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APPENDAGES AND HABITS OF THE UPPER ORDOVICIAN TRILOBITE *TRIARTHRUS EATONI*

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[Plates 1–10]

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Sixteen specimens from the classic locality quarried by C. E. Beecher, in the Frankfort Formation near Rome, New York State, U.S.A., have been examined. Pyrite has replaced the exoskeleton and lines or infills confined spaces such as within the doublure and appendages. Appendages are compressed beneath the flattened exoskeleton and retain their original relationship to one another; biramous appendages have in most cases been rotated, commonly showing the posterior face beneath the cephalon, the anterior face beneath thorax and pygidium. The specimens were collected and prepared by C. D. Walcott, most having been exposed from the ventral side and lie approximately parallel to the bedding, three are oblique-lateral in relation to bedding. Seven have been additionally prepared using a gas pressure abrasion machine, photographs taken in reflected light, the specimens submerged in alcohol, and explanatory camera-lucida drawings made.

The antennae may not have had an originally lyriform configuration. Additional evidence supports the view that the cephalon bore three pairs of biramous appendages as J. L. Cisne claimed (*Science, Wash.* **186**, 13–18 (1974); *Fossils Strata* **4**, 45–63 (1975); *Palaeontogr. Am.* **9**, 99–142 (1981)), but there is no indication that a metastome was present. Coxae are poorly preserved, the last-formed posterior coxa small, triangular, coxae becoming progressively elongate forward along the series, and deeper beneath the cephalon. Neither the ventral membrane nor the coxa–body junction has been observed. The interpretation of the form of the coxa, and attachment of leg branches, by Cisne (1975, 1981), is considered to have been based on misinterpretation of an X-ray stereograph; the leg branch is inserted into the full depth of the abaxial coxal margin. Endites of the podomeres of the leg branch are deep, acutely triangular in shape, on podomeres 1–4 of the posterior branches; podomeres become progressively more elongate forward along the series, endites less acutely triangular, and are present only on the proximal podomere anteriorly, as C. E. Beecher (*Am. J. Sci.* **1**, 251–256 (1896)) showed. The tips of the endites were spinose. We consider that there was no 'post-pygidial abdomen', as claimed by Cisne (1975, 1981), the structure so interpreted being the most posterior, six or seven tiny coxae and leg branches, preserved crowded together and overlapping, backwardly directed across and behind the pygidial doublure. The shaft of the exite was rigidly attached to the upper, posterior side of the coxa, was broad proximally, tapering, and obliquely subdivided. It bore about 50 filaments and a small, setose terminal lobe. The filaments are preserved as imbricated, flattened strips, closely spaced and parallel, always dorsal to the leg branches. The most posterior limb pair was the last-formed, differing growth rates between portions of the earlier-formed limbs led to the graded differentiation shown by the biramous limb series. The differences between coxae and leg branches in particular regions of the body were concerned with capture and ingestion of food.

A new reconstruction is made, the exoskeletal convexity based on uncrushed, enrolled specimens of the similar species *Triarthrus beckii*. Exoskeletal structures show that *T. eatoni* could have enrolled to form an enclosed capsule, within which all the appendages must have been accommodated. The biramous limbs are restored in a hanging stance, the inner ends of the coxae close together. Both branches of the limbs projected well below the margins of the exoskeleton, but only the tips were visible in dorsal view. *T. eatoni* was a benthic animal that walked on the substrate, and could have launched itself off the bottom and drifted above it. It was probably a generalized deposit feeder, scavenger and predator, exploring the surface of the mud and digging into it for small organic fragments, and capable of catching and squeezing small prey in the formidable array of posterior endites and spines. Food was passed forward to the mouth by the interaction of the spinose mesial edges of pairs of coxae, larger cephalic coxae helped push food toward the mouth. *T. eatoni* is preserved predominantly in dark shales, that were formed in muddy environments of the outer continental shelf and upper slope.

1. Introduction

Specimens of a trilobite *Triarthrus eatoni*, showing appendages for the first time (preserved in pyrite), were discovered by W. S. Valiant in September 1892, after an eight-year long search (Schuchert in Raymond 1920) in the Upper Ordovician Frankfort Formation near Rome, New York State. Some specimens were sent to Columbia College by Valiant, and W. D. Matthew (1893) made known the single pair of antennae and fragments of the biramous limbs. C. D. Walcott was intensely interested in the find because of his search for such specimens, and indeed he had earlier discovered (1876, 1879) traces of limbs in thin sections of the Ordovician Trenton Limestone of New York State. Walcott (1894) visited Valiant's locality in 1893, and obtained a small collection, which included the specimens described herein. The classic work on these appendages of *Triarthrus* was by C. E. Beecher (1893, 1894*a*, *b*, 1895, 1896, 1902) who began quarrying the site in 1893, and had mined the bed out by 1895 (Cisne 1973). Beecher prepared over 600 specimens, and he reproduced his restoration of the trilobite in dorsal and ventral view (1896) in relief, so that casts could be widely distributed. His collection remains of great importance because of the large number and range in size of the specimens, and the excellent preservation of appendages in relief. After Beecher's death his unpublished work, including many photographs, was incorporated by Raymond into his memoir (1920), and additional contributions were made by Walcott (1918, 1921).

At the turn of the century it was known that images of pyritized fossils in shale could be obtained by X-rays, and investigations of *Triarthrus eatoni* during the past 50 years have all been illustrated (Størmer 1939; Stürmer & Bergström 1973; Cisne 1975, 1981) by such photographs, supplemented by drawings. Cisne used X-ray stereographs, and summarized his findings in a new reconstruction that differed in a number of important features from that of Beecher, or the slightly modified versions of the latter by Raymond and Walcott. Among the new features claimed by Cisne were the presence of three, not four, pairs of biramous appendages on the cephalon, a coxa showing the position of the coxa–body junction and the two branches of the limb arising from the outer edge, and a supposed tapering, limb-bearing 'post-pygidial abdomen' that projected a short distance beyond the pygidium. A notable omission from his reconstruction of the limbs were the triangular, spinose endites of the leg branches and their increasingly strong development posteriorly, shown so clearly by Beecher, Raymond and Walcott. In other trilobites in which appendages are preserved, no trace of a structure resembling the 'post-pygidial abdomen' is known. This claim, and others made by Cisne, appeared to us worthy of re-investigation, using a modern improvement on Beecher's methods, and in particular photographs taken in reflected light. These show what has been revealed of the specimen after preparation, and have a clarity lacking in the X-ray images, but do not show features concealed in the matrix. Explanatory drawings, showing our interpretation of the morphology preserved, face the plates of photographs. From this evidence, we support Cisne's (1974, 1975, 1981) view that the cephalon bore three pairs of biramous appendages. Our illustrations show the endites of the leg branches much as they were originally described by Beecher, and portrayed in his original restoration (Beecher 1896, plate viii), and those of Raymond (1920, figure 10) and Walcott (1894, plate 1; 1918, plate 32), but not in that by Cisne (1981, text-figure 5; reference hereafter is to Cisne's (1981) monograph, which includes all his previously published illustrations and additional ones). Further, comparisons between our photographs and Cisne's X-ray stereographs, convince us that Cisne's drawings of the coxa and how the limb branches arose from it, and of the 'post-pygidial abdomen', are based on misinterpretations of X-ray stereographs. We therefore urge reconsideration of deductions on the relationships of trilobites that include acceptance of a 'post-pygidial abdomen' in *Triarthrus* (Lauterbach 1980). The pygidial region of *Triarthrus* was formed of fused posterior somites and the telson bearing the anus.

Although the flattening that the specimens of *Triarthrus eatoni* had undergone was recognized by Beecher, neither he, Raymond nor Walcott allowed for it in restoring the convexity of the exoskeleton. Cisne gave it much more convexity, but a new factor for our consideration was Ross' (1979) publication of photographs of enrolled specimens of *T. beckii*, a similar species to *T. eatoni* and contemporaneous in stratigraphical range. The convexity of the exoskeleton in these specimens is far greater than envisaged in previous restorations. If it is assumed, as we do, that *T. eatoni* was very like *T. beckii* in exoskeletal convexity, and that it enrolled and was able to accommodate all the appendages within the exoskeleton, a new reconstruction is required. We have attempted to provide this (figures 38–41, 43), and discuss it in detail. Many questions remain unanswered, especially on the form of the coxa, the nature and position of the coxa–body junction, and the morphology of the exite and its filaments. We have not re-examined any of Beecher's numerous preparations. If these were further prepared and photographed by methods similar to those used here, much new information might be revealed.

2. MATERIAL AND TECHNIQUES

In this study we have selected for illustration 16 of the 55 specimens we received on loan; none has been figured previously. Specimens lying parallel to the bedding had all been prepared from the ventral side, with the exception of two on which an attempt had been made to prepare them from the dorsal side; these latter show little. All these specimens had been prepared long ago by Walcott, and U.S.N.M. 400936–400939 and 400943–400947 are illustrated here as he left them. The scrap of shale containing each specimen was set in a small plaster block; hence the white areas in the photographs where the specimen was broken through, and around the margins of the fragments. In his preparation Walcott presumably used similar methods to those of Beecher (Schuchert in Raymond 1920, p. 6), that is, rubbers and fine abrasive powders in the final, delicate stages. The possibilities of further preparation using the gas pressure abrasion machine were first explored by Dr C. P. Hughes, and subsequent extensive preparation was by J. E. A. on U.S.N.M. 400932–400935 and 400940–400942. The abrasion was as gentle as possible, the gas pressure low, the abrasive powder (used very sparingly) was dolomite. Pyritized structures were protected as soon as exposed by a thin layer of latex, but it proved difficult to avoid damage to delicate structures such as small spines and exite filaments. The photographs were taken by J. E. A. using fibre-optic illumination, the specimens submerged in alcohol; the Kodak Panatomic-X film was developed to give maximum contrast. Drawings were made by H. B. W. using the Wild binocular microscope with a camera lucida attachment.

3. TAPHONOMY AND PRESERVATION

Cisne (1973) discussed in detail the stratigraphy of Beecher's Trilobite bed, concluding that the benthic fauna was killed and buried by a turbidity flow. We accept his argument that the trilobites were whole animals killed by the flow, and are not transported moults. During transport mud penetrated between the limbs and the ventral cuticle, and between branches of the limbs. As a result of compaction, the limbs were bent to conform with the residual convexity of the exoskeleton, and as they crossed over the edge of the exoskeleton, but a layer of matrix remains between limb and exoskeleton and between the limb branches, as the present photographs show. Cisne (1973, pp. 11–12) discussed diagenesis, concluding that parts of *Triarthrus eatoni* are preserved as pseudomorphs in pyrite. In X-ray photographs (Størmer 1939, figure 21; Stürmer & Bergström 1973, plate 24; Cisne 1981, plates 17–23) the tubular cephalic doublure, the similar doublure of the tips of the thoracic pleurae and of the pygidium, appears darker (that is, is densely pyrite-filled), the narrow space between axial ring and its doublure being less dark. The doublure and the appendages may be outlined by a darker rim that is externally smooth, irregular on the inner side (see, for example, Cisne 1981, plate 17; plate 18, figure 3; plate 20, figure 4; plate 23, figure 4). This suggests that the pyrite was formed particularly in confined spaces, and both X-ray photographs and thin sections (Cisne 1982, figure 7) of the limbs support the idea that it lined the inner surface of such spaces and grew inward to fill them. If the filling was hollow, then in the course of preparation the side facing outward might have been wholly or partly removed, leaving only the outline of the limb in pyrite. Left limbs of 400940 (figure 26, plate 7) show this appearance, as does right leg, branch 2. In the confined space inside the cuticle covering small posterior leg branches and their endites, the prominent pyrite infillings appear to have been solid (figure 3, plate 1; figures 32, 33, plate 9), as do the distal portions of the exites. Such thicker infillings may have produced the appearance of a ridge along the ventral margins of endite 1 of left leg branches l, m and n in 400932 (figure 3, plate 1). It is questionable whether such features as the double ridge of right coxa 2 in 400944 (figure 30), or the transverse groove in the coxa of 400946 (figure 34), should be interpreted as original or resulting from compression of a pyrite lining of variable thickness. If the limbs are preserved as infillings of the space within the cuticle of limbs, spines and filaments, then they may well be slimmer in appearance, filaments and spines shorter and blunter, than in life. Besides these infillings, some specimens show the outer or inner surface of the exoskeleton, preserved in a smooth layer of pyrite (figure 4, plate 1; figures 25, 26, plate 7), and in axial section (figures 18, 19, plate 5) the exoskeleton appears to have been replaced by pyrite.

No pyrite layer that can be recognized as having been associated with the uncalcified ventral cuticle is known. Rather, the limbs lie close beneath, or (especially distally) separated by a thin layer of matrix from the pyrite layer of the dorsal exoskeleton. The limbs are approximately in their original relationship to one another, bent to conform with the exoskeleton and over its edges if they extend out beyond it. It is presumed that in life fluid pressure was sufficient to provide hydrostatic support of the trilobite body. Upon death and burial, the body would presumably have collapsed, bringing limbs, hypostome and ventral membrane close up to the dorsal exoskeleton. Decay would have begun, but also formation of ferrous sulphide in confined spaces, and replacing the mineral matter in the exoskeleton. The ventral cuticle was sufficiently resistant to hold the series of appendages and the hypostome in place as pyritization continued, even though no trace of it appears to remain. At the same time compaction of the wet sediment would have begun the process of progressively reducing the convexity of the exoskeleton and pressing the appendages against it. Such compaction would presumably have continued over a far longer period of time than pyritization. Some estimate of the amount of this compaction may be made from comparing Cisne's cross-sections of the thorax (1981, plate 18, figure 2) with the present restoration.

As the body collapsed, and compaction took place, it appears that the limbs were rotated about the coxa–body junction, and flattened from side to side, not dorsoventrally. In specimens exposed from the ventral side (figures 4, 5, 6, 27, 28, 32, 33) the limbs of the thorax and pygidium appear to have been rotated backward so that the anterior face of coxa and leg branch is directed ventrally. The leg branches curve backward to varying degrees, and the endites are seen in profile. In these specimens seen in ventral view, the exite shafts emerge from behind (posterior to) the leg branches; thus filaments are only rarely revealed by preparation beneath cephalon or thorax (figures 4, 36), or posteriorly (figures 5, 14, 33). Anteriorly, these filaments are directed backward and outward, directly backward posteriorly where the leg branch is similarly directed. We consider the evidence suggests that in life (figure 41) the exite shaft was held so that the filaments were proximally directed back at right angles to the leg branch. When, during collapse of the body, the coxa and leg branch were rotated, filaments were not swung to point vertically, but presumably held close beneath the ventral cuticle, and bent at the base. That the filaments are straight and parallel suggests an original stiffness.

Beneath the cephalon rotation of the coxae appears to have been forward (figures 6, 11, 20, 28) so that the posterior face of the coxa faces ventrally. The backward curvature of the leg branches in these specimens implies either twisting or distortion of the leg branch distally. In lateral or oblique-lateral specimens (figures 12, 13) the limbs have been rotated so that leg branches are seen in lateral aspect and curve backward, and the inner side of the exite is exposed. In figures 18, 19, limbs of the left side are nearest the observer, and the upper, outer side of the exite is exposed, with backwardly directed filaments attached, and the limbs appear not to have been rotated. In 400943 (figure 36) the limbs in the anterior portion are directed forward and outward, appearing as narrow ridges, and presumably were compacted dorsoventrally. The varied attitudes of the limbs presumably reflect turbidity during burial as well as early effects of death and decay. Cisne (1981, p. 110) also recognized the forward rotation of limbs beneath the cephalon, but considered those of the thorax to have been flattened dorsoventrally. The evidence of the majority of our specimens, and of many of Beecher's (Raymond 1920, plate 2, figure 6; plate 3, figure 3; plate 4, figure 3; plate 5, figures 2, 3; plate 6, figure 3), contradicts this latter view. Dorsoventral flattening of the more anterior thoracic limbs, as seen in 400943 (figure 36), appears to be unusual.

The limbs on one side of a specimen (figures 4, 6) or both (figure 11) may project out beyond the edge of the exoskeleton. The limbs are shown in this attitude in dorsal and ventral view in Beecher's (1896, plate viii) and Raymond's (1920, figure 10) restorations, and markedly so in that of Cisne (1981, text-figures 1, 2). In our view this attitude reflects preservation rather than being a plausible stance in life (see §6*j*). In the restoration we show the distal portions of the limb branches as steeply inclined, so that in dorsal view (figure 38) only the tips of the limbs are seen, whereas in lateral view (figure 39) the limbs project far below the exoskeleton. The animals were buried in a wide variety of orientations relative to the bedding plane, ranging from the body having been approximately parallel (figures 11, 21), slightly oblique (figure 6), more strongly oblique (figure 13), to almost lateral (figure 12). In the oblique specimens (figures 6, 13, 22; compare the X-ray photographs of Cisne 1981, plate 21, figure 4; plate 23, figure 3), the limbs on one side extend far out beyond the exoskeleton because of lateral displacement. Consideration of the cross sections of the reconstruction (figure 39*a–e*) will show that such displacement would have been possible, after collapse and compaction of the remains, if the vertical plane of the body had been at an angle to the bedding when buried. If, in addition, the sagittal axis had not lain in the bedding plane, a shift of the series of limbs, backward or forward in relation to the exoskeleton, may also have occurred.

