of pyrite running all or part of the way from the base of the limb to areas of origin on the dorsal exoskeleton or the ventral endoskeleton. Modern arthropods furnish no detailed guidelines for the recognition of fossilized extrinsic limb muscles except that, ideally, they radiate to the base of the limb from origins in both the dorsal and ventral parts of the body and that, also ideally, dorsal and ventral sets of muscles are subdivided into anterior and posterior groups. Fossil extrinsic limb muscles are best recognized from their attachments to limbs. Usually, recognizable extrinsic muscles are incomplete, and, as a consequence of post-mortem deformation, somewhat dislocated. Several probable extrinsic limb muscles could not be identified as such because they are detached from their insertions.

Extrinsic muscles of the biramous limbs (*dam*, *dmm*, *dpm*, *vam*, *vpm*) have been identified in 18 of the 68 intensively studied specimens. Most of the preserved muscles are, however, fragmentary. The extrinsic limb musculature was probably much more complex than is suggested in the reconstructions (Text-fig. 8). Each muscle mass may have been comprised of a number of discrete muscles. The frequency of preservation of such delicate structures is less surprising when it is considered that only one or two muscles were found in each specimen, that each specimen, if complete, has about 40 larger limbs, and that each limb should in life have had at least five associated extrinsic muscle masses.

Two extrinsic limb muscles are shown in YPM 28264 (Pl. 20, figs. 3, 4; Text-figs. 19, 20): a ventroposterior extrinsic limb muscle (*vpm*) extends from its endoskeletal bar (*b*) to the base of the fourth thoracic limb ( $T_4$ ), and a dorsoposterior extrinsic limb muscle (*dpm*) extends from its apodeme (*tpa*) anteriorly to the base of the eighth thoracic limb ( $T_8$ ). The dorsomedial extrinsic limb muscle (*dmm*) is shown for the eleventh thoracic limb ( $T_{11}$ ) in MCZ 7190/15 (Pl. 19, figs. 1, 3; Text-fig. 16). In this unusual view, the muscle extends from its apparent origin beneath the pleural furrow (*tpf*) ventrally into the coxa (*cx*) to the coxal proximal furrow (*cpf*) and perhaps ventrally past it. A ventroanterior extrinsic limb muscle (*vam*) extends between the first postfrontal bar ( $b_1$ ) and the base of the first postoral limb ( $G_1$ ) in YPM 28257 (Pl. 22, fig. 2; Text-fig. 26). Probable extrinsic limb muscles (*elm*) are shown in MCZ 7190/1 (Pl. 22, fig. 1; Text-fig. 25). They have, however, been displaced from their areas of origin.

The extrinsic muscles of the antennae, usually in a

fragmentary condition, have been identified in eight specimens: YPM 211, YPM 214, YPM 27802A, YPM 27813, YPM 28265, MCZ 7190/14B, MCZ 7190/15, MCZ 7190/26. The best example of these muscles as a group is the paired ventroposterior muscle (*vpm*) in MCZ 7190/14B (Pl. 20, figs. 1, 2; Text-fig. 18). Both muscles of the pair extend from their origins on the first post-frontal bar ( $b_1$ ) to the base of the respective antenna (*A*).

The intrinsic limb muscles appear as thin, relatively long strands of pyrite within the limbs. They have been identified simply by their forms and positions. As might be expected, the intrinsic limb muscles are fragmentary. When an apparent fossil muscle is observed in one limb, there is no assurance that it is complete. Further, the post-mortem deformation of limbs makes it practically impossible to determine the exact points of origin and insertion for a muscle even if it is complete.

Probable intrinsic muscles of the biramous limbs have been identified in 13 of the 68 intensively studied specimens. Usually, only one or two muscles in one or two out of nearly forty limbs were identified in a given specimen. A typical scrap of muscle is shown in MCZ 7190/22 (Pl. 22, fig. 3; Text-fig. 27), *ilm* on  $C_2$ ; notice also the folds in the  $C_1$  limb anterior to it).

Several muscles, however, have been repeatedly seen in the same anatomical position in different limbs of different specimens. Two have been identified often enough to be worthy of mention. The coxal enditic muscle (*cem*) has been identified in YPM 201, YPM 28259, MCZ 7190/1, MCZ 7190/22, MCZ 7190/25, and AMNH 839/14A. It is serially repeated in MCZ 7190/1 (Pl. 22, fig. 1; Text-fig. 25, *cem*). A muscle running between the distal part of the prefemur (*pf*) and the proximal part of the patella (*pl*) across the femur (*fe*) has been identified in YPM 220, YPM 28257, YPM 28264, and MCZ 7190/15. It is shown in YPM 28257 (Pl. 22, fig. 2; Text-fig. 26, *ilm* on  $C_3$ ).

Intrinsic muscles of the antennae (*A*) appear as multiple strands running along the length of the shaft, and have been identified in YPM 228, YPM 28265, MCZ 3638/3 and MCZ 7190/15. They are best shown in YPM 28265 (Pl. 23, fig. 4).

## Discussion

It is clear from this description that the various parts of the trilobite's exoskeleton were linked together by a complex musculature that included the basic muscles characteristically found in arthropods. Relationships among the muscles and skeleton (Text-figs. 8, 9) are such that the pull



of muscles must have been balanced by one or more antagonists other than the skeletomusculature itself. Based on modern arthropods, it is reasonable to postulate internal hydrostatic pressure and cuticular elasticity as antagonists. For instance, Hessler (1964) demonstrated from experiments on living animals that internal hydrostatic pressure was the principal antagonist in *Hutchinsoniella macracantha*, a cephalocarid crustacean with a skeletomusculature generally similar to that of the trilobite. The dorsal longitudinal muscles (*dlm*) connected more or less directly to the dorsal exoskeleton, should have acted to flex the body dorsally. The ventral longitudinal muscles (*vlm*), connected to the ventral exoskeleton by way of endoskeletal bars (*b*) and their connecting ligaments (*cl*) and by the horizontal muscles (*hom*), should have acted to flex the body ventrally. The longitudinal muscles were linked by dorsoventral muscles (*dva*, *dvp*, *dvv*) which, with the horizontal muscles (*hom*), were probably adjustors. The anteriorly and posteriorly descending dorsoventral muscles (*dva*, *dvp*) should have acted to pull exoskeletal segments together anteroposteriorly. In conjunction with the ventrally descending dorsoventral muscles (*dvv*), they should at the same time have acted to compress individual segments dorsoventrally. It is particularly necessary to hypothesize internal hydrostatic pressure as the antagonist for this muscular action so that segments could have maintained their dorsal telescoping. The lines of action of the extrinsic limb muscles are all directed inwardly with respect to the body cavity; and it is necessary to hypothesize rigidity of the cuticle surrounding the articulations of legs, if not internal hydrostatic pressure, as the antagonist for the action of these muscles.

An unusual feature from a functional standpoint is the gradual origination of the dorsal longitudinal muscle (*dlm*) along the sides of the glabella (Text-fig. 8). The mechanical consequences and the functional significance of such a configuration are unclear. Perhaps it relates to the support of the head during locomotion. Perhaps it also conferred an advantage in molting. It is well known that in the ecdysis of trilobites, and of *Triarthrus* in particular, that the head cuticle opened along sutures and that the animal removed itself from the remainder of the exuvium through the opening thus created (Harrington, 1959; Harrington and Leanza, 1957; Cisne, 1973b). The anterolateral extensions of the dorsal longitudinal muscles could have acted in flexing the soft integument epithelium underneath the cuticle in the initial stages of ecdysis.

It is also unusual that the lateral parts of the dorsal longitudinal muscle (*dlm*) should extend so far ventrally

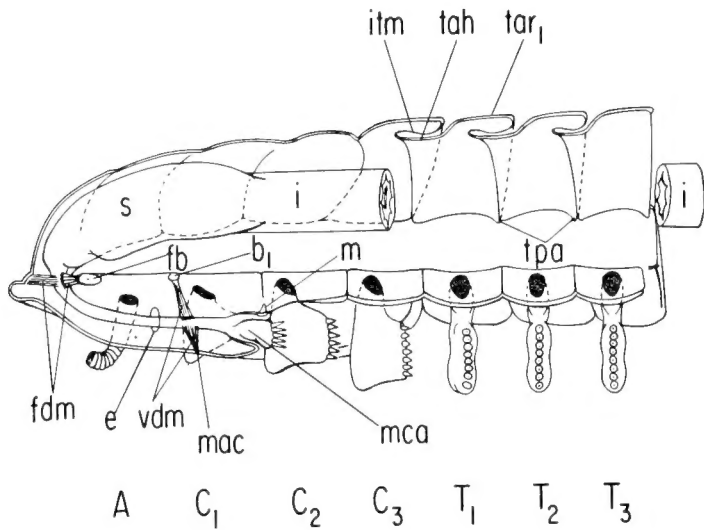
around the interior of the axial region and lie so close to the intertergal hinge at the dorsal axial furrow (*daf*) (Text-fig. 8). Only the more medial slips of the dorsal longitudinal muscle should have had a sufficiently long lever arm to exert much torque about the intertergal hinge. The lateral slips near the hinge may have acted in compressing and reinforcing this joint.

Based on Snodgrass' (1931, 1935) accounts of arthropod anatomy in relation to insect anatomy, Størmer (1939) suggested in his generalized reconstruction of trilobite anatomy that superficial dorsal and ventral muscles ran between successive thoracic exoskeletal segments outside the dorsal and ventral longitudinal muscles. There is no compelling reason to believe that superficial muscles were present. Elaborate development of superficial muscles is correlated with a high degree of flexibility across articulations; and development of two point hinges, as found in trilobites, is correlated with reduction of surficial muscles that otherwise make possible more varied excursions of movement, as Manton (1973a) has demonstrated for myriapods. Careful examination of the *Triarthrus* specimens revealed no traces of surficial muscles, which does not necessarily indicate they were absent.

Another unusual feature of the head musculature in *Triarthrus* is the apparent sets of dorsoventral muscles in the two posterior head segments ( $G_2$ ,  $G_3$ ). These muscles are known in the head from only two specimens (YPM 204 and YPM 28254). Like the sets of dorsoventral muscles in the thorax, these dorsoventral muscles probably served as adjustors. They may have acted in maintaining the relationship between the tergal and sternal sides of the cuticle and in maintaining the shape and flexure of sternal parts. But, unlike thoracic dorsoventral muscles, these muscles could not have regulated the telescoping of the dorsal parts of head segments, owing to the head tergum. Thus, the occurrence of sets of dorsoventral muscles in the posterior part of the head might suggest that the function of dorsoventral muscles all along the body was primarily to maintain the relationship between the sclerotized tergal cuticle and the more flexible sternal cuticle across each segment.

Hupé (1953) included muscles running dorsoventrally across the pleural region connecting the two sides of the exoskeleton in his reconstruction of a generalized trilobite. There is no compelling reason from the comparative anatomy of modern arthropods to postulate the existence of these muscles, and a careful examination of the *Triarthrus* specimens revealed no evidence of any.

Manton (1977, p. 360) objected to my reconstructions on grounds that *Triarthrus* should have stout muscles especially concerned with enrollment, muscles she implies



Text-figure 10.—Interior view of the right halves of the head and first three thoracic segments showing the digestive tract and related musculature. Only the coxae of postoral limbs are shown. See Appendix for explanations of abbreviations. From Cisne (1975).

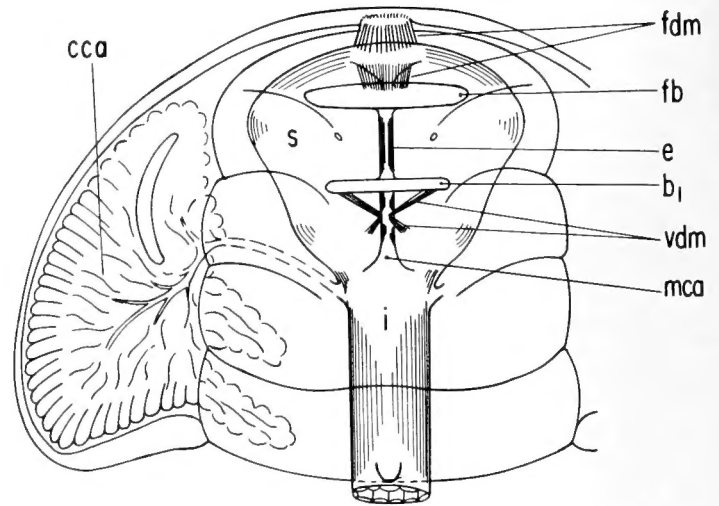
might be like those in tightly enrolling millipedes. *Triarthrus* does have stout muscles concerned with enrollment: the dorsal and ventral longitudinal muscles. There is no reason to believe that muscles developed in conjunction with tight ball-like or spiral enrollment should be present. As already explained (see "Tergites and Intertergal Articulation"), *Triarthrus* could not fully enroll as many other trilobites could.