In some specimens (figures 4, 13) a longitudinal groove traverses part of some, but not all, the exites on the inner, ventral side. In other specimens (figures 6, 12) such a groove is absent. It is uncertain whether this feature was original or whether it results from compaction of a hollow tube of pyrite deposited inside the branch. In 400938 (figure 19) the outer side of the exites x and y is exposed, and there is a marked step in level between the bases of the filaments and the anterior portion of the exite shaft. This may well be original, but may have been exaggerated by compaction. Thus how the specimens are to be interpreted depends on deductions regarding preservation. Furthermore, the method of preparation by removing matrix gradually until pyrite appears, affects what is seen. For example, as a specimen was prepared from the ventral side, the first pyrite encountered would have been the limb as it crossed the tip of the pleura. The major portion of the limb would only have appeared after further excavation. This is why in many specimens the limb has been exposed beneath and outside the pleura, with a gap where it has been lost in preparation as it crossed over the tip of the pleura (figures 4, 25). Thus, whether an X-ray is taken of a prepared, or an unprepared, specimen, affects what is seen.

4. DESCRIPTIONS OF SPECIMENS OF *TRIARTHRUS EATONI* (HALL, 1838)

These specimens are of holaspid individuals from 7 to 28 mm in sagittal length. They come from a single horizon (Cisne 1973) in the Upper Ordovician Frankfort Shale, in Cleveland's Glen, near Rome, New York State, U.S.A. Earlier authors referred them to *Triarthrus beckii* Green, 1832, but Cisne (1973, p. 20) followed Ruedemann in naming the species *T. eatoni* (Hall, 1838). The recent study by Ludvigsen & Tuffnell (1983) has clarified the distinctions between these two species. We follow them in accepting that, because the present specimens have a long palpebral lobe, the centre opposite the second lateral glabellar furrow (figure 26, plate 7; figure 27, plate 8), they should be referred to *T. eatoni*. Authors such as Fortey (1974), Ludvigsen & Tuffnell (1983), and Nikolaisen & Henningsmoen (1985) agree that *Triarthrus* belongs within the family Olenidae Burmeister, 1843, but not on the species to be included within the genus or its relationships and the consequent subfamilial groupings. Nikolaisen and Henningsmoen include in their diagnosis of the family that the hypostome was not attached along a hypostomal suture to the cephalic doublure. What little evidence is available (§5) from specimens of *Triarthrus* suggests that there was such an attachment in *T. beckii* and *T. eatoni*.

The specimens oriented parallel, or slightly oblique to the bedding have been exposed from the ventral side. The terms 'left' and 'right' are used with reference to the anatomy of the animal, hence the left side is on the right side of the illustration and vice versa. These specimens are referred to as *parallel*, in contrast to those oriented strongly obliquely or laterally to the bedding, referred to as *oblique-lateral* or *lateral*. We have used the term *exoskeleton* to denote the mineralized portion of the cuticle on the dorsal side, that extends ventrally as the reflexed doublure and hypostome. Appendages are referred to using the terminology of Whittington (1975, p. 99), except that the outer branch, that extends abaxially to the inner or leg branch, is called an exite rather than a gill branch. Podomeres of the leg branch are numbered 1–6 abaxially from the coxa.

(*a*) *U.S.N.M.* 400932

Figures 1, 2; figures 3, 4, plate 1

Twenty-two successive appendages (figures 1, 2, labelled a–v on the left side) are displayed in relation to the exoskeleton of the thorax and pygidium. The appendage series is displaced slightly to the left, so that the inner ends of the coxae on the right side lie about on the sagittal line, and those on the left just inside the axial furrow. The course of this furrow may be traced on the left, but not on the right side. The limbs are rotated so that the anterior side faces ventrally, and the outer branches thus appear from beneath the most proximal portion of the leg branch. The limbs are slightly flexed and directed outward anteriorly, progressively more strongly backward toward the rear where they are directed straight backward. Posteriorly on the left side the series of coxae (figure 1) become prominent, triangular ridges, directed ventrally and backward, where they lie on the axial furrow of the pygidium. The most posterior coxa recognized (v in figure 1) appears to lie on the doublure of the pygidium, and the limb series may have been displaced slightly backward. The limbs have been rotated back and flattened so that they project back behind the pygidial doublure, the most posterior pair separated by a narrow median gap.

The size and form of the endites on podomeres 1–3 of the leg branch are well displayed in this specimen. The endite of podomere 1 is present on the left branch labelled e, and conspicuous on branches j to t, on which it becomes relatively larger, triangular, and more elongated ventrally going backward in the series. As noted in §3, the ridge along the ventral side of endite 1 of branches l, m and n may be an artefact of preservation. The similar endite on podomere 3 is present on branches j–t, and from branch l backwards an endite on podomere 4. On the right side prominent endites are preserved on podomeres 1, 2 and 3, of the leg branch of limbs beneath the posterior portion of the thorax, and are present on the tiny limbs of the pygidium. The tips of the endites of podomeres 2, 3 and 4 were spinose. On the left side beneath the pygidium podomere 2 of the leg branch is poorly preserved or absent where it lay on the doublure, having been damaged or lost in preparation. Beneath the posterior thoracic segments this podomere is distorted or bent where it crosses the pleural tips. Endites on podomeres

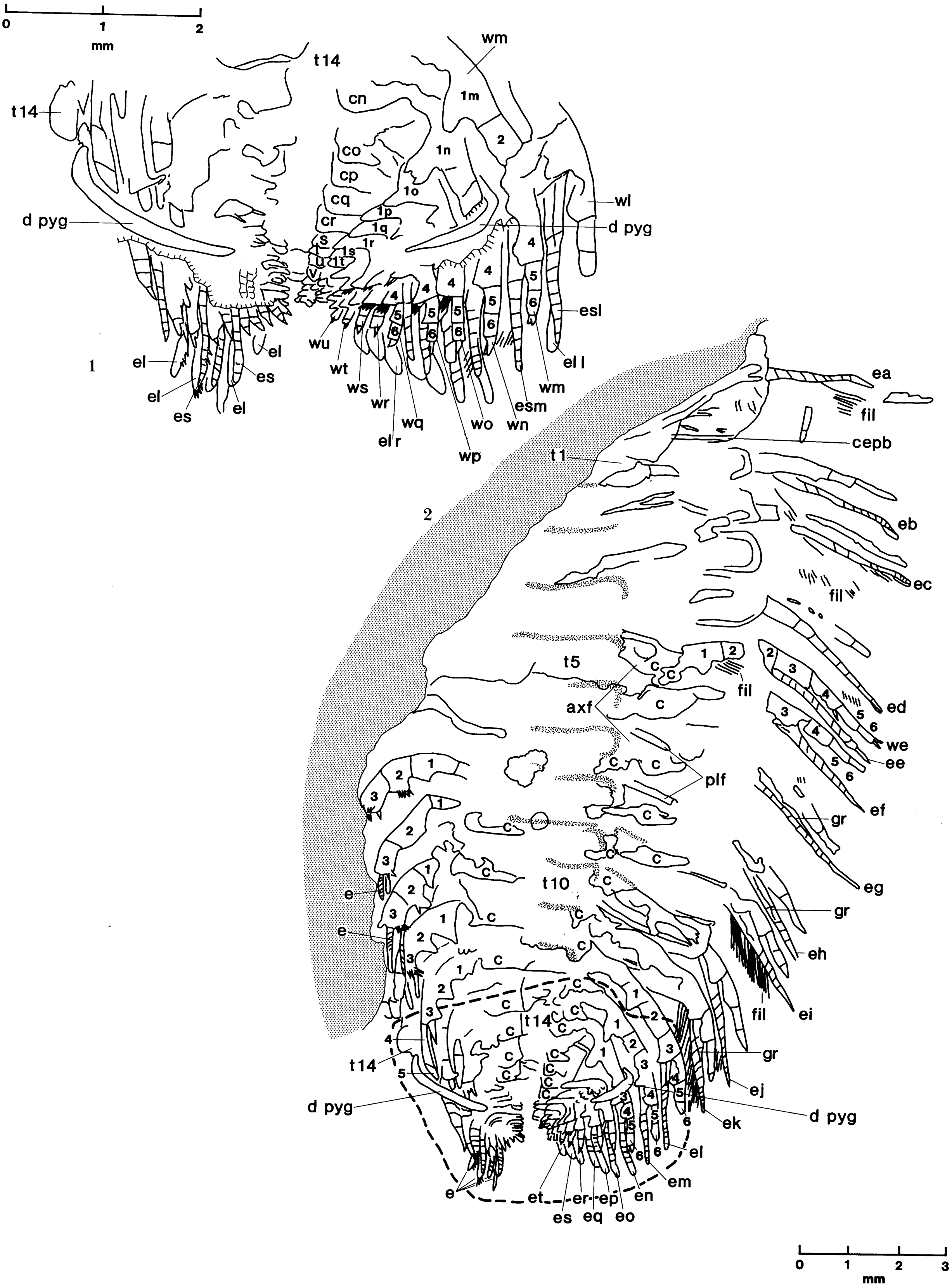
1–3 of the leg branch were progressively deeper, successively posteriorly on thorax and pygidium, and appear also on podomere 4 adjacent to the pygidium.

Exites are visible on all the limbs preserved on the left side, appearing from beneath (that is, originally on the posterior side of) podomere 3 (rarely 2) of the leg branch and curving out behind it. The branch is crossed by oblique, evenly spaced grooves, and in some there is a longitudinal groove or change in level. A spatulate terminal lobe is best-preserved and relatively larger on the exites behind the pygidium; these branches extend well beyond the tiny posterior leg branches l to s, in contrast to the mid-region of the thorax, where leg branch and exite are similar in length. Behind the pygidium, on each side, the shaft of the exite is subdivided, slightly outward-curved, and may be seen to taper and terminate along one side of the terminal lobe. The lobes on the right side have fine marginal setae. Filaments have been revealed in a fragmentary manner, directed obliquely outward or backward behind the exite shaft, and lying at the level of the dorsal side of the branch (that is, farthest from the observer). The proximal portion of the exite is aligned with, and lies beneath (that is, posterior to), podomeres 1 and 2 of the leg branch; filaments are preserved adjacent to these podomeres in branch e, showing that the exite was attached either at the very base of the leg branch or more probably to the distal portion of the coxa, on the posterior side. The left limbs in figure 1 are lettered in series and from e onwards in the series a relation between peripheral limb branches and coxae may be traced. Limb e and its coxa lie largely below the fifth thoracic segment, the dorsal margin of limb and coxa below segment four; limb n and coxa have a similar relation to the first segment of the pygidium and last of the thorax. If limb n was that of the 14th thoracic segment, the enlarged drawing (figure 1) suggests that the pygidium bore at least eight, and possibly as many as 12 pairs of limbs that diminished markedly and progressively in size backward. In front of limb e the relation between branches and coxa is not clear, and limb a may have belonged to the first thoracic segment, or one pair of branches may not be preserved.

(*b*) *U.S.N.M.* 400933

Figure 5, plate 2; figure 7

The first 16 pairs of limbs in the series are preserved on the left and right sides, and also portions of two additional pairs. Coxae and leg branches are prominent, the exites and filaments becoming so posteriorly. Part of the right antenna is preserved anteriorly, but the outline and position of the cephalic exoskeleton is not revealed, and the axial region of only the first five thoracic segments is discernible. The appendage series can be seen, therefore, only in relation to these segments; coxae of the third pair of limbs lie below thoracic segment 1. Coxae are irregularly elongate: oval in outline, some ridged, those of limbs 1–8 directed outward and forward, the inner ends separated by a narrow gap. Behind limb 8 the coxae are more outwardly directed, approximately transverse in limbs 12 and 13. Leg branches are visible along the entire series, flexed proximally at angles between 90° and 180°, the anterior side facing ventrally because of rotation backward of the coxa at the junction with the body. Leg branches have a maximum of six podomeres, 1 and 2 of limb 9 triangular in outline and forming ventrally-directed endites, these endites deeper than long (tr.) in limb 10 onwards; in these posterior branches an endite is developed also on podomere 3. Fragments only of exites are exposed adjacent to leg branches 1–7. An exite (e? in figure 7) immediately behind right leg branch 8 may belong to a concealed next limb in the series, so that the right limb labelled 9 may be in



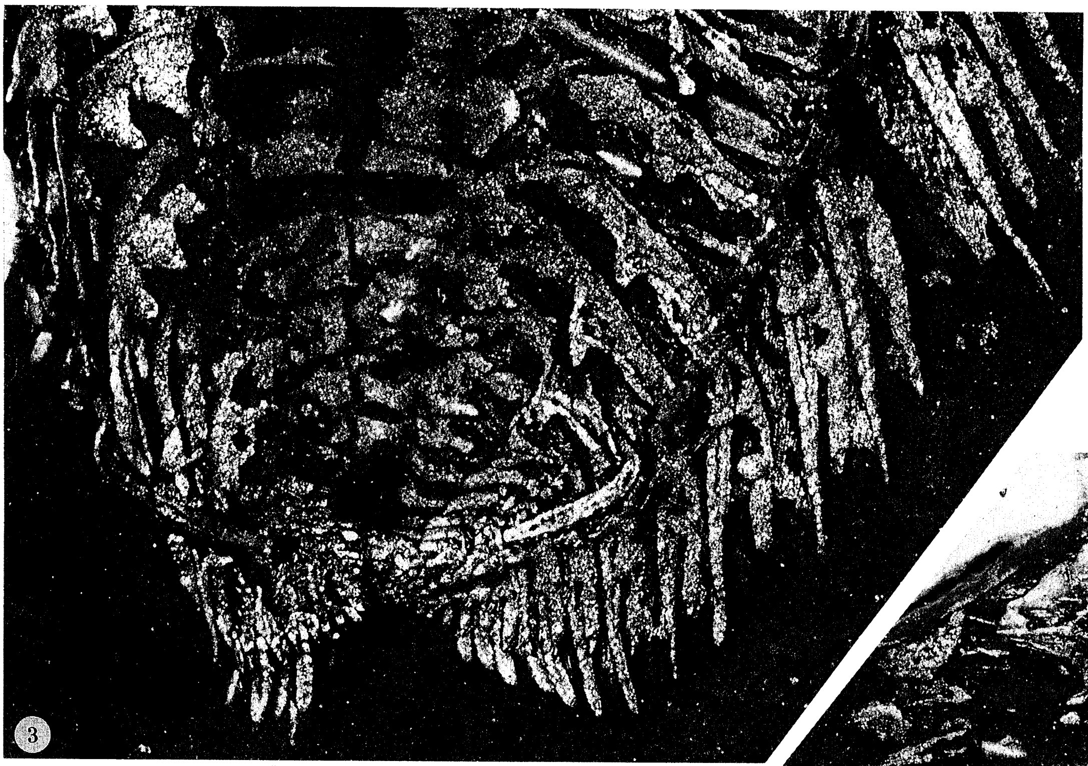
Description of figures 1, 2 and plate 1

Triarthrus eatoni (Hall, 1838)

U.S.N.M. 400932

Figures 1, 2. Explanatory drawings, respectively: posterior portion, shown enclosed by dashed line in figure 2 of entire specimen.

Figures 3, 4. Ventral views, respectively: posterior portion (magn. × 16.5) and entire parallel specimen (magn. × 10.7).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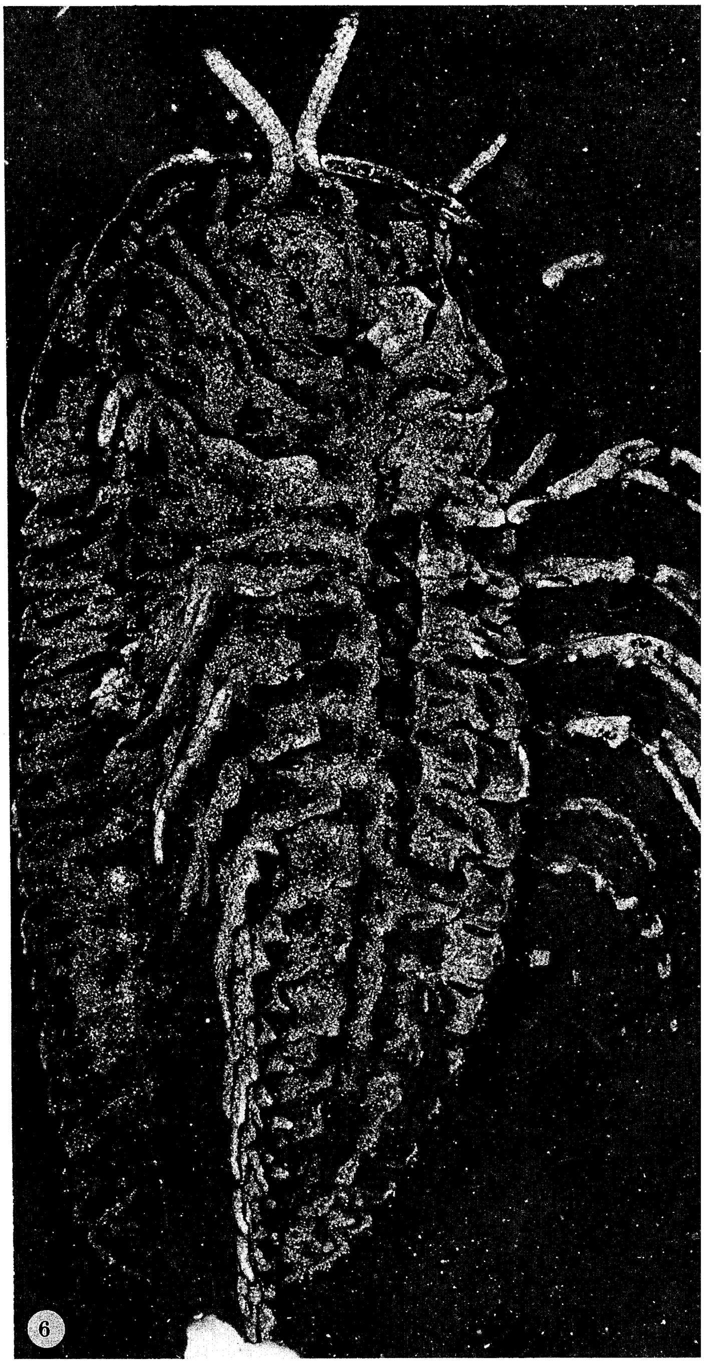
Figures 3, 4. For description see opposite.

(*Facing p.* 10)



FIGURES 5, 6. For description see opposite.

reality limb 10; no other exite on either side appears to be crumpled or displaced, as e? would have to be if it belonged to right limb 8. From limb 9 onwards in the series exite shafts, curved outward and backward, are exposed especially on the left side. All the exites lie on the posterior side (farthest from the observer) of the leg branch. Segmentation is visible in some shafts, and those of left 10–12 show a longitudinal division of the shaft by a groove or step in level, into a broader, unsegmented section on the outer side, and a segmented inner section. These shafts end in a small lobe. The proximal portion of the exite shaft is aligned with the coxa (limbs 1–10), and particularly in limb pair 9, and right 10, the shaft is seen to originate from or very

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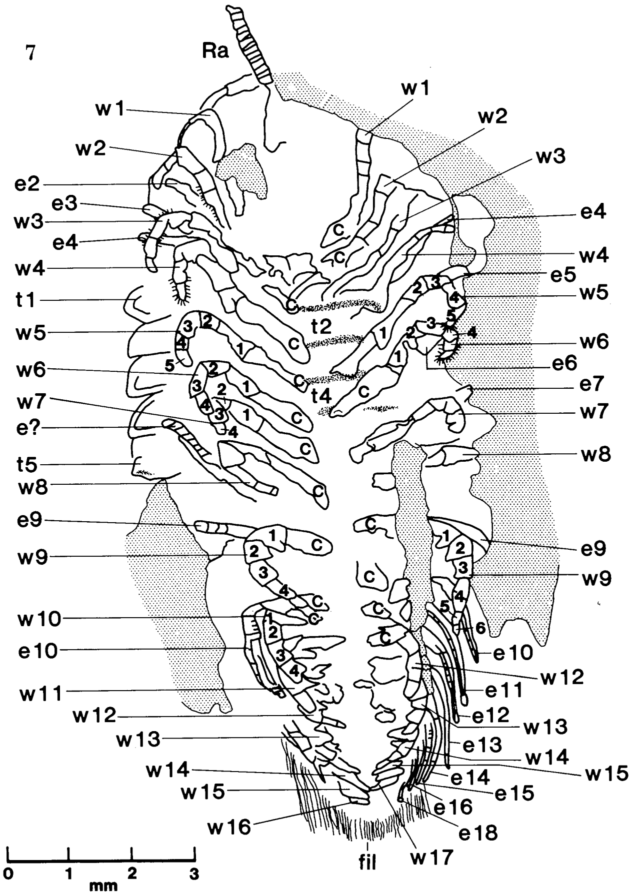

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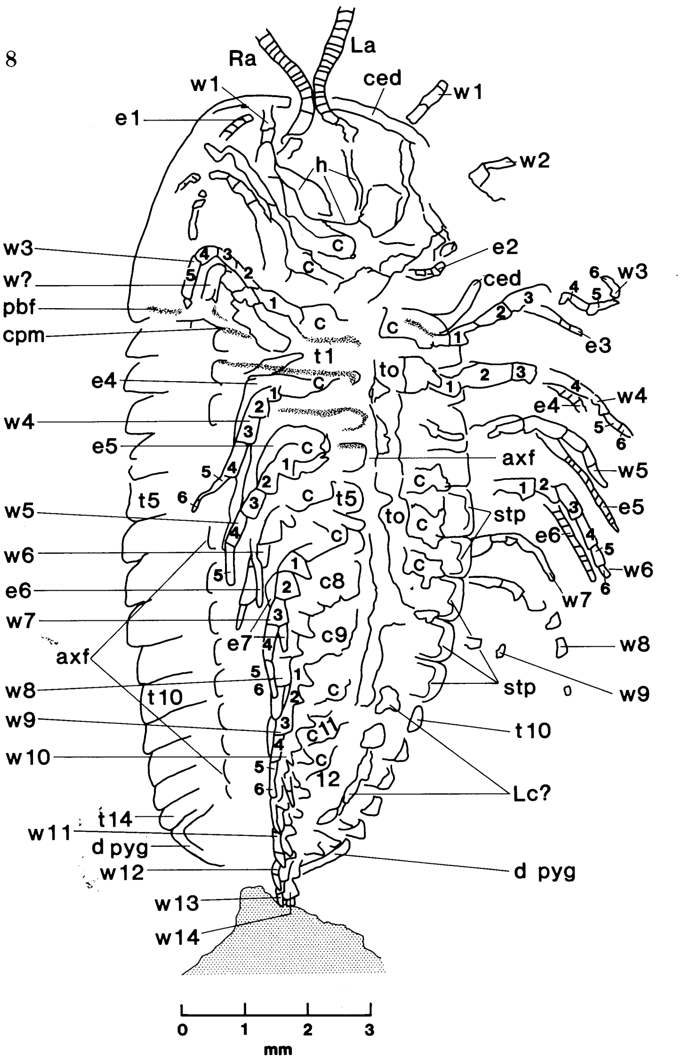

Description of plate 2 and figures 7, 8

Triarthrus eatoni (Hall, 1838)

Figures 5, 7. U.S.N.M. 400933. Respectively: entire parallel specimen (magn. × 14.0), ventral view, and explanatory drawing.

Figures 6, 8. U.S.N.M. 400934. Respectively: entire, slightly oblique specimen (magn. × 12.0), ventral view, and explanatory drawing.

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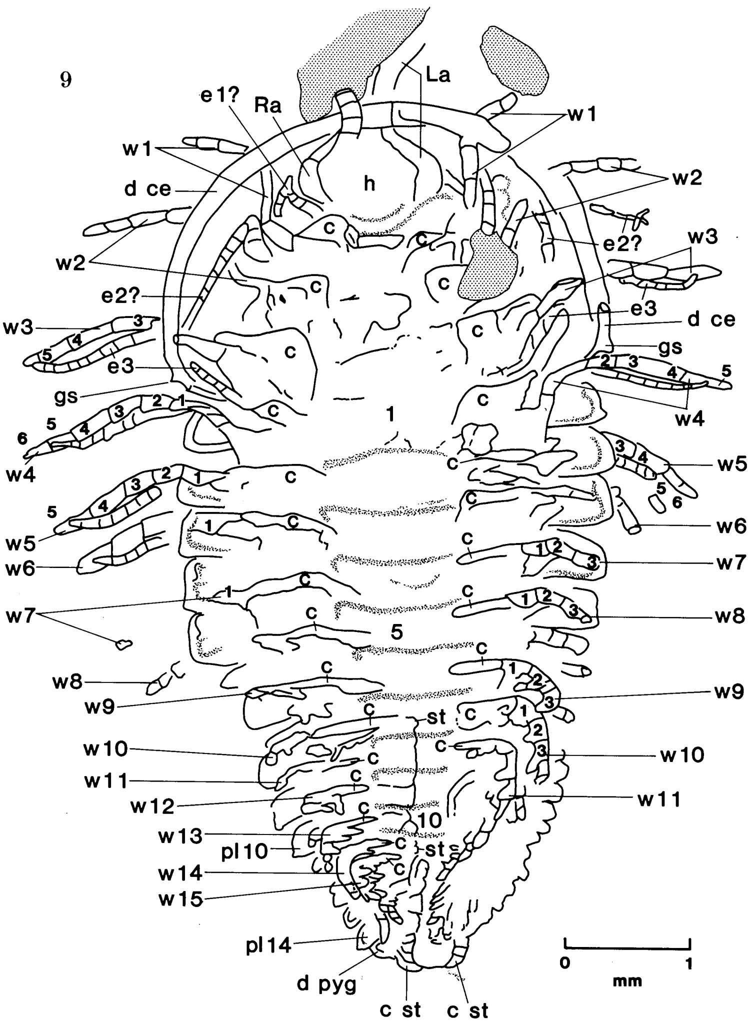

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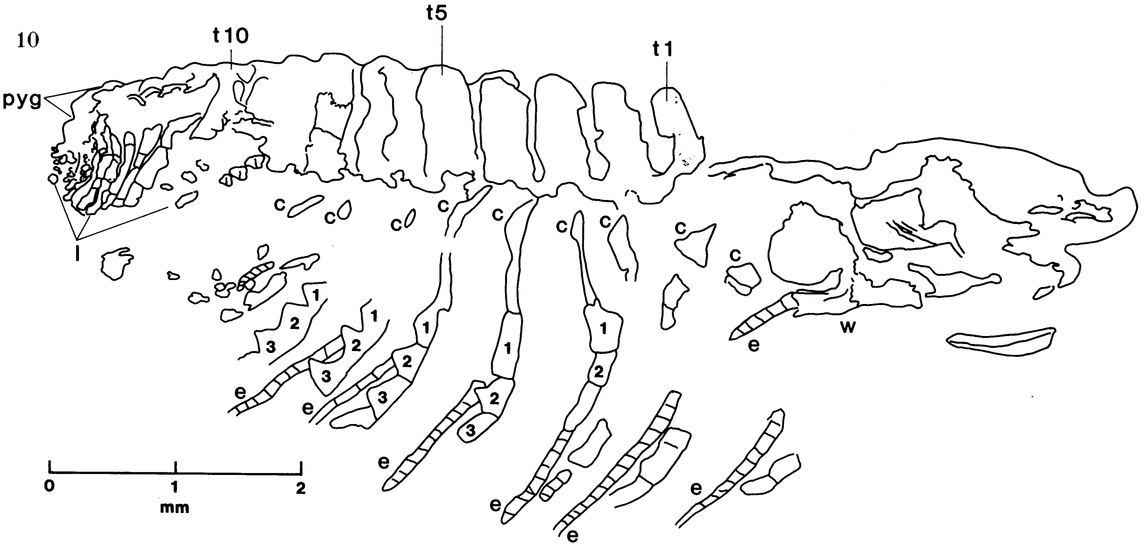
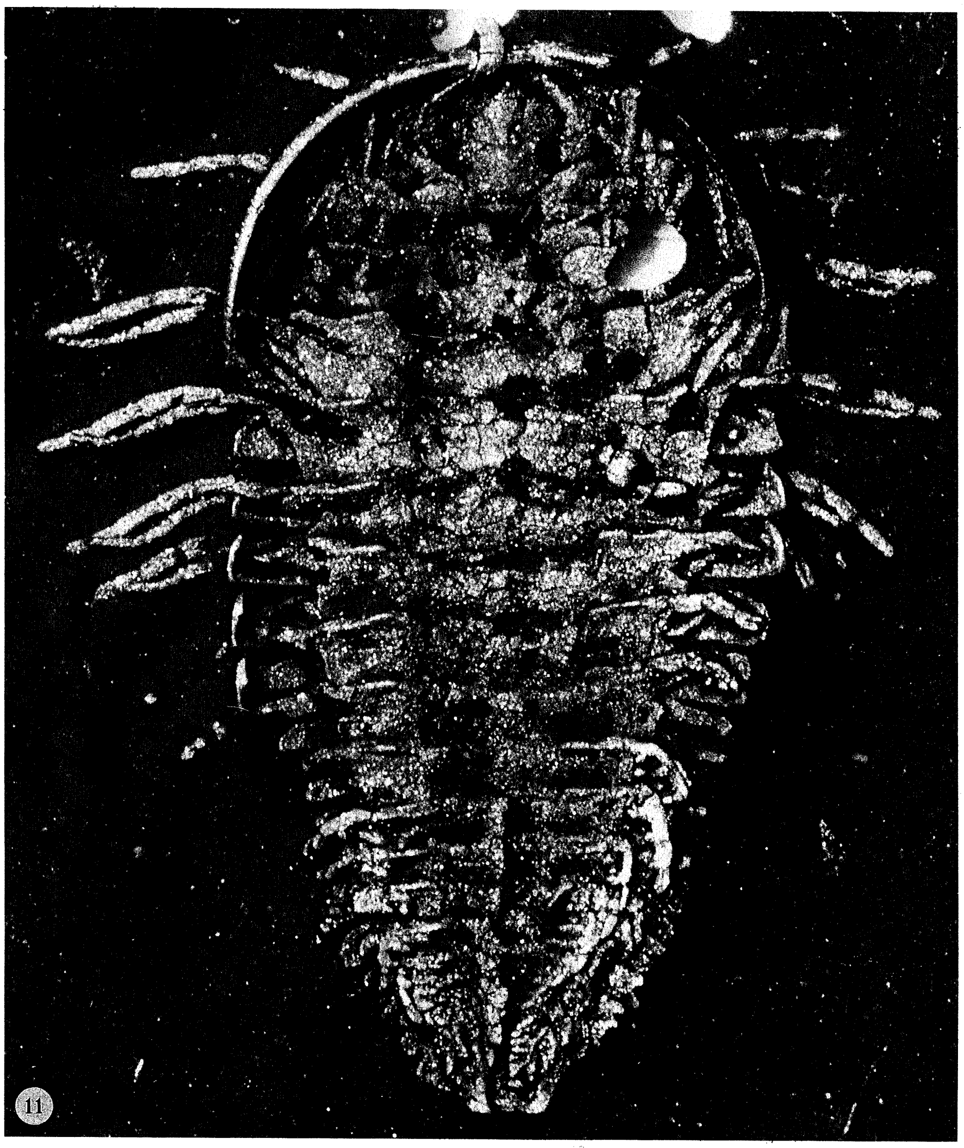


Description of figures 9, 10 and plate 3

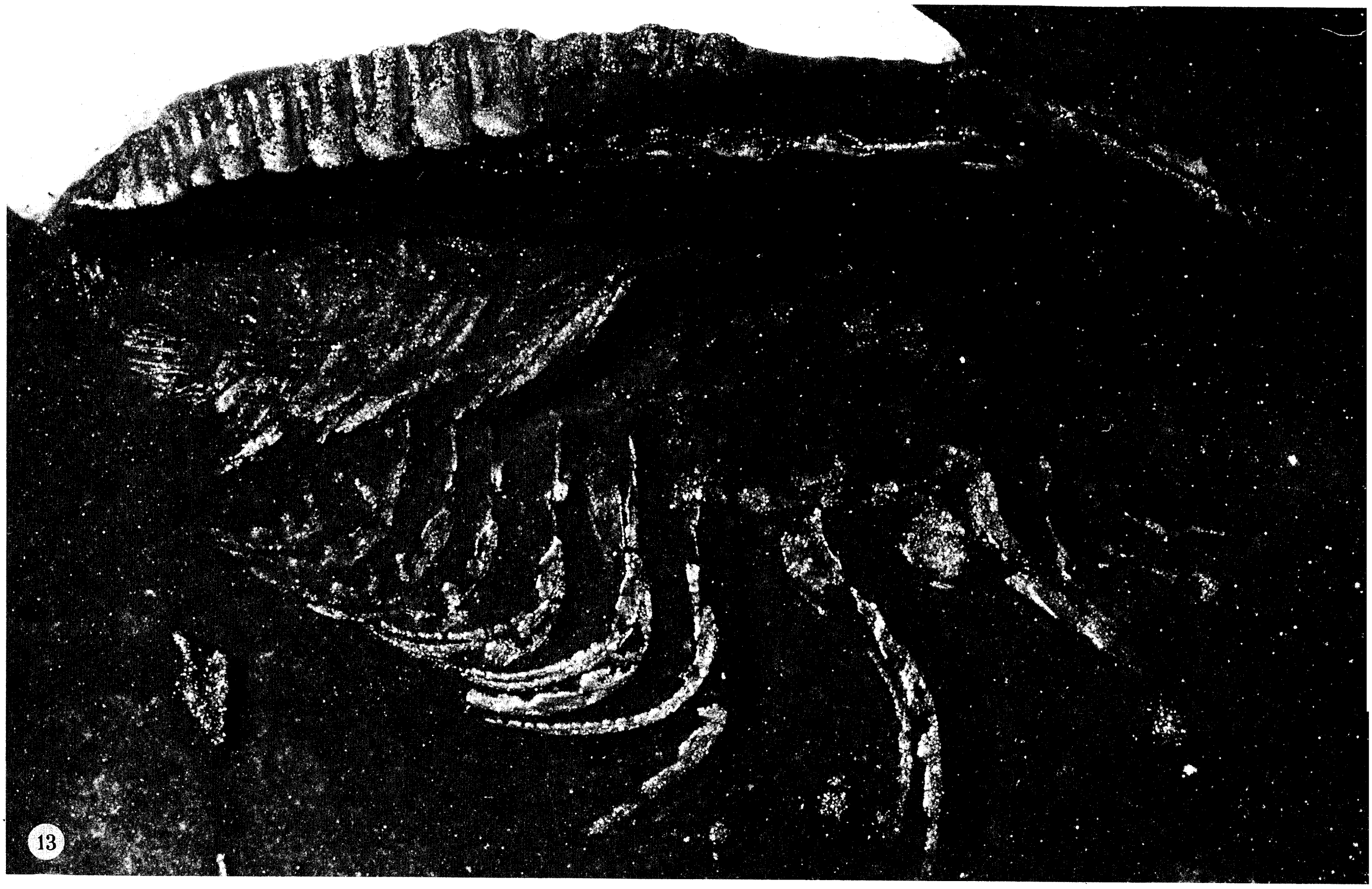
Triarthrus eatoni (Hall, 1838)