#### DIGESTIVE SYSTEM

The three major parts of the gut — foregut (stomodaeum), midgut (mesenteron), and hindgut (proctodaeum) — could not be distinguished on the basis of cuticular lining. If the gut were less well preserved and did not mask the cuticular lining, it might have been possible to distinguish the presumably lined foregut from the presumably unlined midgut. However, the midgut has been recognized more frequently in specimens. Incomplete dilator muscles indicate the pharyngeal region, yet it has not been possible to distinguish the pharyngeal and esophageal portions of the tube connecting the mouth cavity and crop. The term "esophagus" is applied to the entire tube with the understanding that it applies to both esophagus and pharynx in the usual sense.

#### Description

The basic parts of the gut discernible in fossils are the



Text-figure 11.—Dorsal view of the head showing the digestive tract and its related musculature and caeca. See Appendix for explanations of abbreviations. From Cisne (1975).

mouth cavity (*mca*), esophagus (*e*), crop (*s*), intestine (*i*), and anus (*a*). These elements are shown in reconstruction in Text-figures 9-11. Caeca, probably digestive glands, are also preserved (Text-fig. 11).

The mouth cavity (*mca*) is posteriorly directed and opens between the hypostoma (*h*) and metastoma (*m*). More or less at its sides are the coxal endites (*cen*) of the first pair of biramous limbs (*C*<sub>1</sub>).

The esophagus (*e*), into which the mouth cavity tapers anteriorly, is a long narrow tube that extends far forward ventral to the first post-frontal and frontal endoskeletal bars (*b*<sub>1</sub>, *fb*) and then loops anteriorly around the frontal bar and tapers into the crop (*s*). It is likely that the entire esophagus was stomodaeal and had a cuticular lining.

The esophagus (*e*) was probably associated with a complex musculature, and at least the posterior portion adjacent to the mouth cavity appears to have been developed as a pharynx. Ventral dilator muscles (*vdm*) extend from origins on the distal parts of the first post-frontal bar (*b*<sub>1</sub>) to the extreme posterior portion of the esophagus, and it is likely that these muscles were opposed by other muscles taking origin on the hypostoma in the vicinity of the macula (*mac*). It is also likely that other dilator muscles including the frontal dilator muscles (*fdm*) (which are entirely hypothetical), extended in opposition between the frontal area anterior to the glabella and the esophagus, and between the anterior edge of the frontal bar (*fb*) and the esophagus. At least the pharyngeal portion of the esophagus was probably encircled by constrictor muscles.

The crop (*s*) is a relatively flat, oval body lying beneath the frontal glabellar lobe (*fgl*) and the first and second

lateral glabellar lobes ( $lg_1$ ,  $lg_2$ ). It is likely that the crop was stomodaeal and had a cuticular lining. Fossil structures suggestive of longitudinal folds in such a lining have been observed, but denticles have not been seen.

The crop appears to have had a complex of muscle fibers surrounding it, and may have been developed as a triturating organ. The paired depressions of the proximal ends of the first lateral glabellar furrows ( $lgf_1$ ), situated dorsal to the midsection of the crop, may have marked points of attachment for suspensor or dilator muscles of this organ.

The intestine ( $i$ ), into which the crop tapers posteriorly, is a long tube extending from the level of the third lateral glabellar lobe ( $lg_3$ ) to the anus ( $a$ ) at the posterior end of the body. It tapers only slightly posteriorly through the thorax, but then tapers markedly through the pygidial abdomen such that the tube, as it runs through the post-pygidial abdomen, is much smaller than it is in the thorax. It is not known what length of the posterior part of the intestine, if no more than a tiny lip in the telson ( $t$ ), corresponds to the cuticle-lined hindgut.

Highly ramified caeca ( $cca$ ) are present in the genal and lateral glabellar regions of the head (Text-fig. 11). Their connection, or connections, to the gut have not been observed. If indeed they represent digestive glands of the sort found in chelicerates and crustaceans, ducts for the glands should have joined the gut near the intersection of the crop ( $s$ ) and intestine ( $i$ ). The duct or ducts leading into the body or bodies of the glands most likely passed through the first postoral segment ( $C_1$ ) anteriorly around the dorsoventral muscles of more posterior head segments. The extent of the glands in the anterior portions of the genal region is not known. No indications of division of the caeca into discrete segmental masses have been found. Caeca have only been found in the head region.

#### Documentation

Specimens YPM 201 (Pl. 22, fig. 4; Text-fig. 28) and YPM 28259 (Pl. 19, fig. 4; Text-fig. 17) show the entire digestive tract: esophagus ( $e$ ), crop ( $s$ ), intestine ( $i$ ), and anus ( $a$ ). The continuation of the esophagus into the mouth cavity ( $mca$ ) posteriorly can be seen clearly in YPM 228 (Pl. 17; Pl. 21, fig. 3; Text-fig. 23), MCZ 7190/14B (Pl. 20, figs. 1, 2; Text-fig. 18) and MCZ 7190/18 (Pl. 18, fig. 3; Text-figs. 13, 14). The preserved structures have the same general form and arrangement of the gut as in merostomes and more primitive crustaceans, which have posteriorly directed mouth cavities that give the gut its J-shape. This similarity is in part the basis for the identifica-

tion of the preserved structures. Perhaps the best prima facie evidence that the contiguous structure interpreted as the gut is in fact the gut is provided by MCZ 7190/15. The cloud of finely particulate material behind this complete specimen (Pl. 19, fig. 1) appears to originate as a cone coming out of the anus (Pl. 19, fig. 2), which lies at the end of a section of preserved intestine that runs through the abdomen. The cloud of material evidently represents preserved gut contents squeezed out during post-mortem compression.

The esophagus ( $e$ ) has been identified in 30 of the 68 intensively studied specimens. Its remarkable length is well-illustrated in MCZ 7190/18 (Pl. 18, fig. 3; Text-figs. 13, 14), and its relationship to the first post-frontal and frontal bars ( $b_1$ ,  $fb$ ) is well shown in YPM 228 (Pl. 17; Pl. 21, fig. 3; Text-fig. 23), YPM 28259 (Pl. 19, fig. 4; Text-fig. 17) and MCZ 7190/14B (Pl. 20, figs. 1, 2; Text-fig. 18). In addition to specimens already mentioned, the esophagus is also evident in YPM 27813 (Pl. 18, fig. 4; Text-fig. 15) and YPM 28257 (Pl. 22, fig. 2; Text-fig. 26).

The ventral dilator muscles ( $vd_m$ ) of the pharyngeal part of the esophagus, and those muscles originating on the first post-frontal bar ( $b_1$ ), have been identified only in YPM 228 (Pl. 17; Pl. 21, fig. 3; Text-fig. 23) and YPM 28259 (Pl. 19, fig. 4; Text-fig. 17).

The crop ( $s$ ) has been identified in 20 of the 68 intensively studied specimens. It is best shown in YPM 201 (Pl. 22, fig. 4; Text-fig. 28), YPM 28222 (Pl. 21, fig. 2; Text-fig. 22), and YPM 28259 (Pl. 19, fig. 4; Text-fig. 17). Its frontal margin, which appears to have followed the axial furrow at the anterior edge of the glabella, has not been clearly seen. The abrupt change in thickness of the trilobite specimen in this region has made it very difficult to obtain a clear radiographic picture of structures.

Specimen YPM 28222 (Pl. 21, fig. 2; Text-fig. 22) illustrates the complex of probable muscle fibers that surrounds the crop ( $s$ ). Similar lineations in the same morphological position are seen in YPM 28257 (Pl. 22, fig. 2; Text-fig. 26) and MCZ 7190/14B (Pl. 20, figs. 1, 2; Text-fig. 18), but it is not clear whether they represent the same structure, folds in the lining of the crop, or perhaps simply a Bertillon pattern of terrace lines on the inner surface of the hypostoma. A Bertillon pattern has not been observed on the exposed exterior surfaces of the hypostoma in *Triarthrus* though it is a common feature in other trilobites (Harrington, 1959).

The intestine ( $i$ ) has been identified in 44 of the 68 intensively studied specimens. It is usually preserved over only a fraction of its total length. As mentioned earlier, the

intestine and the paired ventral longitudinal muscles have a grossly similar appearance in radiographs. The intestine is distinguished by its connection to the crop and (or) anus, by its lack of connection with the endoskeletal bars and smaller body and limb muscles, and by its heavier, non-fibrous texture. In addition to specimens already mentioned, the intestine is shown in YPM 28264 (Pl. 20, fig. 3; Text-fig. 19).

The caeca (*cca*) appear as masses of finely ramified pyrite filaments occupying the lateral pleural and lateral glabellar regions of the head. The structures bear a striking resemblance to the hepatic caecum in the horseshoe crab *Limulus polyphemus*. In this form the caecum is a large digestive gland occupying the lateral regions of its prosoma. The similarity in form and position is the basis for the identification of the caecum in the trilobite. However, no tubes connecting the caeca with the gut have been observed, though it is suggestive that the ramification of the caeca proceeds outward and away from the axial region.

Caeca (*cca*) have been identified in 11 of the 68 intensively studied specimens. They are illustrated in YPM 201 (Pl. 22, fig. 4; Text-fig. 28) and YPM 27802A (Pl. 21, fig. 1; Text-fig. 21) and, perhaps best, in MCZ 7190/22 (Pl. 22, fig. 3; Text-fig. 27). This last specimen shows an apparent diverticular vessel, on the right side of the head, that branches laterally away from the region occupied by the intestine.

#### REMARKS ON THE FEEDING MECHANISM

Though the functional morphology of the feeding mechanism remains to be explored at length, certain simple deductions concerning it are apparent from anatomy.

*Triarthrus* evidently collected and ingested finely particulate food material. Its mouth is small and posteriorly directed, as is characteristic of trunk-limb feeding crustaceans. Its esophagus is very narrow, less than a fraction of a millimeter in diameter in the largest specimens. Its anus is of comparable diameter. It is clear from the structure and extrinsic musculature of the head limbs that they were not developed as powerful masticatory organs for comminuting whatever food might have been collected. Hence the anatomical evidence suggests that the trilobite fed on fine particulate material, likely deposited detritus, as earlier suggested (Cisne, 1973a, 1973b). The only direct fossil evidence of the food are clouds of finely particulate, pyritic material emanating from the gut, probably gut contents squeezed from the body by post-mortem compression, in YPM 207 (Pl. 23, fig. 3) and MCZ 7190/15 (Pl. 19, figs.

1, 2). This is consistent with the deduction from anatomy. Individual particles in the clouds are very small, irregular, and otherwise not readily identifiable. Such material is commonly seen in the body cavities of specimens, though its origin is not so clear as in the cases mentioned above.

Several lines of anatomical evidence indicate that *Triarthrus* had a trunk-limb feeding mechanism such as found in cephalocarid, branchiopod, and phyllocarid crustaceans. This mechanism involves collection of material from suspension in the current generated by those limbs (see Marshall and Orr, 1960, for review). General similarities between the limbs of trilobites and crustaceans having trunk-limb feeding mechanisms have long been noted, and have long been taken to indicate that trilobites had a similar feeding mechanism (e.g., Störch, 1925; Cannon and Manton, 1927; Eriksson, 1935; Bergström, 1969). Most foresightfully, Burmeister (1846) adduced the feeding mechanism of branchiopods to trilobites even though trilobite appendages were not then known. Bergström (1969) suggested that metachronal variation in the spaces between successive exites was the primary method of current production in trilobites like *Triarthrus*. This, however, is a mechanism unlike that in modern crustaceans in that the planar exites are arrayed horizontally, not dorsoventrally as are the parts of limbs involved in current production in crustaceans. A crucial point on the anatomy of *Triarthrus* is that the trunk coxa is large and blade-like, and that the plane of the coxa is transverse to the body. It has much the same shape and orientation as the protopod in the cephalocarid *Hutchinsoniella*. In this crustacean, metachronal limb movement results in rhythmic variation in the space between successive limbs (primarily the space between successive protopods), which in turn produces a pumping action in the manner of a peristaltic paddle pump (Sanders, 1963). The implication is that the coxae in *Triarthrus* may have been similarly involved in the creation of the feeding current.