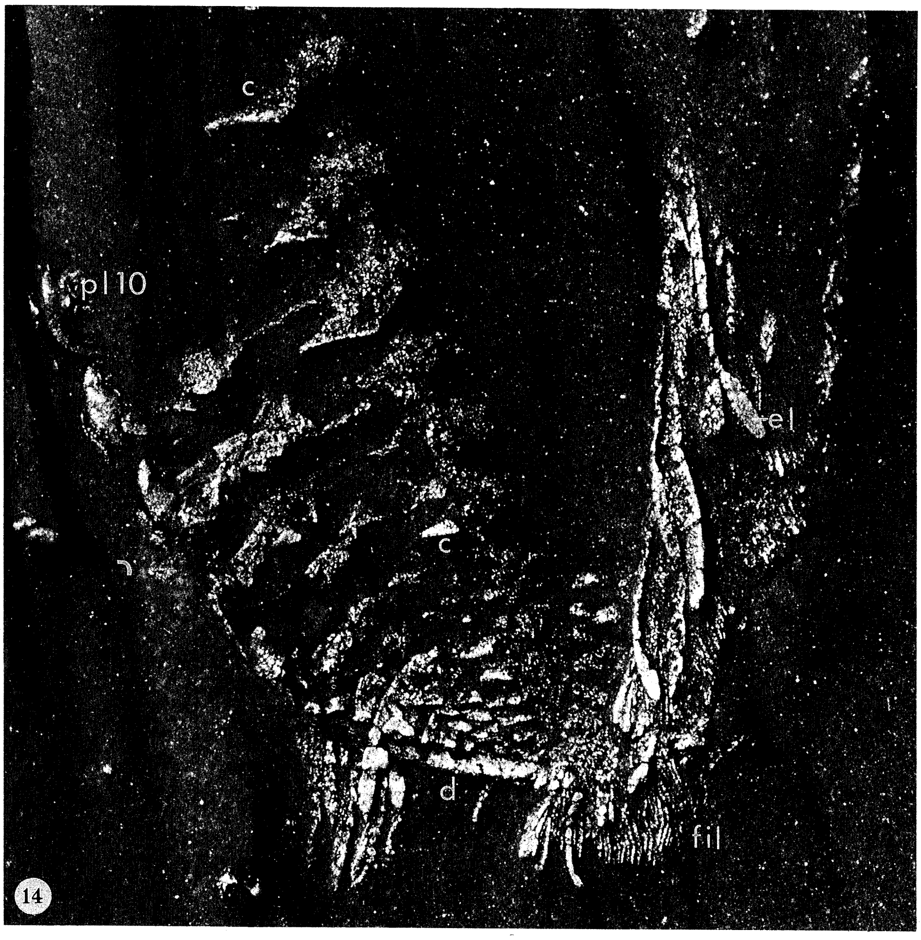
Figures 9, 11. U.S.N.M. 400935. Respectively: explanatory drawing and parallel specimen, ventral view (magn. × 20.0).

Figures 10, 12. U.S.N.M. 400937. Respectively: explanatory drawing and approximately lateral specimen, right lateral view (magn. × 20.0).



FIGURES 11, 12. For description see opposite.





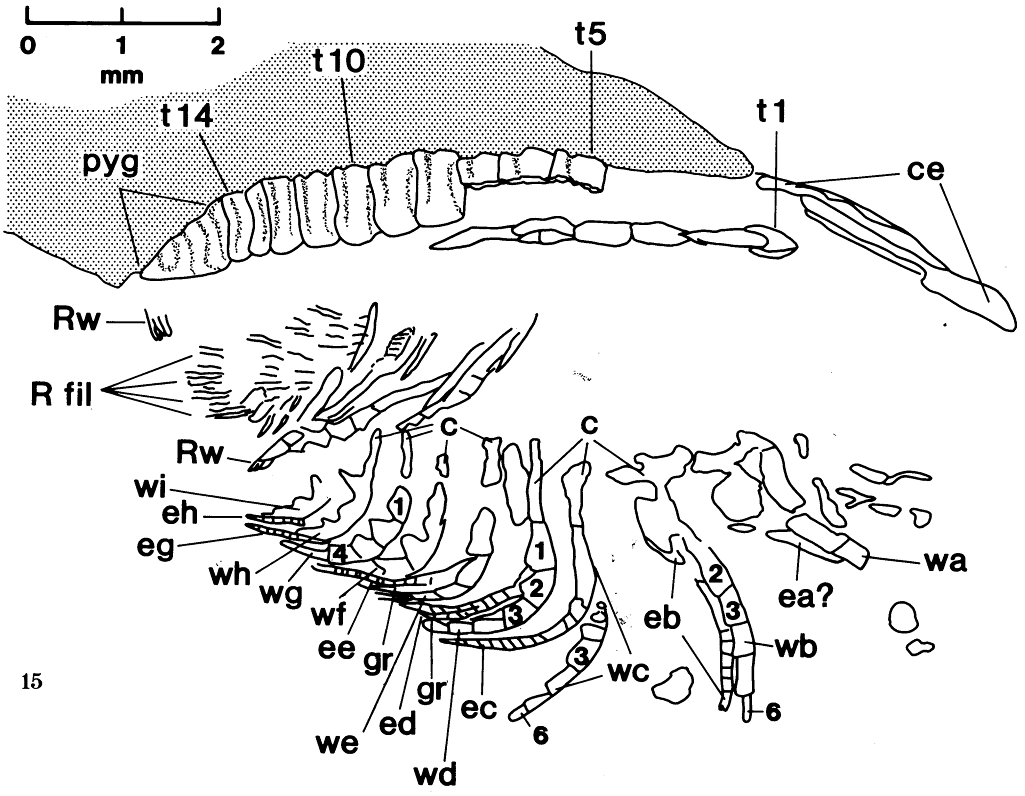
FIGURES 13, 14. For description see opposite.

close to the abaxial portion of the coxa, on the posterior side. Overlapping sheets of filaments are exposed only posteriorly, their position indicating an origin from the dorsal side of the shaft. On the right side the overlap between successive sheets of filaments is seen, and the length of the filaments is considerable, the exact amount uncertain.

(*c*) *U.S.N.M.* 400934

Figure 6, plate 2; figure 8

The exoskeleton (length (sag.) 12.5 mm) is clearly outlined in this specimen, and the tips of left pleurae 5–9 show the projection of the doublure that acts as a stop during enrolment. A series of up to 14 pairs of appendages is exposed in relation to this exoskeleton, displaced to the left so that the gap between the inner ends of the coxae straddles the left axial furrow. The antennae appear to be little, if at all, displaced laterally from their original place of attachment, whereas the hypostome is distorted by leftward displacement and crumpled. The first three pairs of limbs beneath the cephalon are fragmentary, and it is uncertain whether or not the coxae have been rotated forward to show the posterior side; the way right coxa 3 projects



15

DESCRIPTION OF PLATE 4 AND FIGURE 15

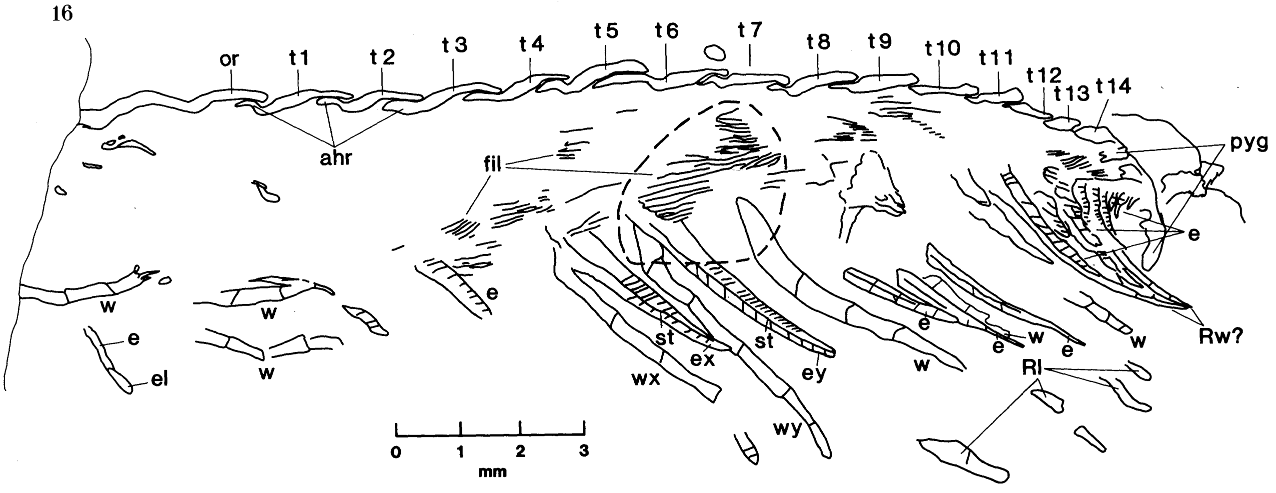
Triarthrus eatoni (Hall, 1838)

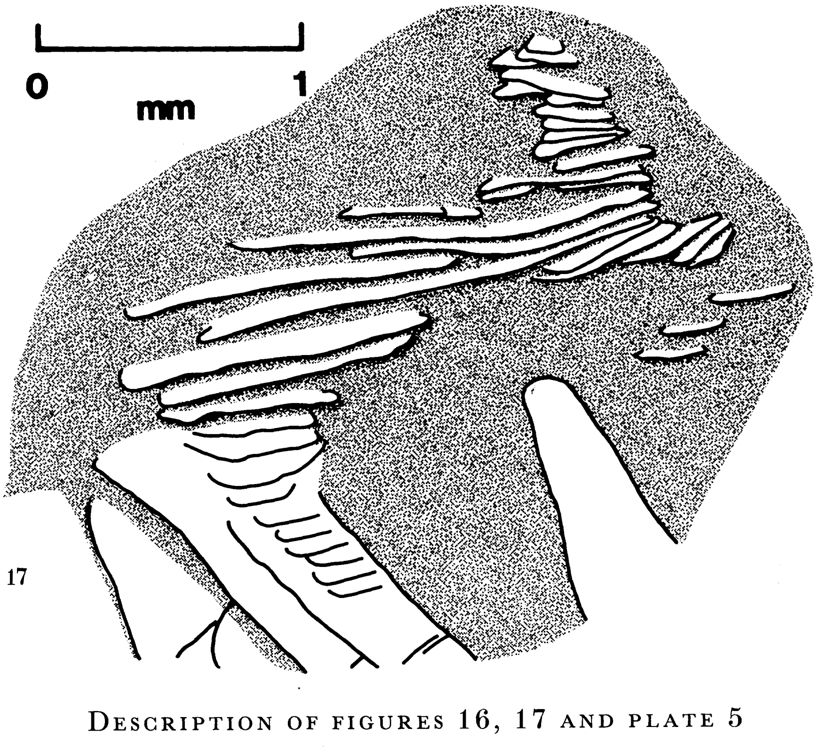
FIGURES 13, 15. U.S.N.M. 400936. Respectively: oblique-lateral specimen, viewed from right side (magn. × 19.5) and explanatory drawing.

FIGURE 14. U.S.N.M. 400945, slightly oblique, incomplete specimen, ventral view of posterior portion of thorax and pygidium (magn. × 14.6).

forward suggests this. Yet distally the leg branches curve backward, implying that the anterior side faces ventrally and that the branch may have been twisted. From the fourth pair of appendages onwards the series appears to have been rotated backward at the coxa–body junction to show the anterior face of the coxa and leg branch. Coxae appear to be directed outward and slightly forward beneath the cephalon, transversely beneath segments 1–4, then

16



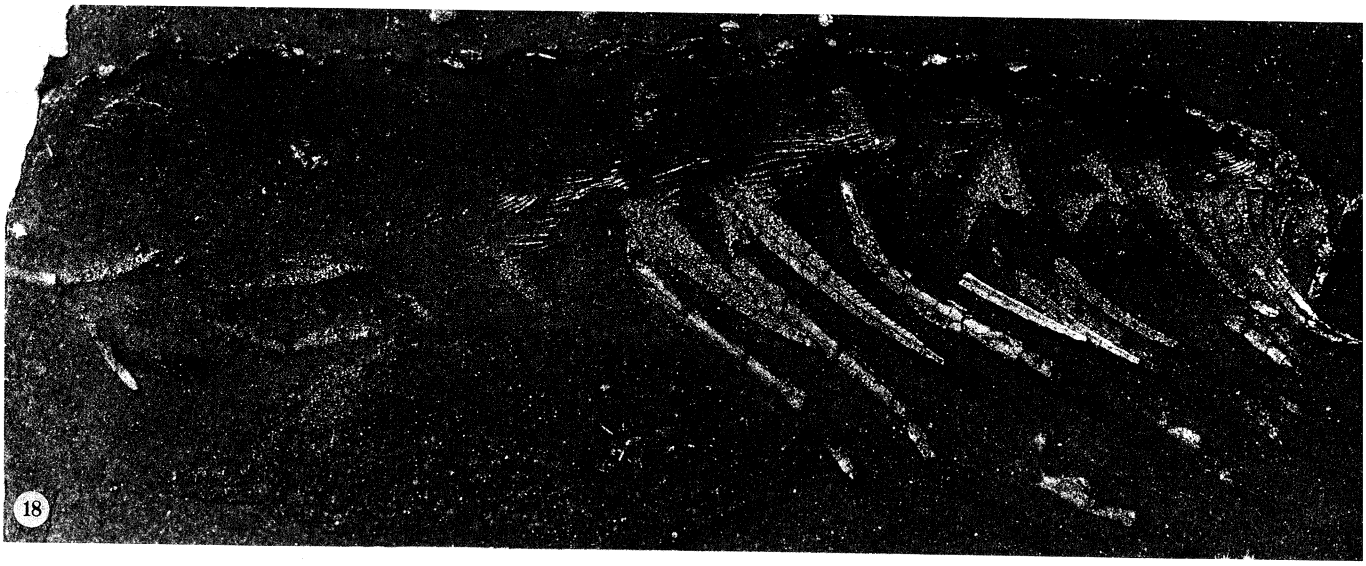


17

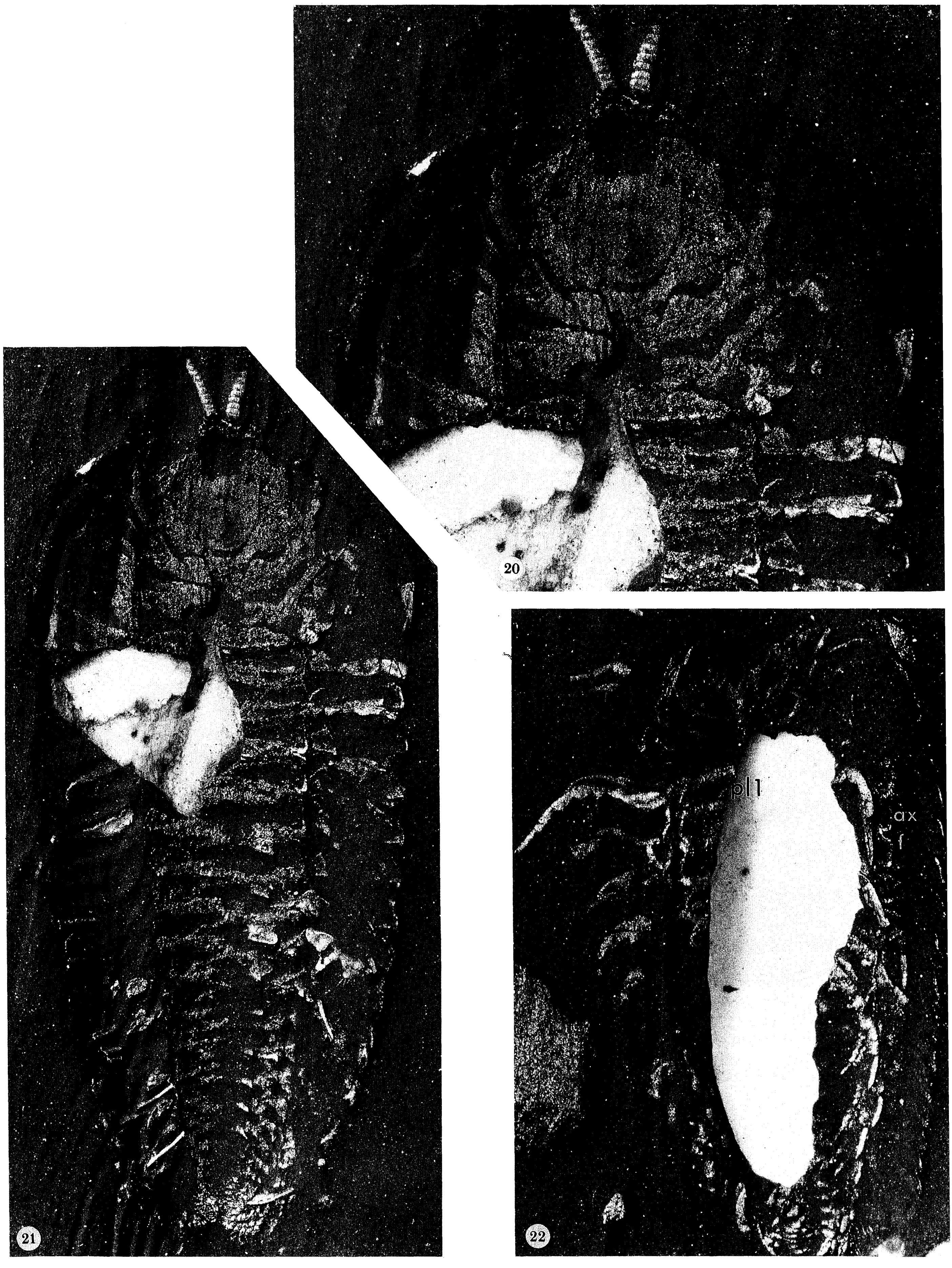
Description of figures 16, 17 and plate 5