*Triarthrus* has anatomical features analogous to those used in food transport mechanisms in cephalocarids, branchiopods, and phyllocarids. With the exception of notostracan branchiopods, these crustaceans have a food groove along the trunk and the posterior part of the head between transversely paired endites. Collected food material is carried forward along the food groove, being passed mechanically from limb to limb while caught on enditic setae in cephalocarids (Sanders, 1963) and phyllocarids (Cannon, 1927), but being carried in suspension in a current flowing anteriorly along the food groove in branchiopods (Cannon, 1928; 1933). In notostracans, material is likewise carried

forward in suspension in the midventral space, though not in a food groove (Cannon, 1933). *Triarthrus* has a food groove (*vt*, Text-fig. 8) extending along the trunk toward the mouth, and like the food groove in cephalocarid crustaceans it is walled by large, blade-like coxae with large, setiferous endites and has the ventral integument along its dorsal margins uninvginated. A food transport chamber as depicted by Bergström (1969), one of a pair of channels, thought to extend above the limbs just lateral to their articulations to the body, is not developed in *Triarthrus*. The exitic filaments project out and away from this region, not into it. In all probability, they could have played no role in mechanical transport of food material anteriorly through this region.

Though the occurrence of a food groove in the trilobite would seem to leave little doubt as to how food material was transported to the mouth once collected in the midventral space, it does not tell us how, in detail, the distal parts of the limb, the exite in particular, might have been involved in the generation of a feeding current. Differences in the structure and arrangement of exites between the trilobite and crustaceans suggest that the process may have been different in detail. The problem could only be solved using working models of the trilobite's feeding mechanism. However, it is possible the food material was collected directly in the food groove, that the trilobite simply scooped up deposited detritus using the trunk limbs and then passed it forward along the food groove.

As compared with the trunk limbs, the three pairs of postoral head limbs ( $C_1$ - $C_3$ ) appear to be modified gradationally as mouth parts. The reduction in the dorsoventral depth of the endite of the first pair ( $C_1$ ), in particular, is evidently correlated with its proximity to the mouth cavity. Near the extreme anterior position in the movement of the limb, these endites probably moved into the lateral edges of the mouth cavity. As noted earlier, a mechanical consequence of the oblique orientation of the axis of swing of the head coxae ( $C_1$ - $C_3$ ) is that their transversely paired endites should move together on the forestroke. The functional significance of this action is that these endites were involved in comminution of collected food material. The space between the first pair of endites, for example, should have opened on the backstroke phase to receive material pushed forward by the second endite pair, and should have closed on the forestroke phase, the endites pushing food material between them together and forward to the mouth cavity. No strongly developed spines or molar areas have been detected on the head endites. The trilobite's masticatory mechanism would not seem to be powerfully developed

and probably would not have been effective on large, tough food items. It is possible that the first pair of endites acted against the metastoma in mastication much as crustacean mandibles act against paragnaths.

The manner of development of the postoral limbs is consistent with development of a muscular foregut for suctional ingestion of food. It is likely that the crop was developed as a triturating organ, but, as pointed out, no internal denticles have been detected.

#### OTHER ORGAN SYSTEMS

Organ systems other than the exoskeletal, muscular, and digestive systems are known only from limited, fragmentary fossil evidence. But that evidence, combined with additional circumstantial evidence, elucidates several important points on the anatomy of the trilobite's nervous, circulatory, and reproductive systems.

#### Nervous System

As is characteristic of arthropods generally, the nervous system of *Triarthrus* was probably comprised of paired ventral nerve cords running the length of the body between the ventral longitudinal muscles and ventral cuticle and connected intrasegmentally in ladder-like fashion by commissures originating from paired segmental ganglia. The nerve cords themselves have not been recognized as fossils. The only (and very questionable) fossil evidence of the nervous system is a possible circum-esophageal commissure (*ecm?*) and associated possible paired ganglia (*gan?*) in MCZ 7190/18 (Pl. 18, fig. 3; Text-fig. 14).

Owing to constraints placed on their spacing by the connecting ligaments (*cl*) between the endoskeletal bars (*b*) and the ventral cuticle, two possibilities can be singled out for the arrangement of the ventral nerve cords in the trunk and posterior part of the head. Either the cords were very closely spaced medial to the connecting ligaments, or they were comparatively widely spaced lateral to the connecting ligaments. (see Text-fig. 8).

#### Circulatory System

As in other small, primitive arthropods, the principal organ of the trilobite's circulatory system was probably a small dorsal vessel running along the axis of the body just beneath the dorsal exoskeleton from the middle part of the head posteriorly along the trunk. Complexity of circulatory systems, such as that of *Limulus*, seem to be a function of

body size. As reconstructed in Text-figure 8, the dorsal vessel (*dv*) is a small tube between the paired sheets formed by the dorsal longitudinal muscles (*dlm*).

Possible parts of the dorsal vessel — straight, thin filaments of pyrite running parallel to the midline just ventral to the dorsal exoskeleton — have been identified in nine of the 68 intensively studied specimens: YPM 202, YPM 213, YPM 219, YPM 227, YPM 27802A, YPM 28260, YPM 28264, YPM 28270J, and MCZ 3638/4. The fossil evidence is fragmentary. All that are seen in radiographs are suggestions of a narrow tube running across a few segments. The simple morphology of the fossil structure, and indeed of a dorsal vessel itself, offers little in the way of diagnostic features. Ostia, the single most characteristic features, have not been recognized in fossils. Fossil dorsal vessels have been tentatively identified by their gross form and position with respect to the dorsal cuticle. Possible parts of the dorsal vessel (*dv*?) are indicated in YPM 27802A (Pl. 21, fig. 1; Text-fig. 21) and YPM 28264 (Pl. 20, figs. 3, 4; Text-fig. 20).

### Reproductive System

No clear evidence of the reproductive system has been found among the 68 intensively studied specimens. However, a small amount of circumstantial evidence on its anatomy comes through consideration of the trilobite's life history and demography. Females (or hermaphrodites) produced a large number of eggs, on the order of hundreds to thousands, in a relatively short, probably annual, breeding season (Cisne, 1973a). The production, if not the storage, of such a volume of eggs would seem to have required a relatively large ovary. If eggs were stored up for release at one or a few times, ample space for the ripe ovary would seem to have been available in the extensive interstitial spaces of the body cavity. An analogy might be drawn with the female *Limulus*, in which the ripe ovary may extend all through the prosoma.

### DEVELOPMENT

From the protaspis larva to the adult holaspis, the development of *Triarthrus* was very gradual (Walcott, 1879; Beecher, 1895c; Whittington, 1957a, 1957b; Cisne, 1973a). The body form changed gradually as segments were added at probably no more than one per molt during pre-adult development.

New teloblastic segments were probably added just in front of the telson. It was unexpected that the telson is so small and that it is separate from the pygidial region. Un-

Table 1. — Least-squares curve equations for data reported in Text-figure 12. (Equations apply only to the holaspis interval [ $8.0 \text{ mm} < L_o < 40.0 \text{ mm}$ ])

$$L_c = 0.424 L_o^{0.876} \quad (N = 49; r = 0.995; p < 0.001) \quad [\text{Equation 1}]$$

$$L_h = 0.208 L_o^{0.933} \quad (N = 33; r = 0.982; p < 0.001) \quad [\text{Equation 2}]$$

$$L_m = 0.078 L_o^{0.452} \quad (N = 14; r = 0.589; p < 0.05) \quad [\text{Equation 3}]$$

$$L_p = 0.069 L_o^{1.13} \quad (N = 37; r = 0.980; p < 0.001) \quad [\text{Equation 4}]$$

$$L_{pp} = 0.031 L_o^{1.12} \quad (N = 25; r = 0.829; p < 0.001) \quad [\text{Equation 5}]$$

$L_o$  = distance between the anterior margin of the head tergum and the posterior margin of the pygidium, excluding the post-pygidial abdomen

$L_c$  = length of the head tergum

$L_h$  = length of the hypostoma (for practical reasons, the distance between the anterior margin of the head tergum and the posterior margin of the hypostoma; the narrow cephalic border is thus included)

$L_m$  = length of the metastoma

$L_p$  = length of the pygidium (distance between the exposed anterior edge of the most anterior axial ring and the posterior margin of the pygidium)

$L_{pp}$  = distance between the ventral intersegmental furrow at the anterior boundary (as best it could be recognized) and the posterior margin of the telson.

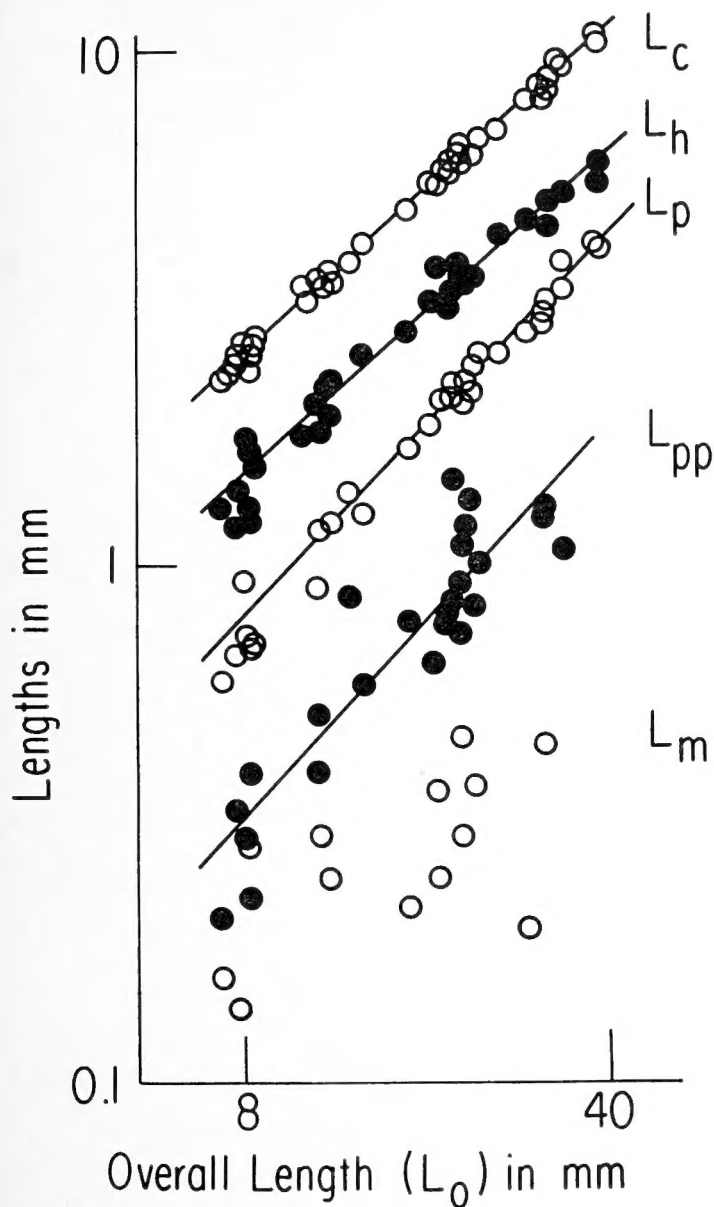
$N$  = number of measurements

$r$  = product-moment correlation coefficient

$p$  = significance probability

fortunately, nothing is known of its development prior to the degree 13 meraspis. It is significant that the structure is present in this last juvenile stage. It was probably present in earlier developmental stages as well.

The first protaspis (Cisne, 1973a, fig. 3A) has a discoidal body about 0.60 mm long. Its head has the same gross form and evidently the same segmental composition as the adult head. Its protopygidial region includes at least two segments, these marked by a single axial ring and the terminal axial segment in the protopygidium. One segment was added to the protopygidium at each molt in progression to the second and third protaspids (Cisne, 1973a, figs. 3B, 3C). In going from the third protaspis to the degree 0 meraspis, an articulation appeared at the posterior margin of the head, and a fifth segment was evidently added to what then was the meraspid transitory pygidium. Starting with the degree 0 meraspis, which has no free thoracic segments, segments were added to the thorax at no more than one per molt. Finally, between the degree 13 meraspis and the first holaspis, the fourteenth thoracic segment was



Text-figure 12.—Graph showing relative growth of various body elements of *Triarthrus eatoni* (Hall) during ontogeny. See Table 1 for equations and explanations of abbreviations.

added. No further segments were added to the thoracic or pygidial regions past this point.

The abdomen in the adult *Triarthrus* can be viewed as an ontogenetic relict of the meraspid period. Through the course of meraspid and holaspid development, the pygidial region maintained its integrity as a tagma of five segments, these expressed as four axial rings and the terminal axial segment on the pygidium. As has been pointed out (*e.g.*, Whittington, 1957a, 1959), the meraspid transitory pygidi-

um does not appear to be segmentally homologous among different meraspid stages. During the juvenile period, segments passed through the pygidial region. At each molt, the most anterior pygidial segment passed into the thoracic region with development of an articulation at its posterior end, while, at the same time, the most anterior post-pygidial segment was incorporated in the pygidial region with development of a tergal portion that fused with those of other segments to form the new pygidium. Presumably, a new segment was added to the post-pygidial region at the same time. The pygidial region thus represents a zone of transition in the development of the tergal cuticle, a zone of gradation between weakly sclerotized cuticular segments in the post-pygidial region and sclerotized, fully articulated tergites in the thoracic region. With cessation of segmental addition to the thoracic and pygidial regions, this gradient in development of segments was frozen in the holaspis.

The concept of the pygidial region as a zone of gradation in the ontogenetic development of segments goes far in explaining three riddles of trilobite anatomy and development. First, it explains why holaspids of the same or closely related species should have similar pygidia even though they differ in number and anatomical development of thoracic segments. The process of segmental addition was arrested at different stages, leaving much the same gradient at the posterior end. Adults of *Triarthrus eatoni* have 14 to 16 thoracic segments as the dominant holaspid number, varying from population to population (see Walcott, 1879; Beecher, 1894a; Whittington, 1957b; Cisne, 1973a). Second, it explains why the transitory pygidium should remain so stable in segmental composition during ontogenetic development—a pattern without parallel among other arthropods that could otherwise be taken to suggest a highly unusual mode of segmental growth (see Tiegs and Manton, 1958). The same gradient is manifested at different stages. And third, it helps explain the occurrence of the post-pygidial abdomen in *Triarthrus*. The post-pygidial region represents the extreme of the ontogenetic gradient. In holaspids, the post-pygidial abdomen may represent simply the “left-overs” from the process of segment addition.

The head tergum, hypostoma, pygidium and post-pygidial abdomen maintained nearly constant proportions to the overall length of the body during the holaspid period and the latter part of the meraspid period during a five-fold increase in body length (see Table 1, Text-fig. 12).

The exponents in Table 1, Equations 1, 2, 4, 5 indicate that the respective structures grew in length in very nearly direct proportion to the overall length of the body. The small deviations from perfect similar growth (exponent = 1)

indicate that the head became relatively smaller and the abdomen relatively larger by small amounts as overall size increased.

It is important to note that the post-pygidial abdomen grew with the length of the body, that it was present even in small stages, and that it varied in size. The variability in size is related both to preservational bias and to variability in number of constituent segments, which does not itself seem to be directly related to the overall size of the animal. Variability in number of segments seems simply an expression of indeterminate growth. Unfortunately, the post-pygidial abdomen was never found in measurable condition in the largest specimens.

The metastoma is variable in size and proportions with respect to the entire body. The relationship between its length ( $L_m$ ) and overall body length ( $L_o$ ) (Table 1, Equation 3) is markedly allometric but not so well-defined as other relationships. It is apparent from examination of specimens that the metastoma itself is variably developed, though the high degree of variability manifest in the scatter of points in Text-figure 12 may in part be due to unavoidable errors in measuring a very small structure. The metastoma in YPM 205, which was used by Raymond (1920; see pp. 155-156, pl. 2, fig. 4) as a prime basis for reconstruction of this sternite, is disproportionately large and peculiarly developed.

## SEGMENTAL CONSTRUCTION OF THE BODY

### TAGMATIZATION

The body of *Triarthrus* is comprised of four tagmata: head, thorax, pygidial abdomen, and post-pygidial abdomen. As revealed by high degrees of serial homology among postoral limbs and segmental elements of the skeletomusculature, these groups of segments are distinguished primarily by manner of development of the tergal cuticle. The head and pygidial abdomen are distinctive in their terga, the thorax in its tergites and their articulations, and the post-pygidial abdomen in the weak sclerotization of the cuticle.

### SERIAL HOMOLOGY

#### Limbs

The one case of strong structural differentiation within the entire set of limbs is that between the uniramous antenna and the biramous limbs of the head and trunk. The antennal shaft strongly resembles an exite shaft in form and

annulation, suggesting that the two structures may be homologous.

The biramous limbs show a high degree of serial homology. All apparently share the same podomeric construction and differ in graded fashion to no great extent in the relative proportions of their constituent parts (Text-figs. 2, 5). As a matter of degree, the head limbs are differentiated from trunk limbs by the relatively smaller size and more ventrally directed orientation of the telopod and exite with respect to the coxa and by the reduced dorsoventral depth of the coxal endite (Text-fig. 5). But there is no truly abrupt transition in the development of limbs between head and trunk. Gradation in the development of the coxa among head limbs (Text-fig. 5) makes the transition between head and trunk limbs to a large extent gradational. A morphologically minor but functionally very important difference between the head and trunk limbs is the graded change in the orientation of the coxa-body joint line, from transverse to oblique, from the thorax toward the mouth (Text-fig. 2). Trunk limbs themselves, ranging over more than an order of magnitude in relative size, are graded primarily by size and secondarily in relative proportions of parts.

#### Musculature

Many segmentally repeated elements of the musculature show a high degree of serial homology among all limb-bearing segments of the head and thorax, and certainly among all postoral segments. From the fossil evidence itself, not from the reconstructions, these serial homologies are best documented for the endoskeletal bars (*fb*, *b*), which bore the insertions of the ventral longitudinal muscle (*vlm*), among others, for the dorsoventral muscles (*dva*, *dvp*, *dvv*), which indicate the areas of insertion of the dorsal longitudinal muscle (*dln*), and for the horizontal muscles (*hom*).

Though the segmental pattern is modified by the muscle's gradual origination in the head, all segments from the antennary (*A*) to the most posterior thoracic (*T<sub>14</sub>*) bear sections of the dorsal longitudinal muscle (*dln*). Segmental sections are very similar in shape from the most posterior head segment (*G<sub>3</sub>*) to the most posterior thoracic segment (Text-fig. 8). This remarkably high degree of serial similarity in the development of the body musculature also holds for the ventral longitudinal muscle (*vlm*). Segmental sections of this muscle show an even higher degree of mutual similarity between the antennary (*A*) and last thoracic (*T<sub>14</sub>*) segments. All post-frontal bars (*b*) of the



head and thorax show a high degree of serial homology that is expressed in their size, shape and relationships to the rest of the musculature, though it is likely that the first bar ( $b_1$ ) is somewhat differently related to the exoskeleton (Text-figs. 8, 9). The frontal bar ( $fb$ ) appears to be serially homologous with other bars in the series; all bear insertions of the ventral longitudinal muscle ( $vlm$ ) and the origins of the horizontal muscles ( $hom$ ) and ventral extrinsic limb muscles ( $vam$ ,  $vpm$  for all post-frontal bars) (Text-fig. 8). All thoracic segments bear serially homologous sets of dorsoventral muscles ( $dva$ ,  $dvp$ ,  $dvv$ ; Text-figs. 8, 9), and this same set of dorsoventral muscles appears to be repeated in two posterior head segments ( $C_2$ - $C_2$ ; Text-fig. 8). All horizontal muscles ( $hom$ ) likewise appear to be serially homologous (Text-fig. 8).

Because the extrinsic limb muscles are not well known from fossils, and because the serial homology principle has been heavily applied in their reconstruction, little can be said concerning the details of their serial homologies. It is, however, likely that, as a set, dorsoanterior ( $dam$ ), dorso-posterior ( $dpm$ ), ventroanterior ( $vam$ ), and ventroposterior ( $vpm$ ) extrinsic limb muscles were repeated in all limb-bearing segments. The dorsomedial extrinsic limb muscle ( $dmm$ ) is probably present, at least as a spatially separate muscle mass, only in the trunk segments. Being situated along a line directed dorsoventrally upward from the coxa-body foramen, it was likely not involved in promotion or remotion of the limb to so great an extent as more anterior and posterior muscles. It was more probably an adjustor muscle that acted in opposition to the ventral extrinsic limb muscles ( $vam$ ,  $vpm$ ). If developed at all in the head segments in the same relation it bears to the coxa in thoracic segments, its origin should be near the distal end of the head furrows ( $ocf$ ,  $lgf_1$ ,  $lgf_2$ ) owing to the rotated orientation of the head limbs. If that is so, the dorsomedial extrinsic limb muscle ( $dmm$ ) should not be clearly distinguishable from the dorsoanterior extrinsic limb muscle ( $dam$ ) in its area of origin. To judge from the direction of the thoracic pleural furrow ( $tpf$ ) beneath which the muscle ( $dmm$ ) takes origin, it is likely that the dorsomedial extrinsic limb muscle is more closely related to the dorsoanterior extrinsic limb muscle than to the dorso-posterior extrinsic limb muscle. It is possible that the dorsomedial muscle ( $dmm$ ) actually represents a slip of the dorsoanterior muscle ( $dam$ ) that has migrated posterolaterally to serve an adjustor function. Though the high degree of serial homology expressed in the external anatomy of the biramous limbs would suggest that they all had a basically similar intrinsic musculature, not enough is known of the intrinsic muscles themselves that their serial homologies can be meaningfully considered.

## SEGMENTATION

### Trunk Segmentation

The trunk is evidently comprised of homonomous segments, each bearing a pair of limbs. During larval and juvenile development, each segment in the holaspide thoracic and pygidial regions behaved as a developmental unit (see "Development"). Despite the lack of definitive evidence on the development of segmental mesoderm, it can be inferred from the development of external anatomy that each limb-bearing segment represents a true metameric segment. By implication, limb-bearing post-pygidial segments represent true segments. However, the possibility that post-pygidial segments, like posterior abdominal segments in the notostracan *Triops*, bear multiple limbs, cannot be rigorously eliminated.

Størmer (1942, 1944, 1951; see also Hessler, 1962) described secondary segmentation of the tergal exoskeleton with respect to the primary segmentation of the trunk in trilobites. Such secondary segmentation, a general feature among arthropods, is now understood to represent an accommodation between sclerites and the attachments of muscles that pull on them (see Hessler, 1962; Manton, 1969b). Muscle attachments do not rigidly follow primary segmental boundaries, though the attachments of major muscle masses may indicate them approximately. The skeletomusculature of *Triarthrus* fails to give unequivocal evidence for Størmer's suggestion that pleural furrows mark primary segmental boundaries, though the origin of the dorsomedial extrinsic limb muscle ( $dmm$ ) falls along this furrow on thoracic segments.

### Head Segmentation

The head includes four segments: three postoral segments that are constructed on very much the same pattern as thoracic segments, and one preoral antennal segment that is somewhat modified over this pattern. The skeletomusculature gives no indications whatever of a reduced segment within this series such as the ventral cephalic tendon in *Triops* gives for the much reduced second maxillary segment (see Hessler, 1964). The anatomy of the adult provides no hard evidence for the existence of a possible pre-antennal segment (see Anderson, 1973, on the question of embryonic pre-antennal and precheliceral segments).