Triarthrus eatoni (Hall, 1838)

Figures 16–19. U.S.N.M. 400938. Section through oblique lateral specimen, viewed from left side; respectively: explanatory drawing of entire specimen, drawing of portion enclosed within dashed line in figure 16, entire specimen (magn. × 9.7), posterior portion (magn. × 14.6).



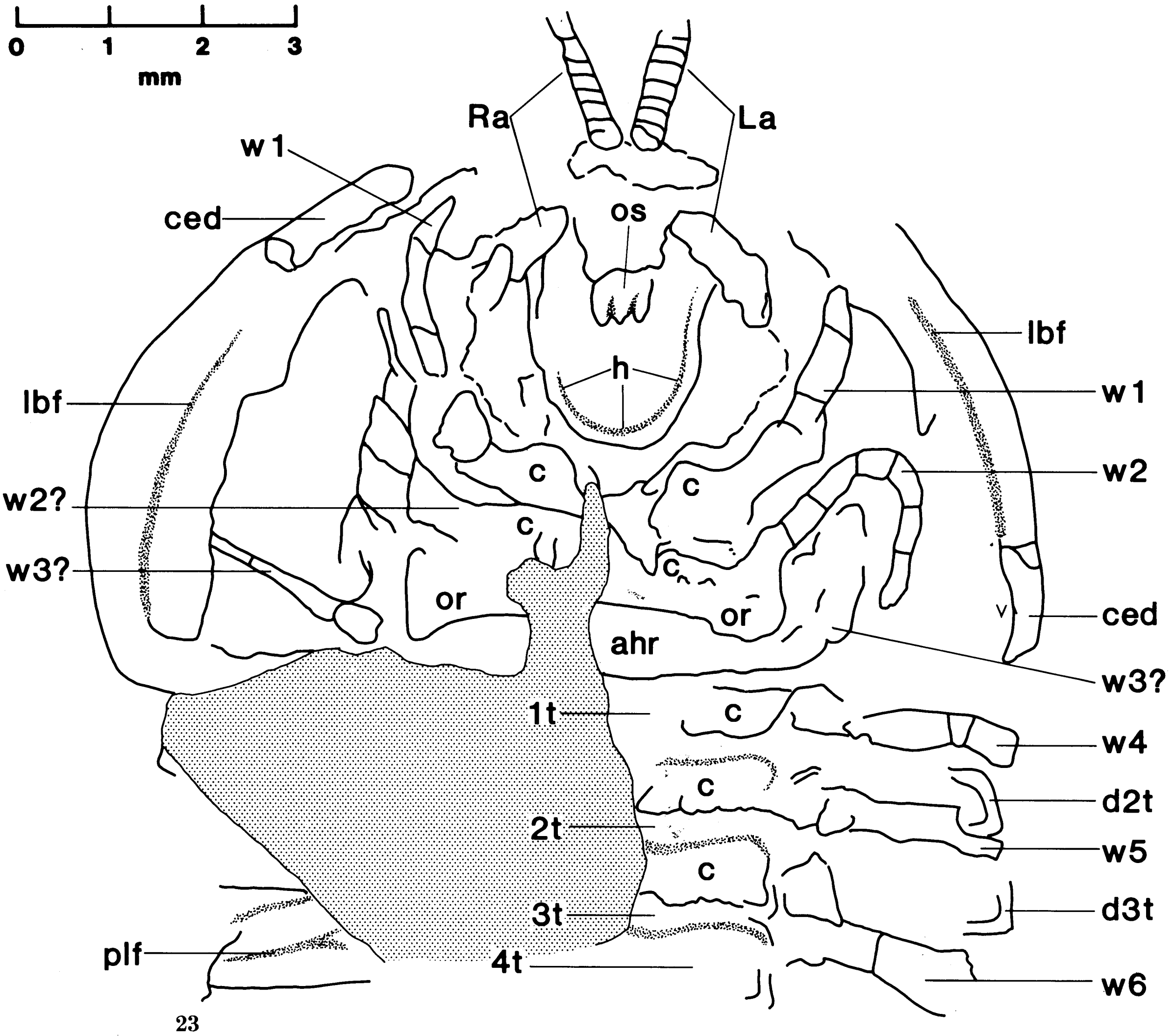
FIGURES 18, 19. For description see opposite.



FIGURES 20–22. For description see opposite.

progressively slightly backward. The directions of the flexed leg branches reflect this arrangement, in right limbs 4–14 the flexure of the leg branch is strong proximally, so that podomeres 2–6 are directed backward, entirely so posteriorly. Triangular endites are present on podomeres 1 and 2 of leg branch 4, on podomere 3 of leg branch 7 and become more prominent backward in the series. In posterior limbs (10 onwards) these endites are as deep or deeper than long (tr.), especially as the limbs diminish in size.

Right limbs 4 and 5 show that the exite arises proximally, apparently from the distal portion of the coxa on the posterior side. Proximally the exites are aligned with the coxa and first one or two leg-branch podomeres, then they curve backward. All lie proximally on the posterodorsal



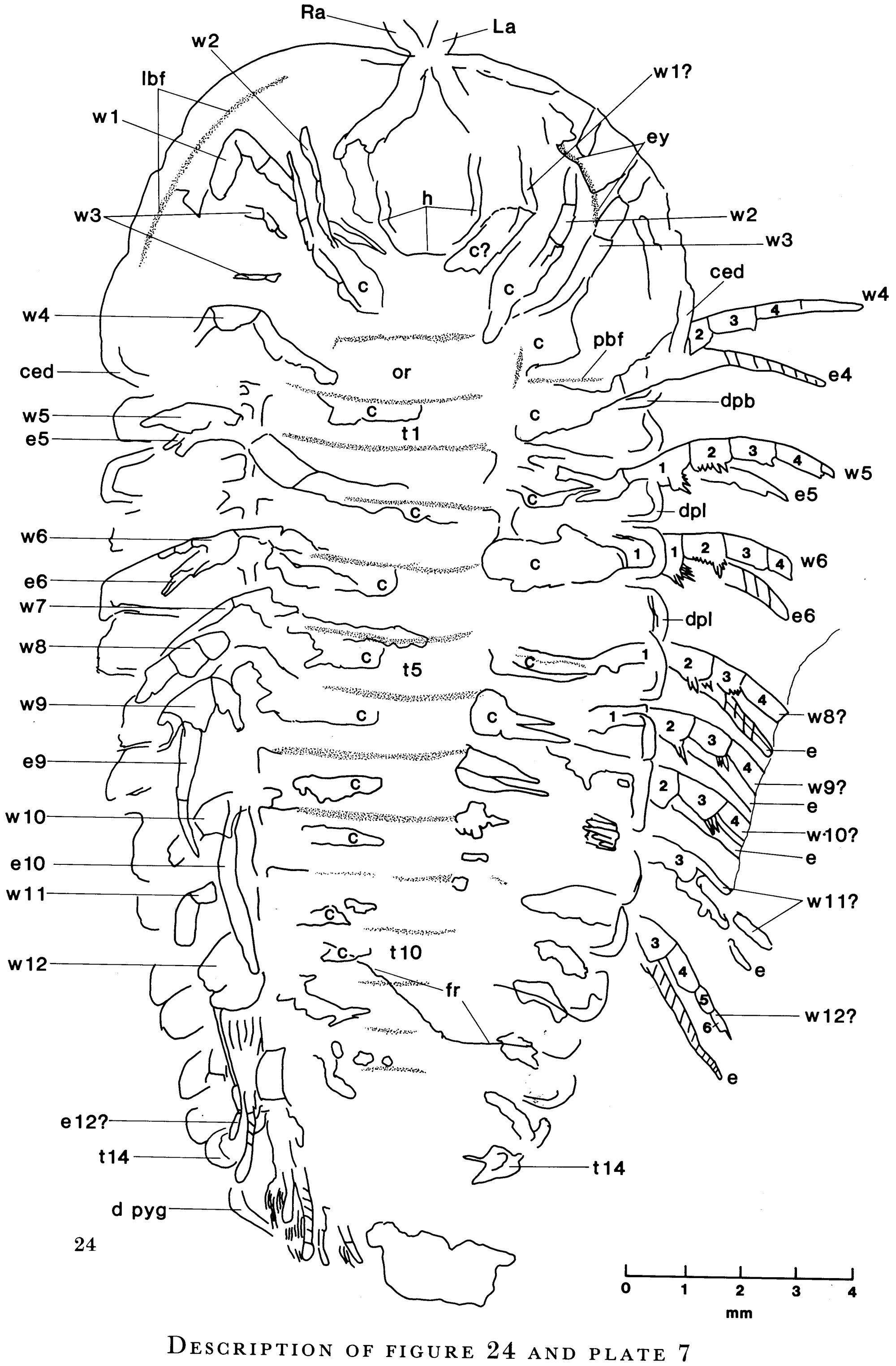
23

Description of plate 6 and figure 23

Triarthrus eatoni (Hall, 1838)

Figures 20, 21, 23. U.S.N.M. 400939. Respectively: parallel specimen, ventral views, anterior portion (magn. × 11.4), entire (magn. × 7.6), drawing of anterior portion.

Figure 22. U.S.N.M. 400946. Slightly oblique specimen, ventral view (magn. × 14.3). See figure 34, plate 10.



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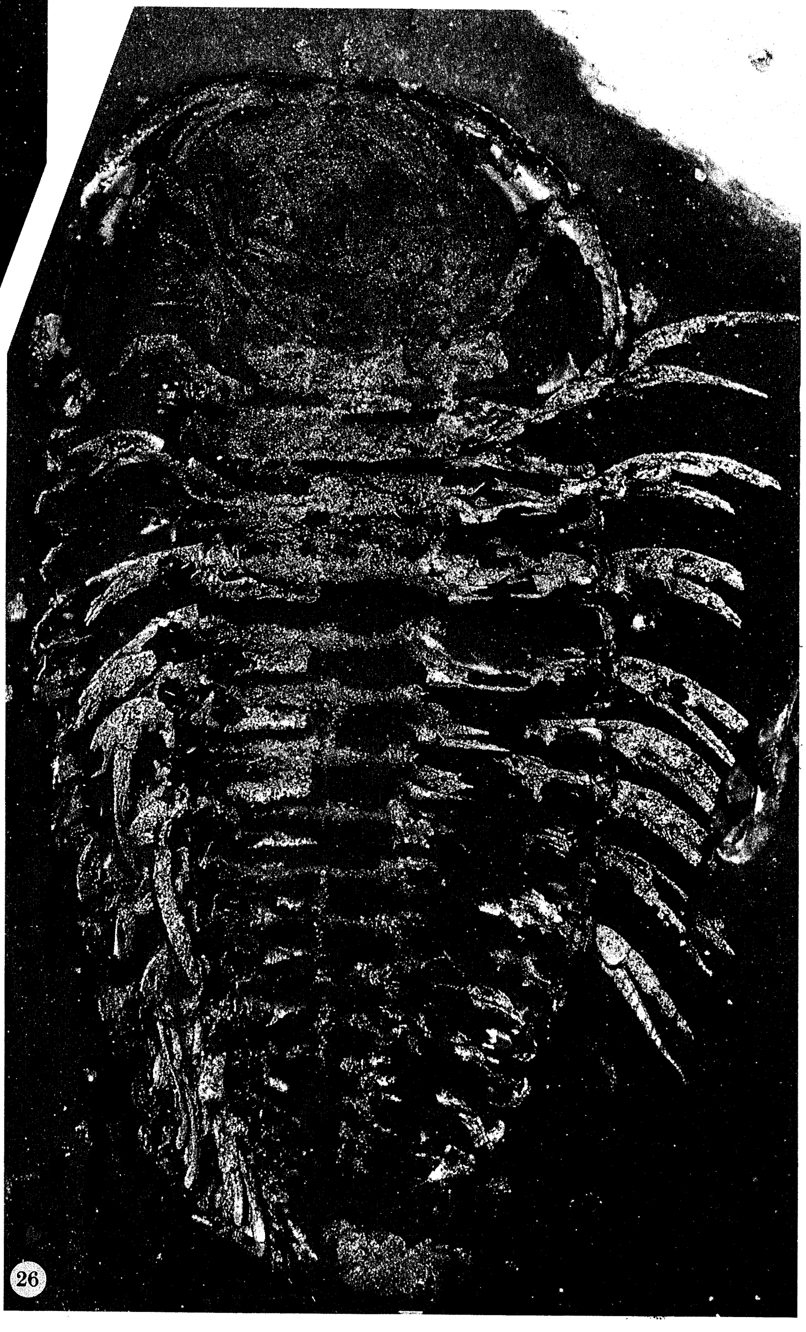
Description of figure 24 and plate 7

Triarthrus eatoni (Hall, 1838)

Figures 24–26. U.S.N.M. 400940. Respectively: parallel specimen, explanatory drawing, ventral view of right anterior portion (magn. × 9.5), ventral view of entire specimen (magn. × 7.6).