Størmer (1942) interpreted a faint groove across the frontal glabellar lobe in protaspids of several species as marking off a pre-antennal segment. Whittington (1957a) strongly criticized this interpretation on the basis of careful re-examination of the evidence with Størmer. As noted by

Beecher (1893a, 1895c), such a groove is present in some protaspid specimens of *Triarthrus*. From my own observation of these specimens, protaspids in the same growth stage may have a furrow-like groove across the frontal glabellar lobe and may even have faint paired indentations along it, or they may have no trace whatever of the furrow (Cisne, 1973a, figs. 3A-3C). It is not clear whether this structure marks areas of muscle attachment, whether it is a flexure somehow imposed on the glabella by the eye ridge, with which the groove is confluent, or whether it might possibly be a manifestation of a swelling pre-antennal mesoderm band.

In view of the many problems of head segmentation, the segmental relations of the hypostoma are unclear. It may represent more than an entirely acronal labrum. Its anterior portion may represent a sternite of the antennal segment. If so, it might be a structure like the clypeo-labrum in uniramians. One interesting possibility for this configuration (suggested by Hessler, pers. comm.) is that only the part of the hypostoma posterior to the macula represents the acron. Perhaps the posterior part of the hypostoma housed a labral gland, as Cannon and Manton (1927) suggested from the widespread occurrence of a labral gland among crustaceans having a trunk-limb feeding mechanism.

The anatomical relationship between the gut and ventral endoskeleton poses an interesting problem for the topological division between preoral and postoral segments. If the frontal endoskeletal bar marks a segmental boundary as post-frontal bars do, the looping of the gut anteriorly around the frontal bar would appear to indicate that the antennal segment was topologically preoral — an incredibly primitive condition that is suggested in embryonic development (see Manton, 1969a) but otherwise unknown in any adult arthropod. However, it is likely that the observed relationship represents a secondarily developed accommodation between the gut and endoskeleton that does not reflect the primary segmentation of the body.

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## PLATES

Stereoscopic pairs on the following plates can only give the viewer some idea of the trilobite's anatomy as studied from high contrast prints. Because x-ray negatives are of very low contrast, they have been printed on very high contrast paper to bring out the maximum information within a certain relatively narrow range in gray-level. Each exposure is a faithful reproduction of the original negative. No photographic artifice (e.g., retouching, dodging, burning in) was employed in making them. Because different parts of a specimen are ordinarily exposed differently in a single negative, owing largely to variation in rock thickness, any one good print is well-exposed for some parts and underexposed or overexposed for others. A whole series of prints at different exposures was necessary for thorough study of

a single specimen at a given magnification; for especially well-preserved specimens, several series at different magnifications were necessary. It is practical to publish no more than a few illustrative samples of the prints actually studied. Each print reproduced here generally was chosen to illustrate one or a few especially interesting features, not the entire specimen in all its detail. Tracings from enlargements made on medium-contrast film (Text-figs. 13-28) illustrate the features of special interest in selected stereoscopic pairs in the manner of a camera lucida drawing. Made independently of the two exposures finally chosen for the plate, the tracings sometimes point out structures other than those the pair is especially meant to illustrate. The margins of the tracings and the pairs do not always coincide exactly.

## EXPLANATION OF PLATE 17

X-radiograph of *Triarthrus eatoni* (Hall)

	Pages
Dorsoventral view of YPM 228, a large (40 mm body length) specimen, perhaps the most beautiful of those prepared by C. E. Beecher .....	105, 109, 110, 119, 120, 125





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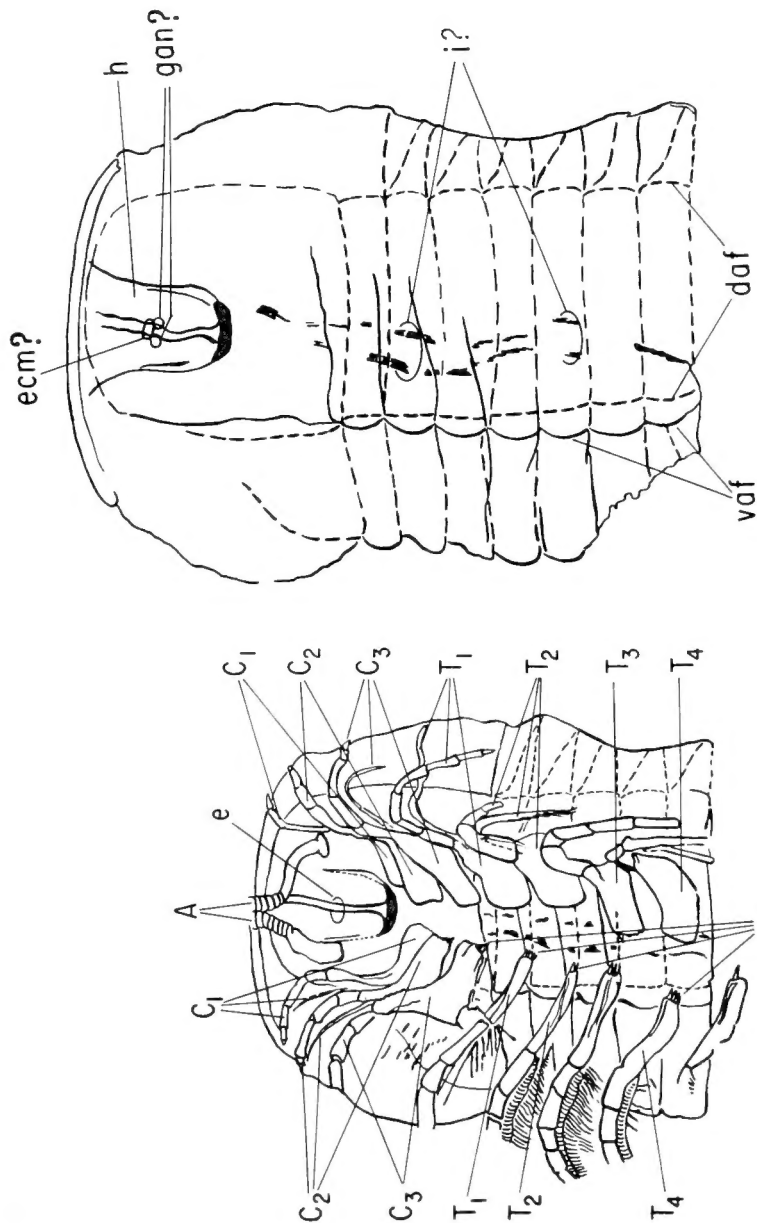
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EXPLANATION OF PLATE 18

X-radiographic stereopairs of *Triarthrus eatoni* (Hall)

Figure	Pages
1. Dorsal view of YPM 28206 (larger specimen) and ventral view of YPM 28250 (smaller specimen) (× 2.87)	101, 104
2. Anterior view of two slices through the mid-thoracic regions of the two specimens shown in fig. 1 (× 2.93)	101, 104
3. Ventral view of MCZ 7190/18 (× 3.30) See Text-figures 13 and 14	108-110, 113, 115, 125, 127
4. Ventral view of YPM 27813 (× 8.45) See Text-figure 15	109, 115, 119, 125



Text-figure 13 — Ventral view of MCZ 7190/18 (Pl. 18, fig. 3) showing in particular the three pairs of postoral head limbs (*C*<sub>1</sub>-*C*<sub>3</sub>), coxal enditic setae (*ces*) on the head and trunk limbs, and the esophagus (*e*). From Cisne (1975).

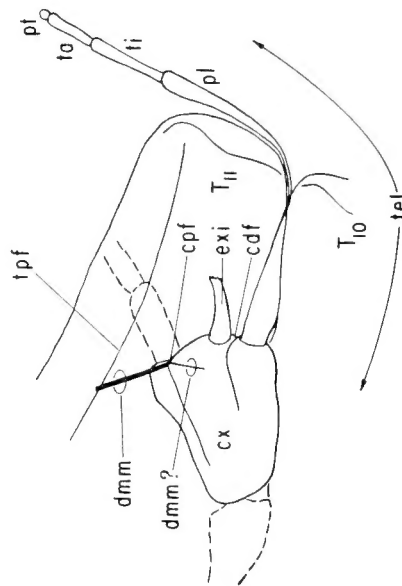
Text-figure 14. — Ventral view of MCZ 7190/18 (Pl. 18, fig. 3) showing displacement of furrows in sternal cuticle (solid lines) with respect to furrows in tergite cuticle (dashed lines). Also shown are the possible circum-esophageal commissure (*ecm?*), possible paired ganglia (*gan?*), and the intestine (*i*).

Text-figure 15. — Ventral view of YPM 27813 (Pl. 18, fig. 4) showing the three pairs of postoral head limbs (*C*<sub>1</sub>-*C*<sub>3</sub>) more or less in their natural upright positions and showing parts of the esophagus (*e*) and dorsal longitudinal muscle (*dlm*).

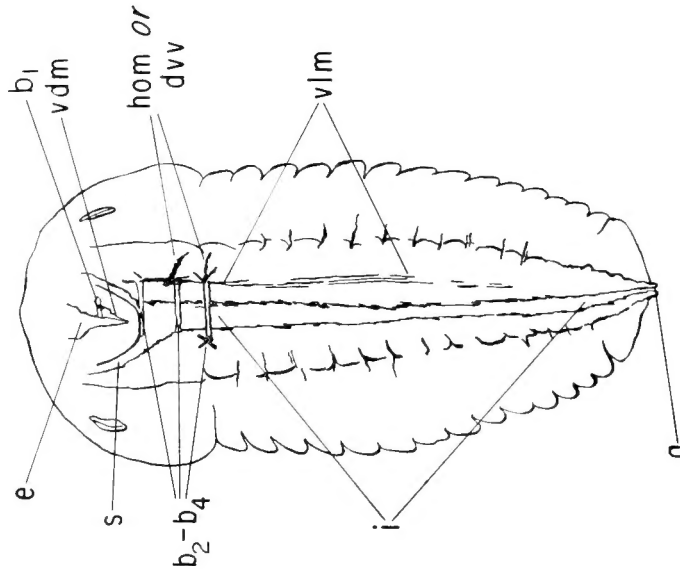
EXPLANATION OF PLATE 19

X-radiographic stereopairs of *Triarthrus catoni* (Hall)

Figure	Pages
1. Ventral view of MCZ 7190/15 showing "cloud" of material emanating from anus ( $\times 3.28$ )	109-111, 122, 125, 126
2. Ventral view of posterior part of abdomen in MCZ 7190/15 ( $\times 13.8$ )	109, 111, 125, 126
3. Ventral view of MCZ 7190/15 showing eleventh thoracic limb, among others ( $\times 17.5$ ). See Text-figure 16	109, 122
4. Ventral view of YPM 28259 ( $\times 6.30$ ). See Text-figure 17	110, 119-121, 125



Text-figure 16.—Ventral view of part of MCZ 7190/15 (Pl. 19, figs. 1-3) showing the eleventh thoracic limb in posterior view. Parts shown include the coxa (*cx*), the dorsomedial extrinsic limb muscle (*dm*), the telopod (*tel*), which projects through the opening between the tenth and eleventh thoracic pleurae (*T<sub>10</sub>*, *T<sub>11</sub>*), and part of the exite (*exi*). Note that structures are rotated about 130° clockwise relative to their position in Plate 19, figure 3.



Text-figure 17.—Ventral view of YPM 28259 (Pl. 19, fig. 4) showing the digestive tract (*e*, *s*, *i*, *a*), the ventral longitudinal muscle (*vlm*) and their relationship to endoskeletal bars (*b*), and the ventral dilator muscle (*vdm*) and its relationship to the esophagus (*e*).





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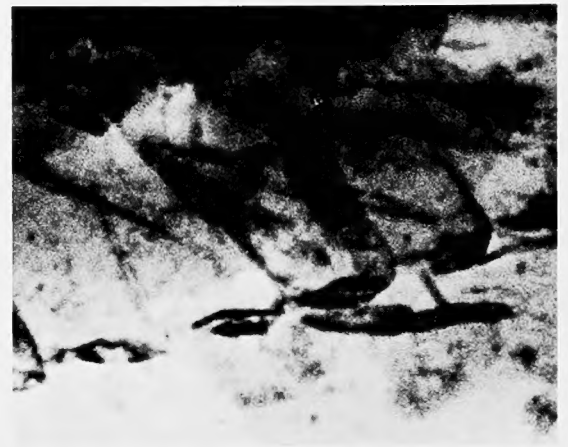
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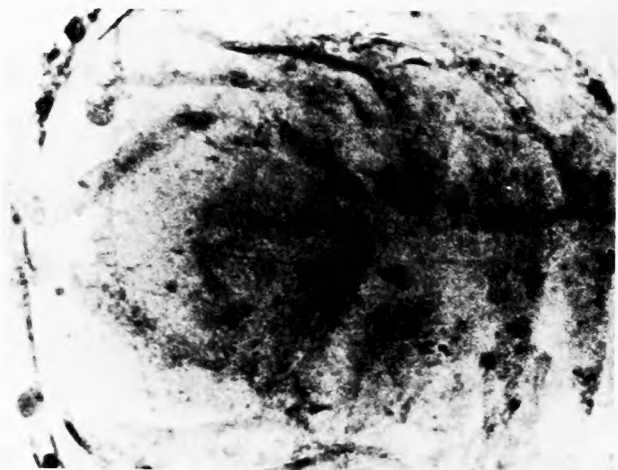


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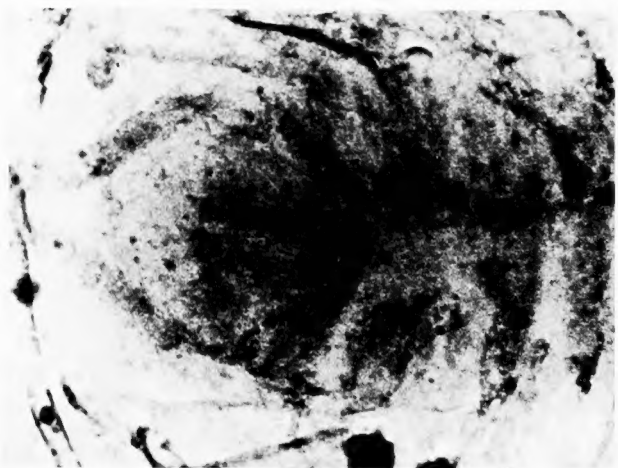


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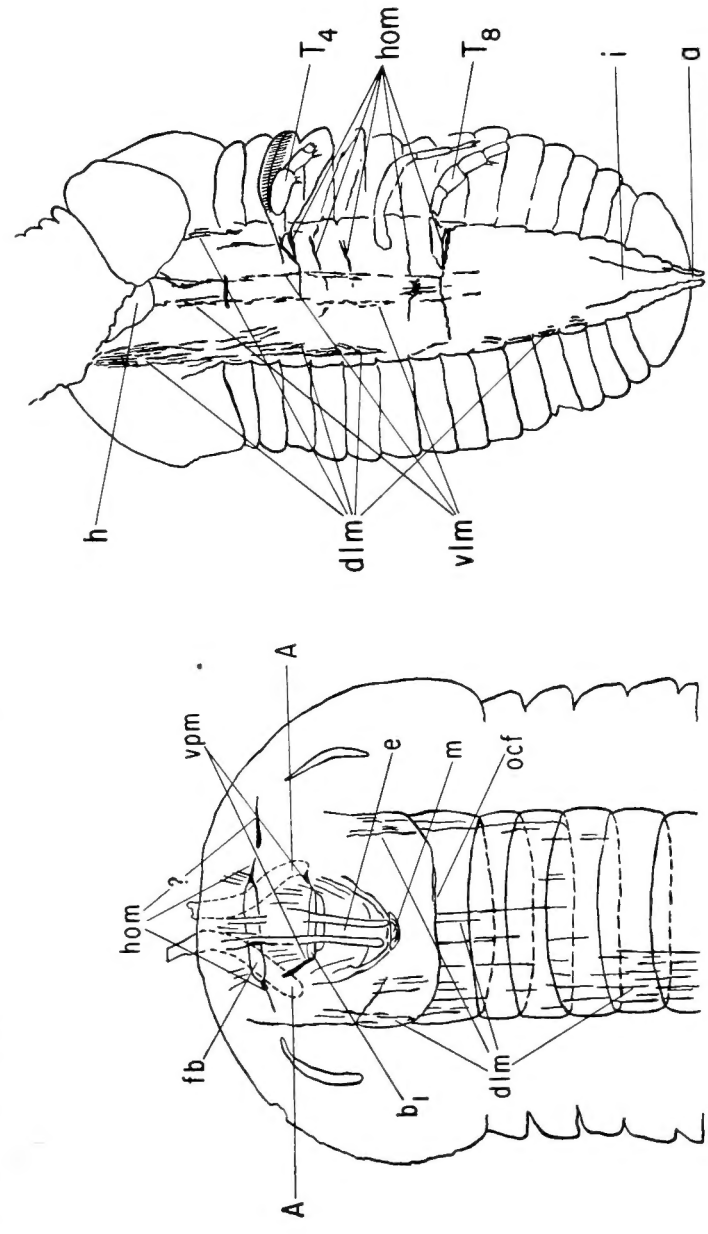


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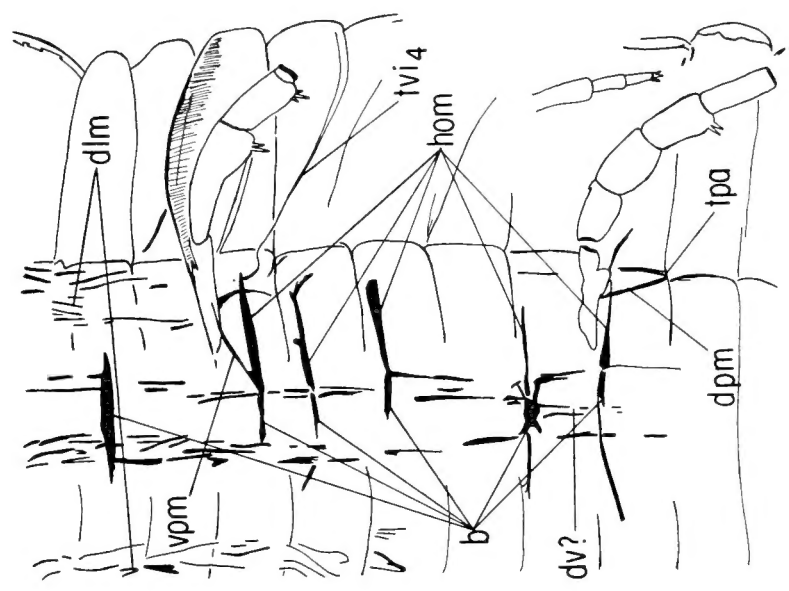
EXPLANATION OF PLATE 20  
 X-radiographic stereopairs of *Triarthrus eatoni* (Hall)

Figure	Pages
1. Ventral view of MCZ 7190/14B (× 4.10)	110, 119-122, 125
2. Ventral view of central part of head in MCZ 7190/14B (× 13.0). See Text-figure 18	110, 119-122, 125
3. Ventral view of YPM 28264, a large specimen with a small <i>Triarthrus</i> draped across its head (× 2.33)	109, 119-122, 126, 128
4. Ventral view of mid-thoracic region in YPM 28264 (× 4.6). See Text-figures 19 and 20	109, 119-122, 128



Text-figure 18. — Ventral view of anterior half of MCZ 7190/14B (Pl. 20, figs. 1, 2) showing the esophagus (*e*) and its relationship to endoskeletal bars (*fb*, *b*), showing horizontal muscles (*hom*) and a ventroposterior extrinsic limb muscle belonging to the antenna, and showing the dorsal longitudinal muscle (*dilm*).

Text-figure 19. — Ventral view of YPM 28264 (Pl. 20, figs. 3, 4), a large specimen with a small individual beneath part of its head. Of particular interest are the dorsal and ventral longitudinal muscles (*dilm*, *vlm*) and the horizontal muscles (*hom*) (see Text-fig. 20 for further details). From Cisne (1975).



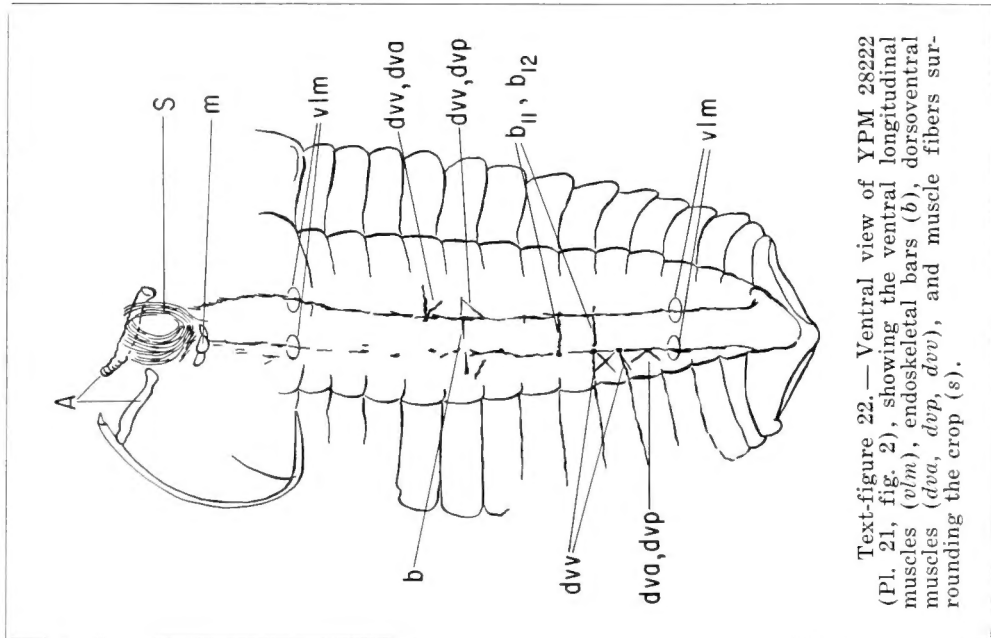
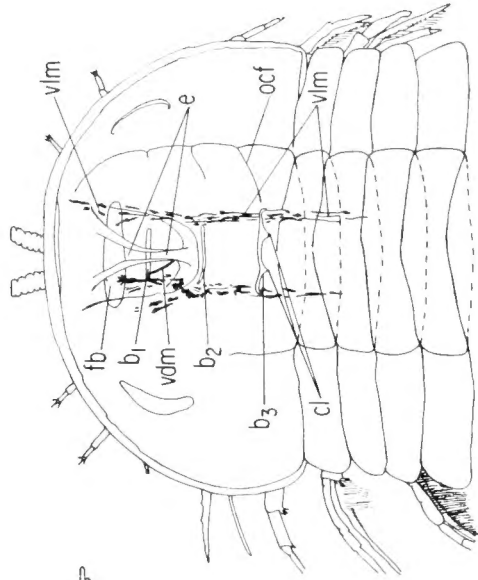
Text-figure 20. — Ventral view of the mid-thoracic region of YPM 28264 (Pl. 20, figs. 3, 4) showing in greater detail than shown in Text-figure 19 the relationship among endoskeletal bars (*b*), horizontal muscles (*hom*), and ventral longitudinal muscles (*vbm*) and showing in addition dorsoposterior and ventroposterior extrinsic limb muscles (*dpm*, *vpm*) and the possible dorsal vessel (*dvi?*).

EXPLANATION OF PLATE 21

X-radiographic stereopairs of *Triarthrus eatoni* (Hall)

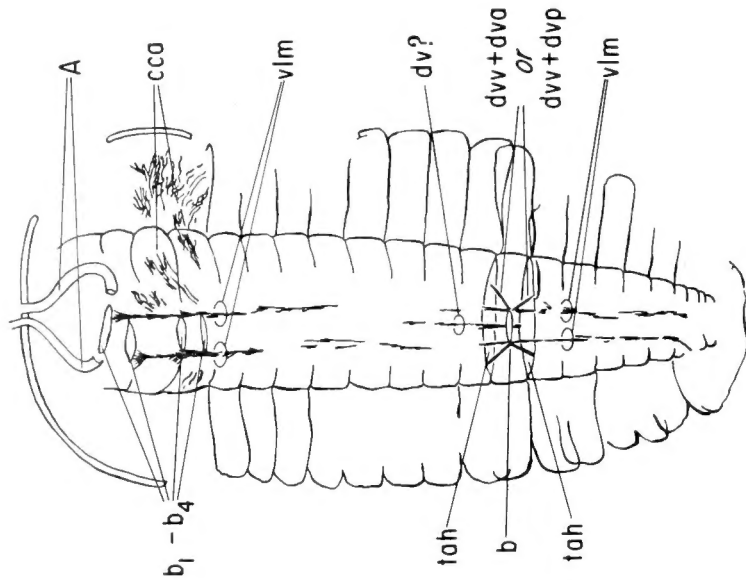
Text-figure 23. — Ventral view of anterior part of YPM 228 (Pl. 17; Pl. 21, fig. 3) showing tips of postoral limbs, the ventral longitudinal muscles (*vlm*), endoskeletal bars (*fb*, *b*) and a ventral dilator muscle (*vdv*), and their relationship to the esophagus (*e*), and showing connecting ligaments (*cl*) on the third post-frontal bar (*b*). From Cisne (1975).