25



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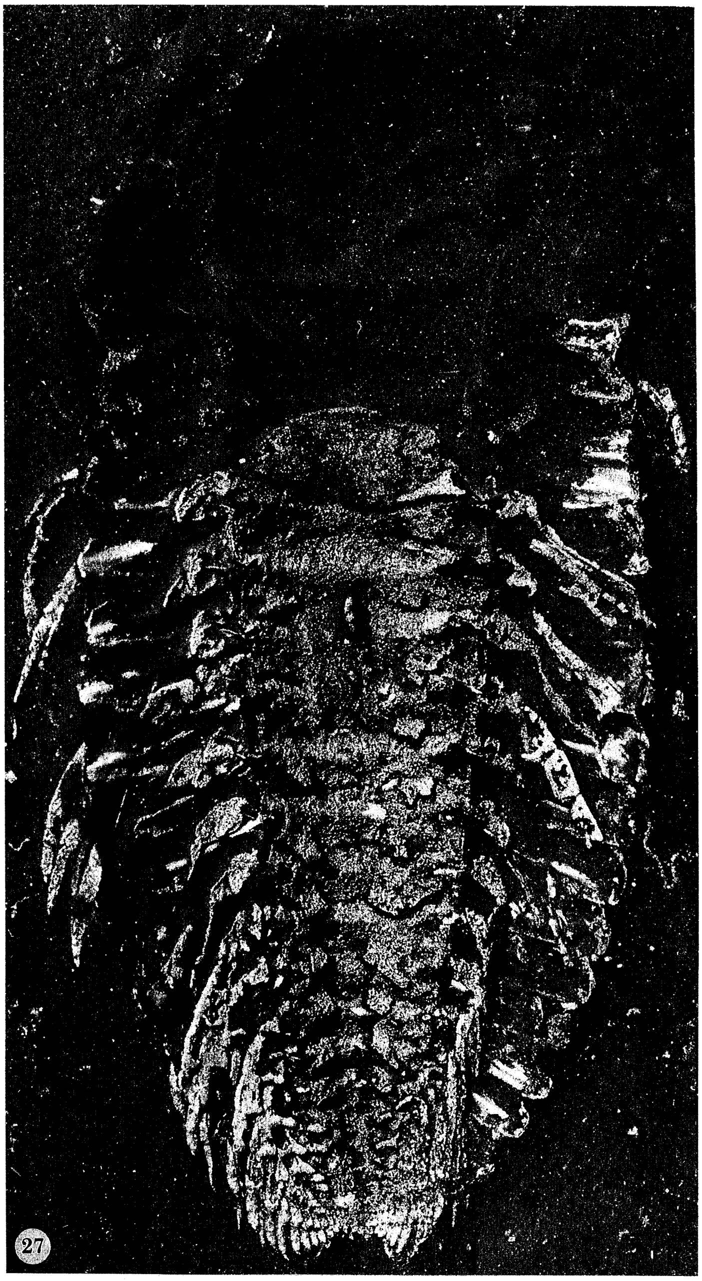
FIGURES 25, 26. For description see opposite.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28


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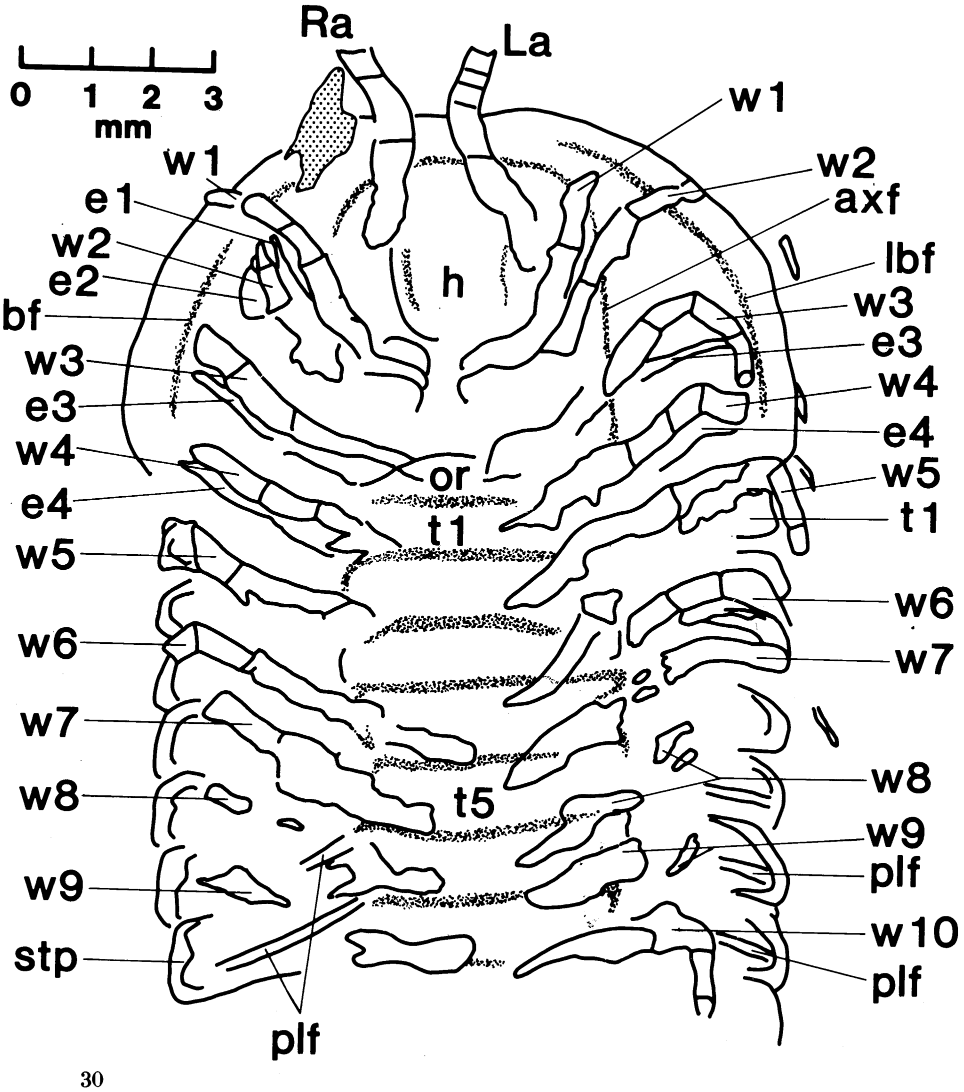
FIGURES 27–29. For description see opposite.

side of the leg branch, distally they attain the same level as the leg branch or may even lie on the anterior face of it. Right limb 6, for example, has the distal portion of the exite lying on the leg branch. Oblique segmentation is seen in left exites 5 and 6, but no longitudinal division.

On the notation adopted here coxae of limb 3 lie on the occipital ring, so that three pairs of albeit fragmentary appendages lie beneath the cephalon. The coxae of the anterior pair lie close behind the hypostome. The notation of appendages of the right side, behind 3, is open to question, because the fragments lying immediately behind the coxa and leg branch 3 (w?



30

DESCRIPTION OF PLATE 8 AND FIGURE 30

Triarthrus eatoni (Hall, 1838)

FIGURE 27. U.S.N.M. 400942. Parallel specimen, ventral view (magn. × 7.6). See figure 32, plate 9.

FIGURES 28, 30. U.S.N.M. 400944. Parallel specimen, respectively: ventral view (magn. × 7.6) and drawing of anterior portion. See figure 33, plate 9.

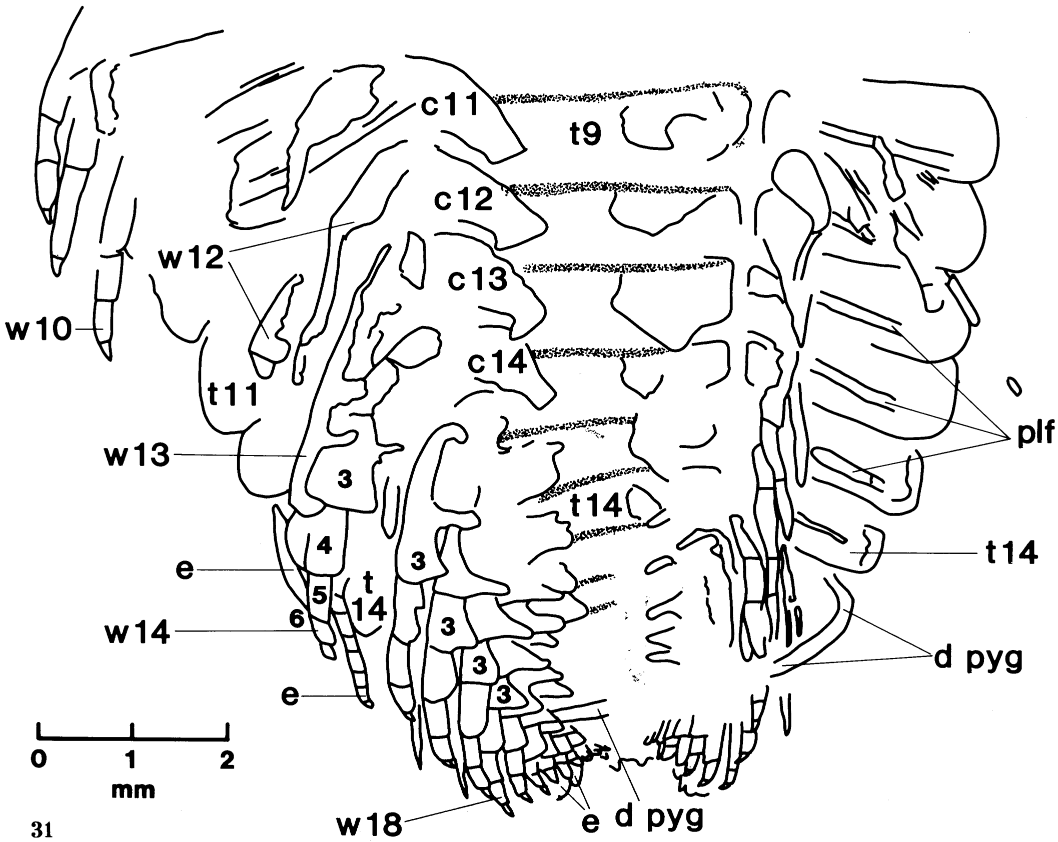
FIGURE 29. U.S.N.M. 400947. Parallel specimen, ventral view of left anterior portion (magn. × 14.3).

in figure 8) may represent a partly hidden limb. A feature of the thorax in this specimen is a trough ('to' in figure 8) running longitudinally beside the left coxae, immediately outside the axial furrow. Whether this trough is an artefact of preparation, or results from collapse of the alimentary canal (and underlying ventral integument) in the early stages of preservation is uncertain. The significance of areas of pyrite behind the trough and below the pleural region is uncertain; some may perhaps be the remains of coxae of the left limbs (Lc? in figure 8).

(*d*) *U.S.N.M.* 400935

Figure 9; figure 11, plate 3

This specimen, approximately 7 mm in length (sag.), has 14 thoracic segments and is an holaspis. The length is at the low end of the range of size of late meraspides with 14 thoracic segments of *Triarthrus beckii* (a closely similar species, Whittington 1957*a*, *b*, figure 20; where the species is referred to *T. eatoni*). The thorax narrows (tr.) rapidly behind segment 5, and a



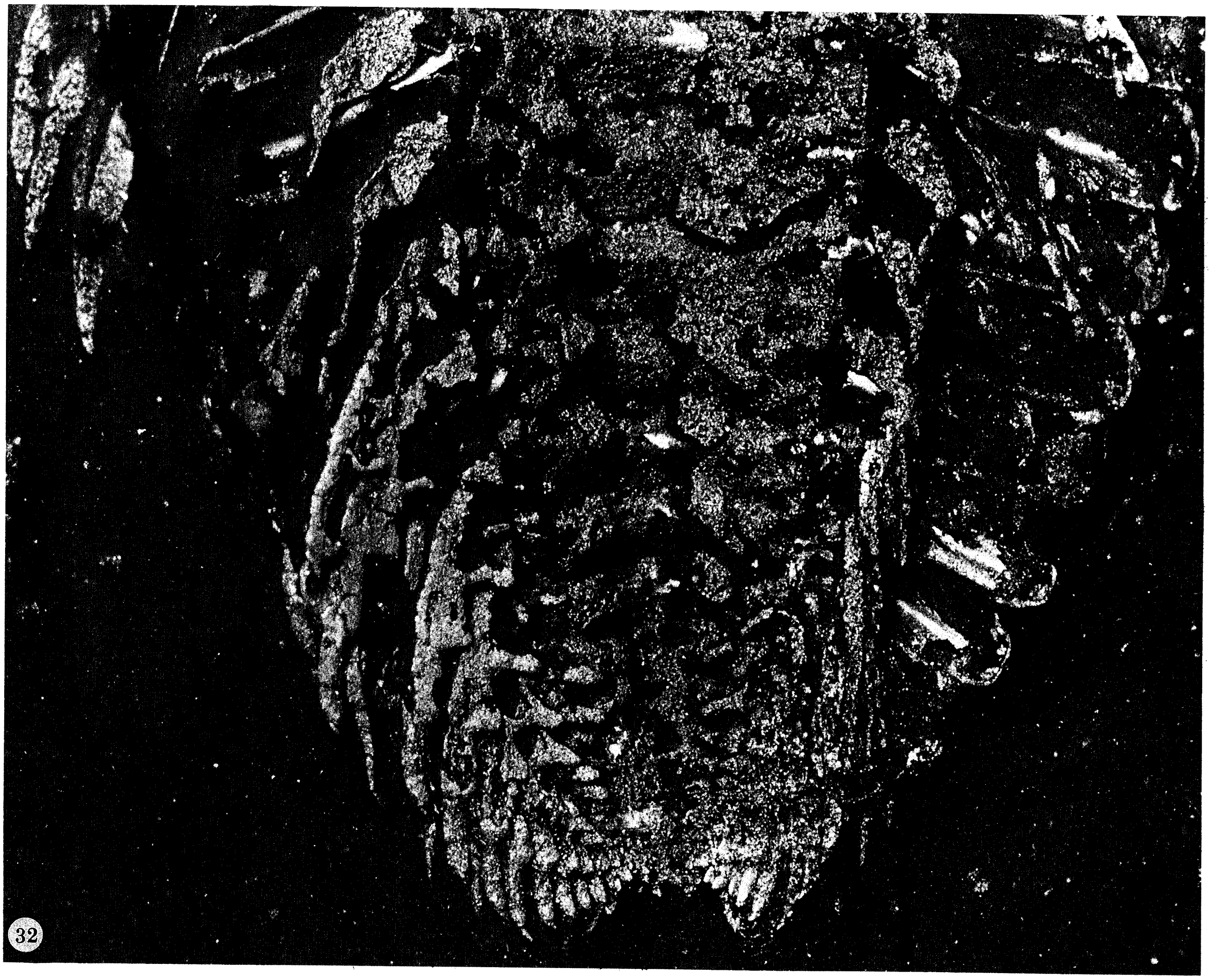
31

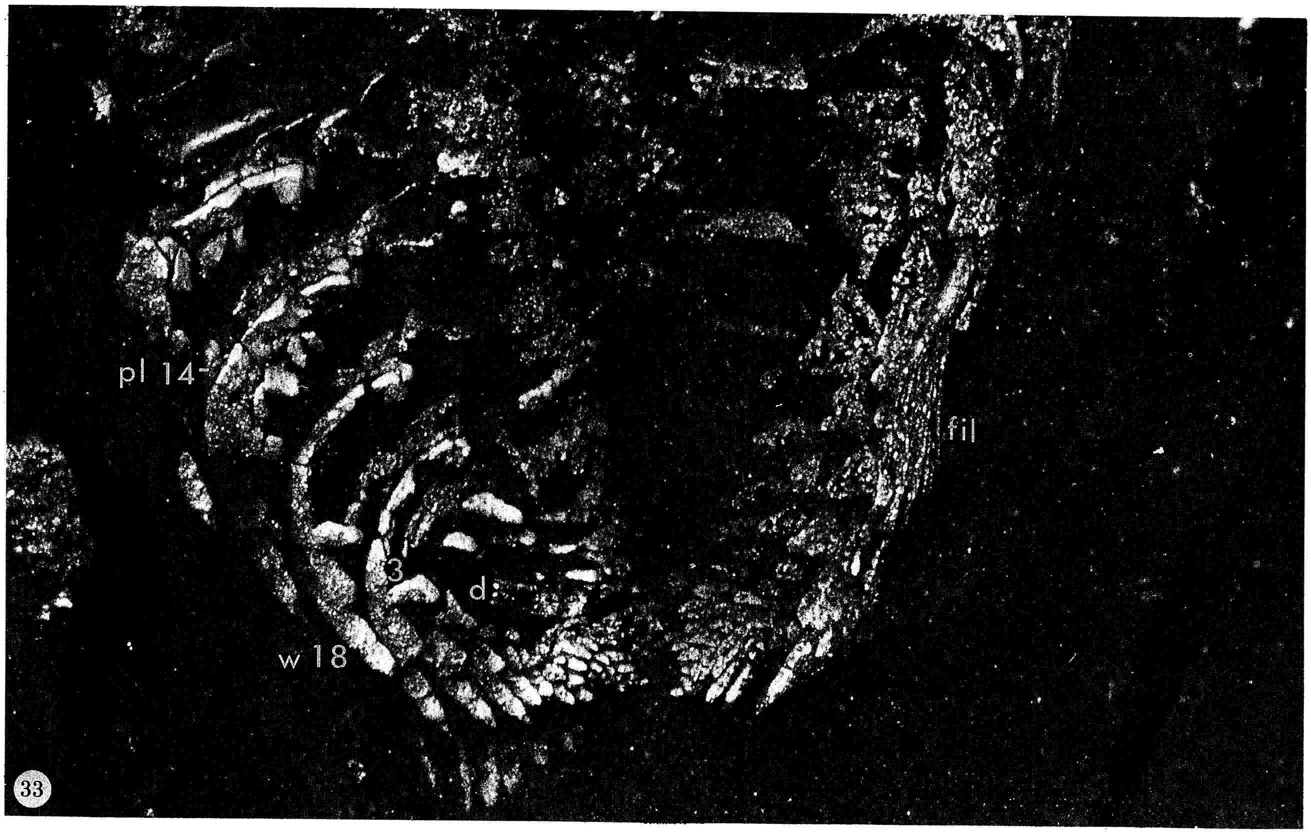
DESCRIPTION OF FIGURE 31 AND PLATE 9

Triarthrus eatoni (Hall, 1838)