- |   |                        |
|---|------------------------|
| Figure  | Pages                  |
| 1. Ventral view of YPM 27802A (X 4.10). See Text-figure 21                      | 110, 119-121, 168, 128 |
| 2. Ventral view of YPM 28222 (X 2.6). See Text-figure 22                        | 119-121, 125           |
| 3. Ventral view of central part of head in YPM 228 (X 5.90). See Text-figure 23 | 110, 119, 120, 125     |
| 4. Ventral view of YPM 204 (X 3.42). See Text-figure 24                         | 103, 110, 119, 120     |



Text-figure 22. — Ventral view of YPM 28222 (Pl. 21, fig. 2), showing the ventral longitudinal muscles (*vlm*), endoskeletal bars (*b*), dorsoventral muscles (*dva*, *dvp*, *dvp*), and muscle fibers surrounding the crop (*s*).

Text-figure 24. — Ventral view of YPM 204 (Pl. 21, fig. 4) showing the dorsal and ventral longitudinal muscles (*dvm*, *vlm*) and dorsoventral muscles (*dva*, *dvp*, *dvp*) and their relationship to head furrows (*lgf*, *ocf*). From Cisne (1975).



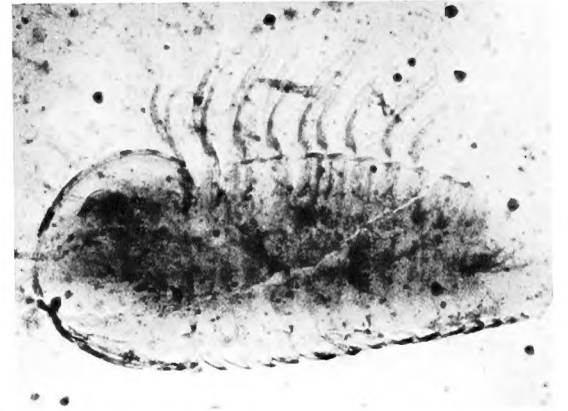
Text-figure 21. — Ventral view of YPM 27802A (Pl. 21, fig. 1) showing the ventral longitudinal muscles (*vlm*), endoskeletal bars (*b*), dorsoventral muscles (*dva*, *dvp*, *dvp*), caeca (*cca*), and the possible dorsal vessel (*dv?*).



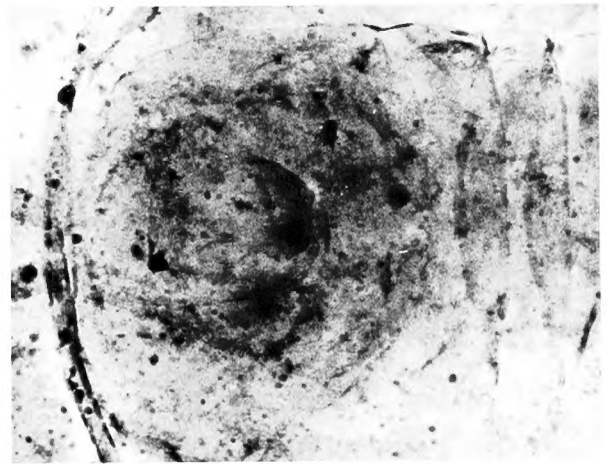
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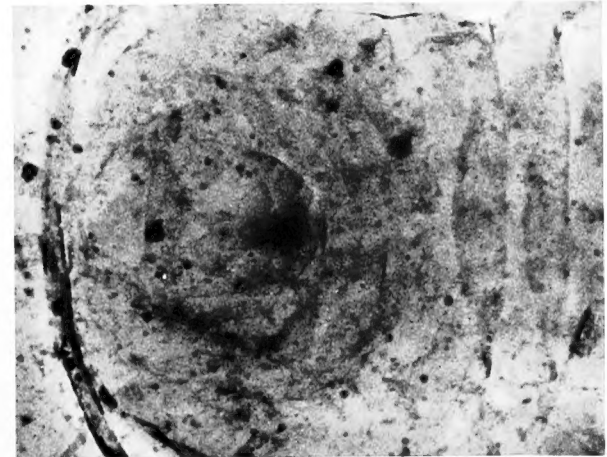
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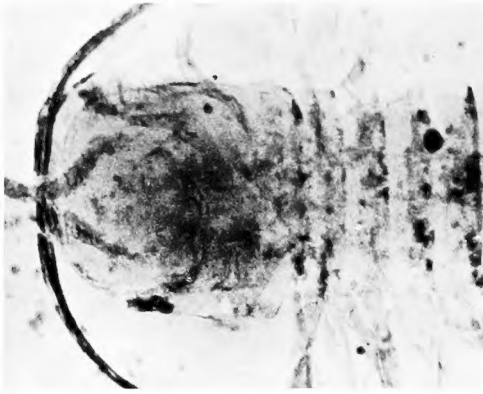


4



3





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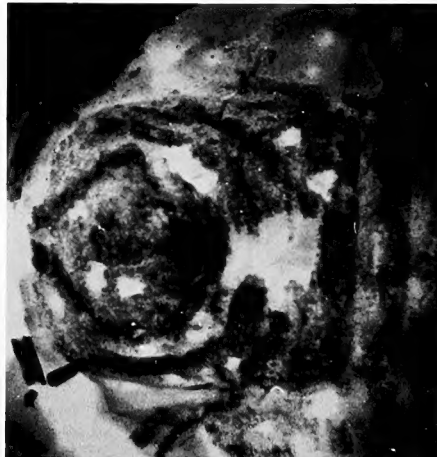
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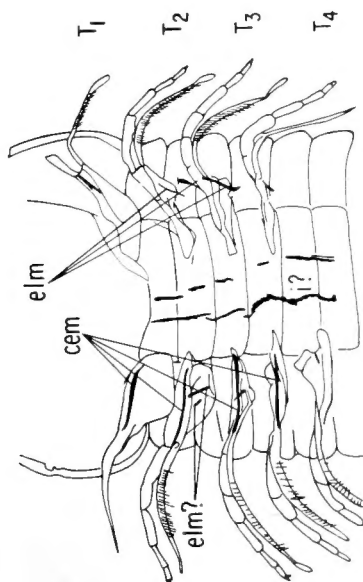


3

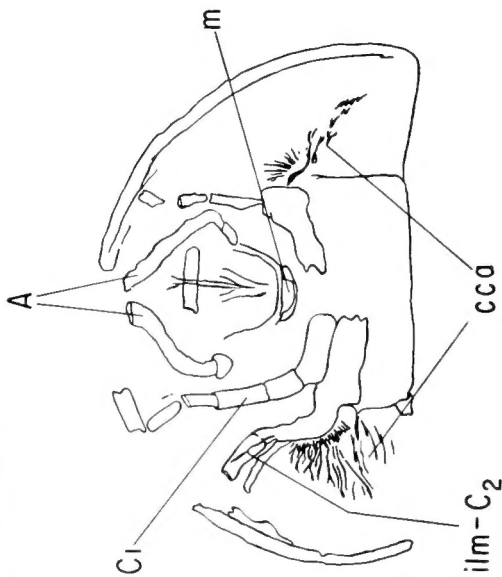


EXPLANATION OF PLATE 22  
X-radiographic stereopairs of *Triarthrus eatoni* (Hall)

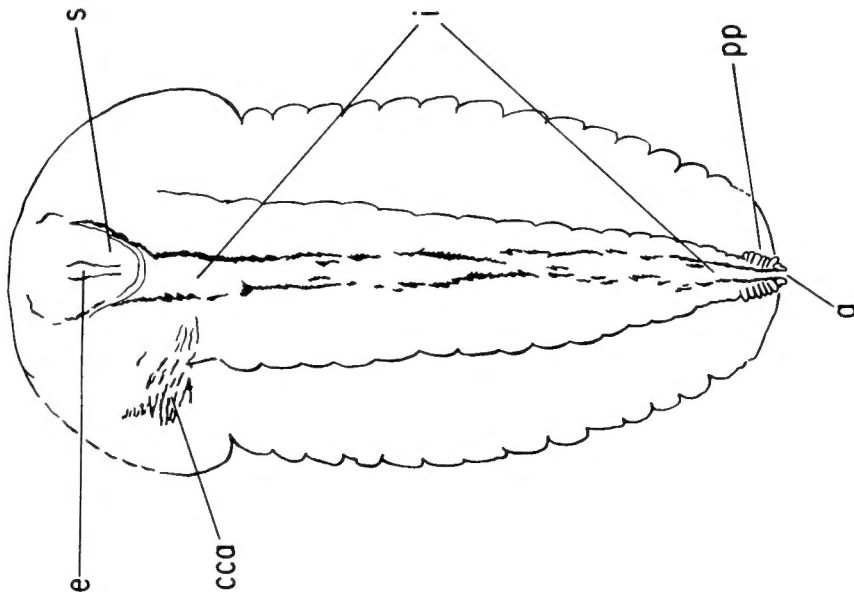
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2. Ventral view of head in YPM 28257 (X 5.20). See Text-figure 26	109, 120, 122, 125
3. Ventral view of head in MCZ 7190/22 (X 8.65). See Text-figure 27	110, 122, 126
4. Dorsal view of YPM 201 (X 4.51). See Text-figure 28	110, 125, 126



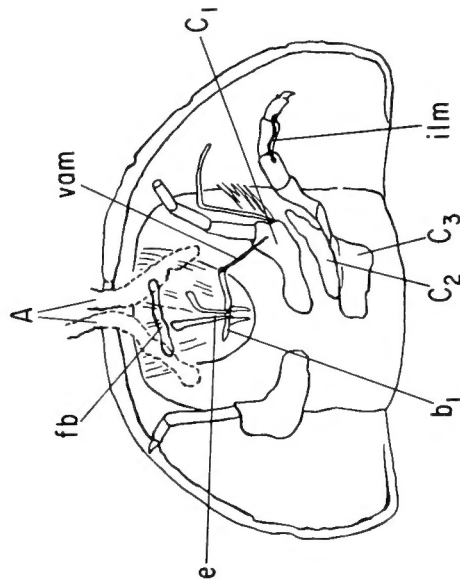
Text-figure 25. — Ventral view of the anterior part of MCZ 7190/1 (Pl. 22, fig. 1) showing the limbs, the coxal enditic muscle (*cem*), indeterminate extrinsic limb muscles (*elm*), and the probable intestine (*i?*).



Text-figure 26. — Ventral view of the head of YPM 28257 (Pl. 22, fig. 2) showing in particular the ventroanterior muscle (*vam*) of the first post-toral limb (*C1*) and its relationship to the first post-frontal bar (*b1*), and showing an intrinsic muscle (*ilm*) in the third post-toral limb (*C3*).



Text-figure 28. — Dorsal view of YPM 201 (Pl. 22, fig. 4) showing the digestive tract (*e, s, i, a*) and caeca (*cca*).



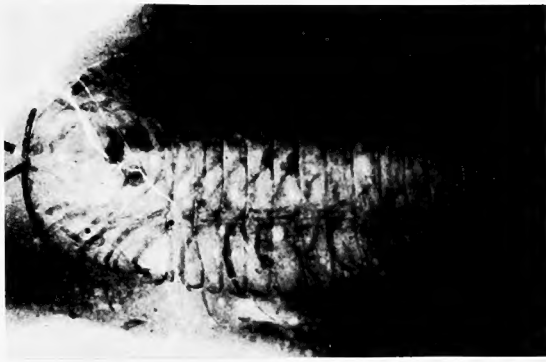
Text-figure 27. — Ventral view of the head of MCZ 7190/22 (Pl. 22, fig. 3) showing caeca (*cca*) and an intrinsic muscle (*ilm*) in the second post-toral limb (*C2*).

## EXPLANATION OF PLATE 23

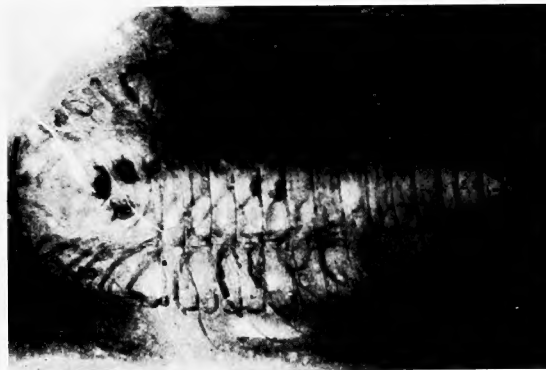
X-radiographic stereopairs of *Triarthrus eatoni* (Hall)

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2. Ventral view of YPM 220 ( $\times 1.92$ ) .....	110, 111
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4. Ventral view of YPM 28265, the extreme anterior part of a large individual's head ( $\times 9.1$ ) .....	122





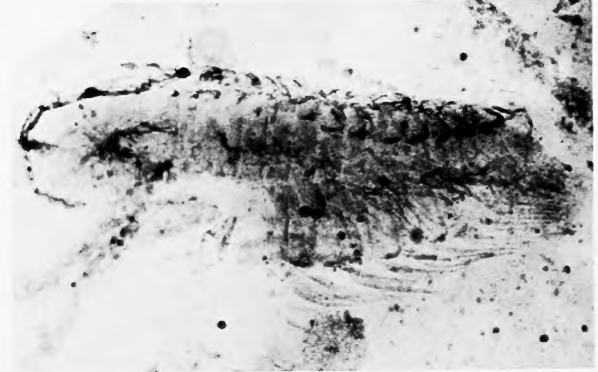
2



4



1



3





Abbreviations of explanations)

*A* .....  
*a* .....  
*axt* .....  
*b* .....  
*C* .....  
  
*cbf* .....  
*cca* .....  
*cdf* .....  
*cem* .....  
*cen* .....  
*ces* .....  
*cl* .....  
*cpf* .....  
*cx* .....  
*daf* .....  
*dam* .....  
*dln* .....  
*dmm* .....  
*dpm* .....  
*dv* .....  
*dva* .....  
*dvp* .....  
*dvo* .....  
*e* .....  
*ecm* .....  
*elm* .....  
*erh* .....  
*ets* .....  
*exf* .....  
*exi* .....  
*fb* .....  
*fdm* .....  
*fe* .....  
*fgl* .....  
*g* .....  
*gan* .....  
*h* .....  
*hbo* .....  
*hom* .....  
*i* .....  
*ihl* .....  
*ihp* .....  
*ilm* .....  
*isf* .....  
*itm* .....  
*lgf* .....  
*lgl* .....  
*m* .....  
*mac* .....  
*mca* .....  
*ocf* .....  
*ocr* .....  
*P* .....  
*pa* .....  
*pah* .....  
*par* .....  
*pdi* .....  
*pdr* .....  
*pf* .....  
*pl* .....



Note: page numbers are in light face; plates numbers are in bold face type.

Abbreviations of Morphological Terms (see "Appendix" for explanations)

<i>A</i>	106, 110, 118, 122, 124, 130, 135, 137-139
<i>a</i>	106, 107, 117, 124, 125, 136, 137, 139
<i>axt</i>	106, 107, 116
<i>b</i>	116-125, 127, 130, 131, 136-139
<i>C</i>	106-110, 114, 115, 117, 118, 120, 122-125, 127, 130, 131, 135, 139
<i>cbf</i>	107, 108, 114, 117, 118
<i>cca</i>	124-126, 138, 139
<i>cdf</i>	107, 108, 116, 118, 136
<i>cem</i>	116, 118, 122, 139
<i>cen</i>	107, 108, 116, 118, 124
<i>ces</i>	107, 108, 116, 135
<i>cl</i>	116, 117, 120, 123, 127, 138
<i>cpf</i>	107, 108, 112, 116, 118, 122, 136
<i>cx</i>	107, 108, 117, 118, 122, 136
<i>daf</i>	106, 109, 117, 123, 135, 138
<i>dam</i>	115-118, 122, 131
<i>dln</i>	115-119, 123, 128, 130, 135, 137, 138
<i>dmm</i>	112, 116, 117, 118, 122, 131, 136
<i>dpm</i>	115-118, 121, 122, 131, 137
<i>dv</i>	116, 128, 137, 138
<i>dva</i>	116, 117, 119, 120, 121, 123, 130, 131, 138
<i>dvp</i>	116, 117, 119, 120, 121, 123, 130, 131, 138
<i>dvv</i>	116, 117, 119-123, 130, 131, 136, 138
<i>e</i>	108, 124, 125, 135-139
<i>ecm</i>	108, 127, 135
<i>elm</i>	122, 139
<i>erh</i>	107, 108, 112, 115
<i>ets</i>	107, 108, 112
<i>exf</i>	107, 108, 112, 115
<i>exi</i>	107, 108, 136
<i>fb</i>	116-121, 124, 125, 130, 131, 137-139
<i>fdm</i>	124
<i>fe</i>	107, 108, 118, 122
<i>fgl</i>	106, 107, 116, 120, 124
<i>g</i>	107
<i>gan</i>	108, 127, 135
<i>h</i>	106, 107, 124, 135, 137
<i>hbo</i>	106, 107, 116, 119
<i>hom</i>	116, 119, 120, 121, 123, 130, 131, 136, 137
<i>i</i>	116, 117, 119, 124, 125, 135-137, 139
<i>ihl</i>	113, 114
<i>ihp</i>	113, 114
<i>ilm</i>	118, 122, 139
<i>isf</i>	106, 107
<i>itm</i>	113, 114, 116, 124
<i>lgf</i>	107, 115-118, 120, 125, 131, 138
<i>lgl</i>	106, 107, 110, 125
<i>m</i>	106, 107, 109, 124, 135, 137-139
<i>mac</i>	106, 107, 124
<i>mca</i>	106, 107, 124, 125
<i>ocf</i>	106, 107, 115, 117-120, 131, 137, 138
<i>ocr</i>	106, 107, 110, 118
<i>P</i>	106-109, 117, 119
<i>pa</i>	106
<i>pah</i>	106, 107, 115, 117
<i>par</i>	106, 107, 111
<i>pdi</i>	106
<i>pdr</i>	106, 107
<i>pf</i>	107, 108, 122
<i>pl</i>	107, 108, 118, 122, 136

<i>pp</i>	106, 107, 139
<i>pt</i>	107, 108, 113, 136
<i>ptl</i>	108
<i>pts</i>	106, 107, 111
<i>ptt</i>	108
<i>pvi</i>	106
<i>pvf</i>	106
<i>s</i>	106, 107, 117
<i>T</i>	119, 124, 125, 136, 138, 139
<i>t</i>	104, 106-110, 113, 114, 117, 118, 122, 124, 130, 135-137, 139
<i>ta</i>	106, 107, 117, 125
<i>tah</i>	107, 108, 136
<i>tar</i>	106, 107, 113-117, 120, 121, 124, 138
<i>tdi</i>	106, 107, 113, 114, 118, 120, 124
<i>tdr</i>	106, 107
<i>tel</i>	106, 107, 109, 114
<i>ti</i>	107, 108, 136
<i>tfa</i>	107, 108, 136
<i>tpf</i>	114, 117, 122, 124, 137
<i>tr</i>	106, 107, 118, 122, 131, 136
<i>tvi</i>	107, 108
<i>tvr</i>	106, 107, 121, 137
<i>vaf</i>	106, 107, 109
<i>vam</i>	106, 109, 121, 135
<i>vdm</i>	115-118, 120, 122, 131, 139
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ABBREVIATIONS OF MORPHOLOGICAL TERMS USED IN THIS PAPER

<i>A</i>	antenna/antennal segment	<i>itm</i>	intertergal membrane
<i>a</i>	anus	<i>lgf</i>	lateral glabellar furrow
<i>axt</i>	axial tubercle	<i>lgl</i>	lateral glabellar lobe
<i>b</i>	endoskeletal bar	<i>m</i>	metastoma
<i>C</i>	postoral head limb/postoral head segment	<i>mac</i>	macula
<i>cbf</i>	coxa-body foramen	<i>mca</i>	mouth cavity
<i>cca</i>	caeca	<i>ocf</i>	occipital furrow
<i>cdf</i>	coxal distal furrow	<i>ocr</i>	occipital ring
<i>cem</i>	coxal enditic muscle	<i>P</i>	abdominal limb/abdominal segment
<i>cen</i>	coxal endite	<i>pa</i>	pygidial abdomen
<i>ces</i>	coxal enditic seta	<i>pah</i>	pygidial articulating half ring
<i>cl</i>	connecting ligament	<i>par</i>	pygidial axial ring
<i>cpf</i>	coxal proximal furrow	<i>pdi</i>	pygidial dorsal pleural furrow
<i>cx</i>	coxa	<i>pdr</i>	pygidial dorsal ring furrow
<i>daf</i>	dorsal axial furrow	<i>pf</i>	prefemur
<i>dam</i>	dorsoanterior extrinsic limb muscle	<i>pl</i>	patella
<i>dln</i>	dorsal longitudinal muscle	<i>pp</i>	post-pygidial abdomen
<i>dmm</i>	dorsomedial extrinsic limb muscle	<i>pt</i>	pretarsus
<i>dpm</i>	dorsoposterior extrinsic limb muscle	<i>ptl</i>	pretarsal lateral seta
<i>dv</i>	dorsal vessel	<i>pts</i>	terminal axial segment of pygidium
<i>dva</i>	anteriorly descending dorsoventral muscle	<i>ptt</i>	pretarsal terminal seta
<i>dvp</i>	posteriorly descending dorsoventral muscle	<i>pvi</i>	pygidial ventral pleural furrow
<i>dvv</i>	vertically descending dorsoventral muscle	<i>pvf</i>	pygidial ventral ring furrow
<i>e</i>	esophagus	<i>s</i>	crop
<i>ecm</i>	circum-esophageal commissure	<i>T</i>	thoracic limb/thoracic segment/thoracic tergite
<i>elm</i>	extrinsic limb muscles	<i>t</i>	telson
<i>erh</i>	exite shaft	<i>ta</i>	tarsus
<i>ets</i>	exitic terminal segment	<i>tah</i>	thoracic articulating half ring
<i>exf</i>	exite filaments	<i>tar</i>	thoracic axial ring
<i>exi</i>	exite	<i>tdi</i>	thoracic dorsal interpleural furrow
<i>fb</i>	frontal endoskeletal bar	<i>tdr</i>	thoracic dorsal ring furrow
<i>fdm</i>	frontal dilator muscles	<i>tel</i>	telopod
<i>fe</i>	femur	<i>ti</i>	tibia
<i>fgl</i>	frontal glabellar lobe	<i>tfa</i>	tergal posterior apodeme
<i>g</i>	glabella	<i>tpf</i>	thoracic pleural furrow
<i>gan</i>	ganglion	<i>tr</i>	trochanter
<i>h</i>	hypostoma	<i>tvi</i>	thoracic ventral interpleural furrow
<i>hbo</i>	head border	<i>tvr</i>	thoracic ventral ring furrow
<i>hom</i>	horizontal muscle	<i>vaf</i>	ventral axial furrow
<i>i</i>	intestine	<i>vam</i>	ventroanterior extrinsic limb muscle
<i>ihl</i>	intertergal hinge line	<i>vdm</i>	ventral dilator muscles
<i>ihp</i>	intertergal hinge point	<i>vlm</i>	ventral longitudinal muscle
<i>ilm</i>	intrinsic limb muscle	<i>vpm</i>	ventroposterior extrinsic limb muscle
<i>isf</i>	intersegmental furrow	<i>vt</i>	food groove

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## PREPARATION OF MANUSCRIPTS

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Collinson, J.

1962. *Size of lettering for text-figures*. *Journal of Paleontology*, vol. 36, p. 1402.

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