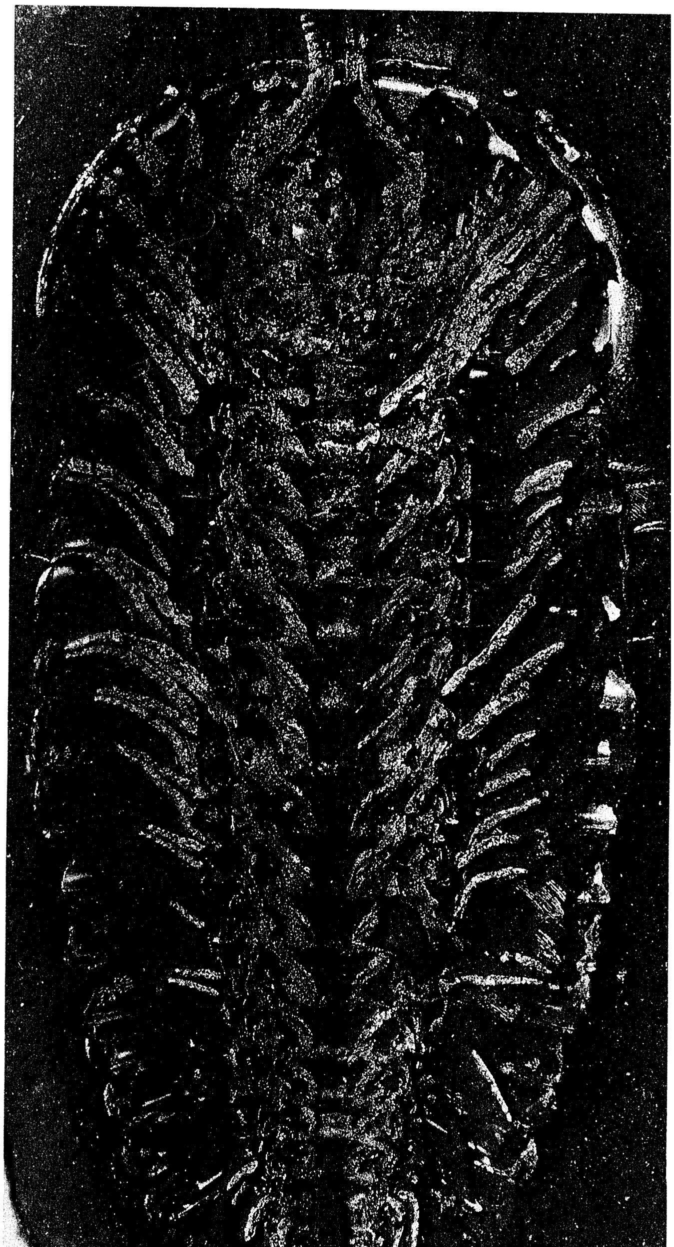
FIGURES 31, 32. U.S.N.M. 400942. Respectively: drawing and ventral view (magn. × 17.0) of posterior portion of specimen (see figure 27, plate 8).

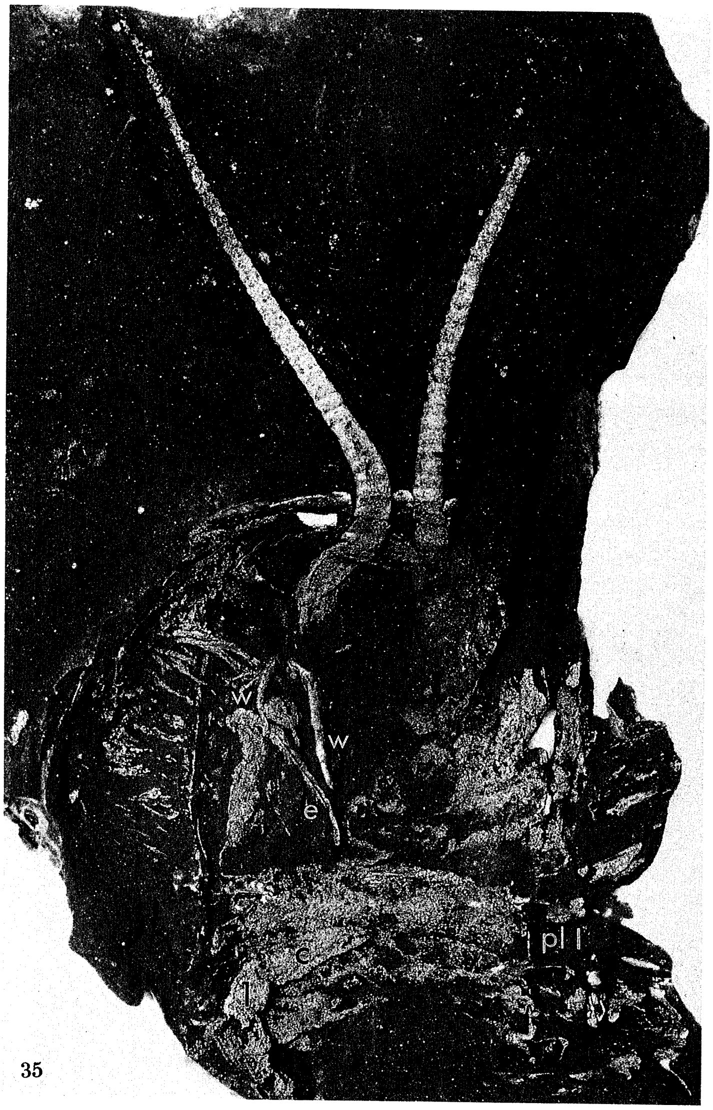
FIGURE 33. U.S.N.M. 400944. Ventral view (magn. × 20) of posterior portion of specimen (see figure 28, plate 8).





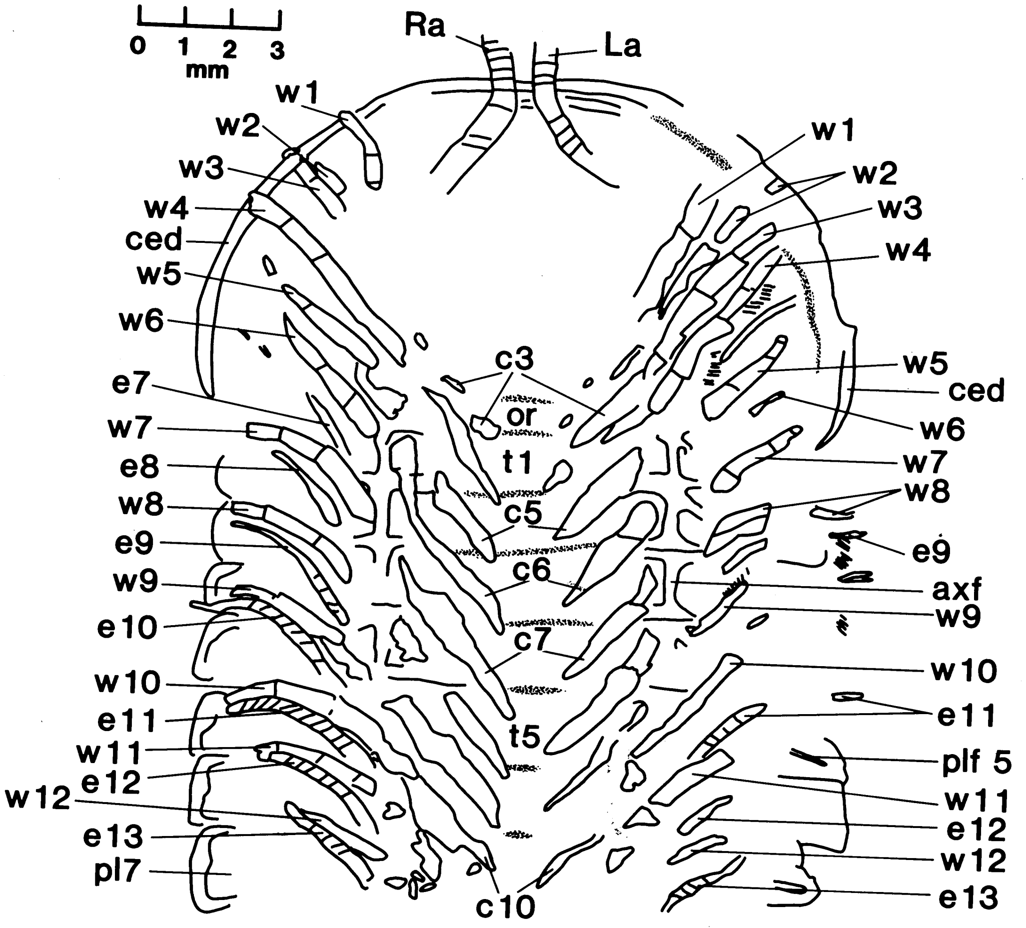
FIGURES 32, 33. For description see opposite.





FIGURES 34–36. For description see opposite.

portion of the doublure of the tiny pygidium is visible. The narrow, cylindrical doublure of the cephalon is complete on the right side, and a small genal spine is present, presumably the relic of a larger librigenal spine of earlier growth stages. The slight displacement of the cephalic doublure behind the right genal spine may be where the doublure was crossed by the posterior branch of the facial suture. Posterolateral cephalic doublure and genal spine are preserved on the left side. The doublure and adjacent lateral portions of some of the thoracic pleurae are exposed, those of segments 1–5 on the right side best preserved. At about its midlength (exs.), the doublure at the pleural tip shows a slight projection, being depressed behind it and raised in front of it. This ridge forms the enrolment stop as each pleura slides beneath the one in front during enrolment.



37

Description of plate 10 and figure 37

Triarthrus eatoni (*Hall*, 1838)

Figure 34. U.S.N.M. 400946. Ventral view (magn. × 23.8) of right anterior portion of original of figure 22, plate 6.

Figure 35. U.S.N.M. 400941. Ventral view (magn. × 6.2) of incomplete cephalon and anterior three thoracic segments.

Figures 36, 37. U.S.N.M. 400943. Respectively: ventral view (magn. × 5.7) of entire parallel specimen, drawing of cephalon and anterior seven thoracic segments.

A series of 15 pairs of biramous appendages is remarkably well preserved in this small individual, with fragments of at least five more pairs behind. The first three pairs of coxae, that lie beneath the cephalon, are inclined forward as well as ventrally, the adaxial end projecting and angulate, overlying the dorsal side of the next coxa in front. These coxae are large, especially the third pair, which shows obscure evidence of transverse subdivision. The anterior pair of coxae lie beside the ridge formed by the posterior border of the hypostome. Separated from this border by the border furrow is the slightly inflated posterior lobe of the middle body, the lateral and anterior portions of the hypostome not defined beside the prominent bases of the antennae. Leg branches 1–6 are largest and best preserved, and podomeres are labelled. Coxae 4 are smaller than those of limb 3, and similarly oriented, coxae 5 and 6 appear to slope steeply downward and forward, the ventral edge forming a prominent transverse ridge. Podomere 1 of right leg branches 3–6 has a triangular form and is developed into a ventrally directed endite; the latter is inclined slightly backward, as may be more distal podomeres as a result of slight twisting of the leg branch so that the anteroventral face is directed ventrally. Segmented outer branches of limbs 1 and 2 beneath the cephalon are doubtfully identified, twisted back and close beneath the exoskeleton. The exite of limb 3 appears to arise from the posterodorsal side of the outer portion of the coxa. These exites, and those of limbs 4–6, lie below (posterior) to the leg branch, except at the tip, which lies on the ventral side of the branch. Coxae of limbs 6–15, as transverse ridges beneath the inner portions of the pleurae, and the more proximal portions of the leg branches 6–15 are best preserved, and diminish progressively in size backward. Triangular endites of podomeres 1–3 are conspicuous from branch 9 onwards, the anterior side facing ventrally, suggesting a backward rotation of these limbs. In the axial region of the specimen, from segment 7 back, is a marked step in level (st in figure 9) running along approximately the sagittal line, at the margin of a pyrite layer; the significance of this feature is uncertain. Posteriorly, on each side of the sagittal line, are curved structures (c st in figure 9), showing faint segmentation, that appear to project slightly behind the pygidium; these may represent the most posterior, tiny limbs matted together.

Judging by the prominent ventromesial margin of the coxae beneath the cephalon, the dorsal sides of the first pair lie just behind the hypostome, those of the third pair beneath the occipital ring and adjacent parts of the genae. Limbs 4–13 seem similarly related to thoracic segments 1–10. Thus there appears to be no posterior displacement of the limb series, and the evidence that the cephalon bore three pairs of limbs is strong.

(*e*) *U.S.N.M.* 400936

Figure 13, plate 4; figure 15

A specimen oriented oblique-laterally, length (sag.) *ca.* 9.5 mm, along the upper edge is the right outer pleural region of thorax and pygidium, and incomplete right edge of the cephalon. The pleurae of the thorax, the pygidium, and presumably the cephalon have been sharply flexed at more than 90° along the exsagittal line of the right fulcrum, so that the remainder of the exoskeleton is concealed at a lower level. The outer portions of right pleurae 8–14 are complete, the rounded tips overlapping so that the facets are partly concealed. The pleural furrows die out before reaching the tip; five furrows may be seen on the flank of the pygidium. Fragments of the outer portions of pleurae 1–7 are preserved, only what appear to be the tips of pleurae 1–4 being recognizable. Ahead of these is the rolled border and part of the genal region of the right side of the cephalon, the border intact anteriorly, but broken laterally.

Shale has been removed below the right side of the exoskeleton to reveal, nearest the observer, fragments of the right limbs beneath the posterior portion of the thorax and the pygidium. Better preserved and farther from the observer is the series of limbs of the left side, labelled a–i, exposed from the inner side. Fragments are visible that may represent portions of the left limbs lying in front of the more recognisable podomeres here labelled walking leg branch a. The series of branches b–i are more complete, so that coxae and podomeres may be recognized and numbered. These branches are oriented obliquely, the anterior face sloping upward and backward from the matrix, the branch curved, the distal podomere 6 preserved in b, c and d. The outline of the outer edge of each leg branch forms a continuous curve, that of the inner edge typically serrated, as a result of the endites developed on podomeres 2–4. These endites are more strongly developed posteriorly, as may be seen on branches d–i, and are developed also on podomere 1. The coxae of limbs c–h appear as thick, elongate bars of pyrite; in limbs a and b as more irregular and larger areas. In limbs b–e the shaft of the exite, showing many transverse or oblique divisions and a deep longitudinal groove in those of limbs d and e, curves back inside the curve of the leg branch. The shaft emerges from *below*, that is, from below the posterior faces of podomeres 1 and 2 of branches b–e. It is thus aligned proximally with podomere 1, and must be attached to either the posterior face of this podomere or that of the coxa; we think more probably the latter. Between this series of left limbs and the posterior portion of the exoskeleton, and at a level in the shale nearer the observer, are downward and backward curving fragments of right limbs. These are considered to belong to the right side because of their relative position in the shale, their different direction and curvature, and because the serrated outline of leg branch fragments may be seen facing those of left branches f–i. Fine threads of pyrite, running directly backward, are interpreted as fragments of exite filaments, and are nearer to the observer than the leg branch fragments. The left margin of the concealed portion of the exoskeleton must lie roughly along a line passing beneath the proximal portions of the coxae of left limbs a–h, if it is assumed that this major portion of the exoskeleton has been flattened, not crumpled. The limb series, however, has not apparently been displaced forward or backward in relation to the exoskeleton, nor in the relation of one limb to another. This suggests that, in the earliest stages of preservation, the limbs were held in series and in relation to the exoskeleton by the ventral integument. Collapse of the body as decay proceeded, and flexing of the exoskeleton during compaction, have combined to bring the limbs into their present position in relation to the exoskeleton. Disintegration of the ventral integument cannot have occurred until a later stage, otherwise the limbs would have been more scattered in relation to each other and the exoskeleton.

(*f*) *U.S.N.M.* 400937

Figure 10; figure 12, plate 3

This specimen (length (sag.) 8.5 mm) is regarded as showing an approximately exsagittal section of the left side of the exoskeleton, below which a series of limbs hang downward, curving back distally. The outer branch of the limbs beneath the thorax emerges from beneath podomeres 2 and 3 of the leg branch and is recognizable by its closely spaced divisions, no filaments being visible. Because the outer branch is farther away from the observer than the inner (that is, outside it) the limb series is regarded as that of the left side. The section of the exoskeleton thus appears to cut through the left genal and pleural regions, the inner sides of left thoracic pleurae 1–7 readily recognizable. How the masses of pyrite cut through in the cephalic section are to be understood is uncertain; what appear to be portions of the two branches of a limb run horizontally beneath them. The series of downward-curving limbs are interpreted as shown, each coxa emerging from the matrix as a ridge, projecting adaxially and slightly backward, thickest and highest at the adaxial end, the ridges having a radial arrangement. Endites are progressively more strongly developed going backward along the series of leg branches; like the coxae the anterior face is exposed, inclined upward (toward the observer) and backward. Beneath the most posterior thoracic pleurae and the pygidium are a number of closely spaced leg branches that diminish in length rapidly posteriorly. The tiny, hindmost limbs are grouped close together beneath the tip of the pygidial axis, none originates behind the posterior margin of the pygidium.

(*g*) *U.S.N.M.* 400938

Figures 16, 17; figures 18, 19, plate 5

An oblique lateral compression, the cephalon incomplete anteriorly, the exoskeleton having been abraded in preparation along the axis to give longitudinal sections of part of the glabella, the occipital ring, and each of the 14 axial rings and articulating halfrings of the thorax and the pygidium. Posteriorly the thorax was flexed slightly downward, the pygidium steeply inclined. Ventral to the exoskeleton of the thorax and pygidium fragments of overlapping layers of subparallel filaments are preserved, directed longitudinally. Farther ventrally to them, and ventral to the cephalon, are parts of the biramous limb series, curved downward and backward. Jointed leg branches and associated exites are recognisable, and farthest posteroventrally are further limb fragments. The latter may be tips of the limb series of the right side (farthest below the surface of the specimen), the main series of limbs exposed being those of the left side. In this left series, filaments and exites are nearest the observer, leg branches slightly below them. Beneath segments 11–14 and the pygidium, exites and filaments are visible, a rapid reduction in size posteriorly taking place beneath the pygidium. No limb originates beyond the posterior margin of the pygidium. Beneath the tip of the pygidium are two slim, apparently jointed branches, that may be leg branches of the right side, appearing from below exites of the left side.

Two large limbs (labelled x and y in figure 16) are well exposed, the proximal portions lying beneath segments 4–6. In each, but most clearly in y, the dorsal, outer side of the exite shaft is divided by a longitudinal step in level. On the anterior, lower side of the step the shaft shows well-spaced divisions running diagonally, similar to those seen on the inner side of the exite shaft in 400932 (figure 2). On the posterior, upper side of the step in level oblique, closely spaced divisions are present, which are seen proximally to coincide with successive filaments. We conclude that the filaments were attached to the upper, outer side of the shaft, and that these close spaced divisions are the bases of successive filaments, most of which were removed in the original preparation. The exite shaft was divided into short segments, these divisions (more widely spaced than filaments) being visible on the anterior and inner sides of the exite shaft. Exite y shows that there were about three filaments attached to each division of the shaft. The lobe at the tip of the shaft is visible in the most anterior exite preserved, the tips of more posterior shafts having been removed. An enlargement of the filaments in a median portion of the specimen (figures 17, 19) shows the flat, blade-like appearance of the imbricated, narrow strips that slope outward and slightly downward from the matrix toward the observer. Thus they appear to have been flattened strips, and not cylindrical in cross-section. In other portions of the specimen the filaments are preserved in the same way.

(*h*) *U.S.N.M.* 400939

Figures 20, 21, plate 6; figure 23

A parallel specimen of length (sag.) 19.5 mm. What appears to be the raised, narrow convex border of the hypostome disappears anteriorly beneath the most proximal portions of the antennae. The trilobed object lying on the anterior median lobe of the hypostome may be an ostracod valve. This object is similar in size and morphology to the valve figured by Ruedemann (1926, plate 23, figures 17–20), that came from a higher horizon than the Frankfort Formation. Each antenna shows the characteristic inward curve as it crosses the anterior border medially and then curves forward and outward. Fragments of the narrow, convex, pyrite filling of the space between doublure and dorsal exoskeleton are preserved on each side. In the left, most posterior portion, this doublure becomes a narrow ridge, and there is a shallow depression in the inner side, a vincular depression, for the reception of the tip of the second pleura in enrolment (compare *T. beckii* in Ross 1979, plate 1, figures 3, 9, 12). Appendages appear to have been rotated forward to show the posterior face of the coxae and, with the hypostome and proximal portions of the antennae, lie close beneath the inner surface of the exoskeleton. Coxae of the first two pairs of appendages lie close to the midline, their triangular outline pointing in toward the hypostome. Leg branches are best preserved on the left side, the second curved to point backward. An irregular pyritized area (a filling of the anterior portion of the gut?) lies on either side of the hypostome and extends immediately behind it. A pyrite area suggesting a filling between the occipital ring and articulating half-ring outlines the latter; the fragments of a third, cephalic pair of appendages are tentatively recognised. On the left side of the first four thoracic segments fragments of appendages 4–6 are labelled, possibly rotated in a similar manner to those of the cephalon, and lying close beneath the inner surfaces of the segments. Fourteen thoracic segments are visible, and portions of the pygidial doublure. Incomplete portions of leg branches include those below the eighth and ninth pleurae on the left side showing triangular, spinose endites, and overlapping groups of the tiny posterior branches below and behind the pygidium. These more posterior leg branches have been rotated backward, the anterior side of the endite facing ventrally. A slight posterior displacement of the appendage series may have occurred, but beneath the cephalon there seems to have been little displacement.

(*i*) *U.S.N.M.* 400940

Figure 24; figures 25, 26, plate 7

A relatively large specimen, length (sag.) *ca.* 20 mm, showing portions of the antennae, limbs 1–12 in series, and a few additional fragments of limbs posteriorly on the right side. The entire series appears to be displaced slightly to the left in relation to the exoskeleton. Various features of the cephalic exoskeleton are preserved including the furrow at the outer margin of the eye lobe, the lateral border furrow, and traces of the lateral and posterior borders of the hypostome. The series of appendages has been rotated back so that the anterior side faces ventrally, curvature is backward, and the exites lie below (posterior to) the leg branches proximally.

Three pairs of limbs appear to belong to the cephalon, coxae recognizable on the left side with incomplete leg branches, fragments of these branches on the right side, the second swung forward to lie across the first. In the thorax the leg branch and outer branch are aligned proximally, distally separating as the outer branch curves more strongly backward. The relatively large coxae are rectangular in outline, those on the left beneath thoracic segments 1–7 preserved as inclined ridges, thickest at the adaxial end. These inner ends lie beneath the left axial furrow, the adaxial ends of the right coxae at the sagittal line. Notable in this specimen (figure 25) are the spinose endites of the leg branches preserved on the left side, on podomeres 1 and 2 on the fifth and sixth limbs, on podomere 3 of the fifth and what may be the eighth to tenth limbs (the gap in the series beneath left segment 4 suggests the absence of left limb 7). The largest group of spines is at the ventral, angular tip of the endite, but other, smaller spines occur along the ventral edge of podomere 2 of leg branches 5 and 6, for example. Exite shafts on the left side show oblique divisions, and there is a median groove in e8? On the right side the outer branches of limbs 9 and 10 are preserved, curving backward as they emerge from beneath the leg branch (that is, they lie on the posterior side of the limb). More posterior exites (12? onwards) show oblique subdivisions of the shafts, the lobe at the tip and filaments. The most posterior of these lobes lie beneath the doublure of the pygidium, and may not have been displaced posteriorly. The patch of pyrite lying to the right of the tips of these limbs in figure 26 has an irregularly reticulate surface, but may represent matted filaments of left posterior exites.

(*j*) *U.S.N.M.* 400941

Figure 35, plate 10

Portions of the cephalon (length (sag.) 9.5 mm) and the first three thoracic segments, and of appendages, are exposed from the ventral side. The antennae taper distally from a robust basal section situated below the anterolateral portion of the glabella. More than 30 segments may be counted in the right antenna, that become successively longer (exs.) and narrower distally. The curvature of the antennae is not symmetrical, the left much more evenly and gently curved than the right. Other appendages are fragmentary, but beneath the right side of the glabella are the distal portions of two leg branches, and a strongly flexed shaft of an outer branch showing a median groove, diagonal divisions and the terminal lobe. An elongate, wedge-shaped coxa, and proximal podomeres of a leg branch lie beneath the right axial region of the thorax, the first podomere appearing to be inserted into the full depth of the distal end of the coxa. Other fragments beneath the genal and pleural regions are of an uncertain nature.

(*k*) *U.S.N.M.* 400942

Figure 27, plate 8; figure 31; figure 32, plate 9

Length (sag.) of exoskeleton *ca.* 20 mm, the external mould of the cephalon shows the glabellar outline, the occipital furrow, glabellar furrows 1S and 2S, the right genal region, the long palpebral lobe and posterior branch of the facial suture. Beneath the thorax and pygidium lie fragments of limbs that have been rotated backward to show the anterior face of the leg branch. The coxae lie beneath the outer portion of the axial region, so that podomeres of the backwardly directed leg branches lie largely beneath the pleural region. In figure 31 we have assumed backward rotation of the coxae, so that coxa 11, belonging to the somite of thoracic segment 8, lies partly below the axial ring of that segment and partly below the following ring of segment 9. Leg branch 18 of the right side, the anterior of the pygidium, is followed by six recognizable branches that diminish rapidly in size; there may be more close to the midline but they cannot be distinguished. The great increase in relative depth, successively backward, of the endites of podomeres 2–4 of these branches is visible. Right leg branches show clearly the stout spine (or spines?) inserted into the tip of podomere 6. On the left side the limbs are more strongly backwardly deflected, and consequently overlap more, and details are less clear. Only distal fragments of exites are preserved on either side.

(*l*) *U.S.N.M.* 400943

Figure 36, plate 10; figure 37

The interest of this relatively large specimen (sagittal length of exoskeleton 28 mm) lies in the orientation of the more anterior coxae and limb branches, directed forward and outward at about 45° to the sagittal line. These limbs appear to have been rotated to a limited extent, if at all, because the leg branches are sub-parallel-sided, and show almost nothing of the endites. This specimen thus contrasts strongly with others illustrated here that are exposed from the ventral side and show the anterior face of the leg branches. The coxae appear as narrow, straight ridges, that is, they are thick along the ventral and adaxial edges; they are close together at the inner ends, the outer ends not reaching the axial furrow. The anterior six pairs of limbs are extended in a straight line, but beneath thoracic segments 1–7 the two branches of limbs 7–13 diverge and curve to run outward. As is best seen on the right side, the distal portion of each exite lies in front of the corresponding leg branch, and curves to lie against the branch in front; proximally the exite shaft goes below (that is, dorsal to) the leg branch. Presumably the exite was attached proximally to the upper, posterior surface of the coxa, as other specimens suggest. Beneath segments 8–14, the coxae of the right side appear oval in form, sloping downward and forward, so here presumably having been rotated to slope anteroventrally; limb branches are poorly preserved. Under the pygidium a few leg branches are visible, proximally flexed and distally directed backward. These branches show the anterior faces of the triangular endites, pointing inward, and hence have been rotated backward in the manner seen in other specimens illustrated. Beneath the pleural region of the left side a few areas show fine, parallel lines of pyrite directed outward and backward. These are the edges of exite filaments, and are directed obliquely to the exite shaft.

(*m*) *U.S.N.M.* 400944

Figure 28, plate 8; figure 30; figure 33, plate 9

A complete specimen, length (sag.) of exoskeleton 22 mm, the appendages exposed from the ventral side, moderately well preserved but apparently not displaced. The first three pairs of biramous limbs lie beneath the cephalon, the coxa of the left third limb lying on the infilling of the doublure of the occipital ring. The thickened ventromesial edge of the coxae of the first two pairs is curved forward and inward toward the posterior border of the hypostome; a double ridge is present on the right second coxa. Presumably these coxae have been rotated forward and the posterior side faces ventrally, yet the limb branches curve backward presumably with the dorsal margin facing anteriorly; such an attitude requires that the branches were twisted through 180°. Beneath the first eight thoracic segments coxae, leg branches and only traces of exites are partly preserved, the branches curved and directed backward distally. The coxae lie beneath the axial region, and appear as irregular, elongate areas that may have been rotated backward, since the anterior side of the leg branch faces ventrally.

Beneath the posterior thoracic segments and pygidium (figure 33) the curved leg branches, with increasingly prominent triangular endites developed posteriorly, are exposed under the right side. If the numbering of the limbs is continued from figure 30, then w 18 (figure 33) is the first belonging to the pygidium, and at least nine additional leg branches may be counted. In branches 19–23 the prominent triangular endite of podomere 3 lies successively farther outside the pygidial doublure, and the progressive increase in relative depth of the endite of podomere 4 is shown. A spine is preserved at the tip of branches 18–22, and the lobes at the tips of the exites are poorly exposed behind them at a lower level. Beyond here the overlapping rows of endites of successive branches are visible as inwardly directed projections; individual branches, being crowded together at the tip of the axis, are difficult to distinguish.

On the left side the leg branches are more strongly backwardly directed and overlapping, the endites transversely directed; outside them are portions of exites and backwardly directed filaments.

(*n*) *U.S.N.M.* 400945

Figure 14, plate 4

A slightly oblique specimen, prepared from the ventral side, showing portions of limbs below thoracic segments 9–14 and the pygidium. The convex doublure at the tips of right pleurae 10–12 are exposed and show the enrolment stop. Below the right side of the exoskeleton, immediately outside the axial furrow, is a line of triangular projections, which are the ventromesial edges of successive coxae directed steeply backward. Associated leg branches, with triangular endites on podomeres 1–3, are best seen beneath the pygidium, being only fragmentary beneath the right pleurae. Filaments and portions of exites are exposed below the leg branches, behind the doublure of the pygidium. On the left side the tips of the pleurae project up toward the observer, as do backwardly directed distal portions of leg branches and exites. The most anterior exite visible may belong to the ninth or tenth thoracic segment (limb pair 12 or 13) and shows the subdivisions of the shaft and the large terminal lobe. Between limb branches and pleural region, backwardly directed, overlapping layers of filaments are exposed; exites and filaments extend back beyond the tips of the leg branches of the pygidium, as they do on the right side.

(*o*) *U.S.N.M.* 400946

Figure 22, plate 6; figure 34, plate 10

A small, incomplete, oblique specimen, exposed from the ventral side. The right anterior five pleurae are lying sloping slightly inward, a more complete limb immediately outside the first, fragments only of limbs on and outside more posterior right pleurae, the limbs rotated back to show the anterior face. The more complete limb (figure 34) has the elongate coxa lying with the adaxial edge on the tip of the first pleura, the lower margin curved convexly ventrally. A faint transverse groove divides the coxa, but it is uncertain whether this is an original feature, or results from partial collapse of a hollow pyrite lining of the coxa. The six podomeres of the leg branch are preserved, and two blunt spines at the distal tip; podomeres 1, 2 and 3 are extended ventrally to form endites. Podomere 1 of the leg branch is inserted into the full depth of the abaxial edge of the coxa. The poorly preserved exite, broad proximally and rapidly tapering distally, emerges from below the upper, posterior side of the coxa, and curves out above podomeres 1 and 2 of the leg branch, to disappear behind podomere 3.

Much of the right and central axial region of the specimen is missing, but a portion of the left side and left pleurae are preserved; the left axial furrow may be traced anteriorly, and the tips of the left pleurae are directed ventrally, toward the observer. Fragments of limbs, in which distal portions of leg branches are prominent, curve back below the left axial region. Posteriorly leg branches of both sides curve backward and slightly inward; overlapping endites are directed transversely.

(*p*) *U.S.N.M.* 400947
Figure 29, plate 8

The anterior portion only of this specimen (sagittal length 12 mm) is figured. Beneath the left cheek region of the cephalon and pleurae of the first three thoracic segments, portions of limbs 1–6 are preserved, directed forward and outward, podomeres 3–6 of leg branches 4, 5 and 6 lying outside the margin of the exoskeleton. Figure 29 shows the gap in each limb branch where it crosses the convex cephalic border or pleural tip; this gap results from preparation by abrasion from the ventral side. Judging by the fragments of more proximal podomeres of these branches, they have been rotated so that the anterior side faces ventrally; the three distal podomeres appear cylindrical in form. Exites 4, 5 and 6 emerge from beneath (posterior to) the corresponding leg branch immediately outside the exoskeletal margin, the gently curved shafts lying in front of the leg branch. The shafts show some of the well-spaced, slightly oblique divisions, and a large lobe, steeply inclined and so in edgewise view, is preserved at the tip of exite shaft 5. Fragments of filaments lie against the inner surface of the genal region of the cephalon and the first pleura.

5. Bases of the reconstruction

The external form of the exoskeleton is based on Beecher's photographs reproduced by Raymond (1920), particularly plate 1, figure 1; plate 2, figure 2; plate 4, figure 6, and illustrations in Ludvigsen & Tuffnell (1983, plate 1, figure 5; plate 2, figures 6–8). Ludvigsen & Tuffnell (1983, p. 572) remark that *T. eatoni* lacks genal, occipital and thoracic spines, and in their illustrations this is so. However, Beecher's photographs (Raymond 1920, plate 1, figure 1; plate 2, figure 3; plate 3, figure 4; plate 6, figure 2) show a median tubercle, highest close to the posterior margin, on the occipital ring and the axial rings of thorax and pygidium. A tiny genal spine is present on a small holaspid (figures 9, 11), but is probably not retained in larger individuals. One specimen figured by Ludvigsen & Tuffnell (1983, plate 2, figure 8) is less compressed than most examples, and shows a narrow, posterior, marginal band on the mid-portion of the pleura, defined by a furrow that dies out abaxially. In a photograph of another specimen kindly supplied by Dr R. Ludvigsen, there is a small fulcral process at the anterior margin of the inner, horizontal portion of each pleura. This process fitted into a socket beneath the posterior marginal band of the pleura. The outer portion of the pleura was moderately steeply inclined, and bore the articulating facet. In the compressed specimens the width (tr.) of the pleura is less than that of the axial ring; in our reconstruction the width of the pleura

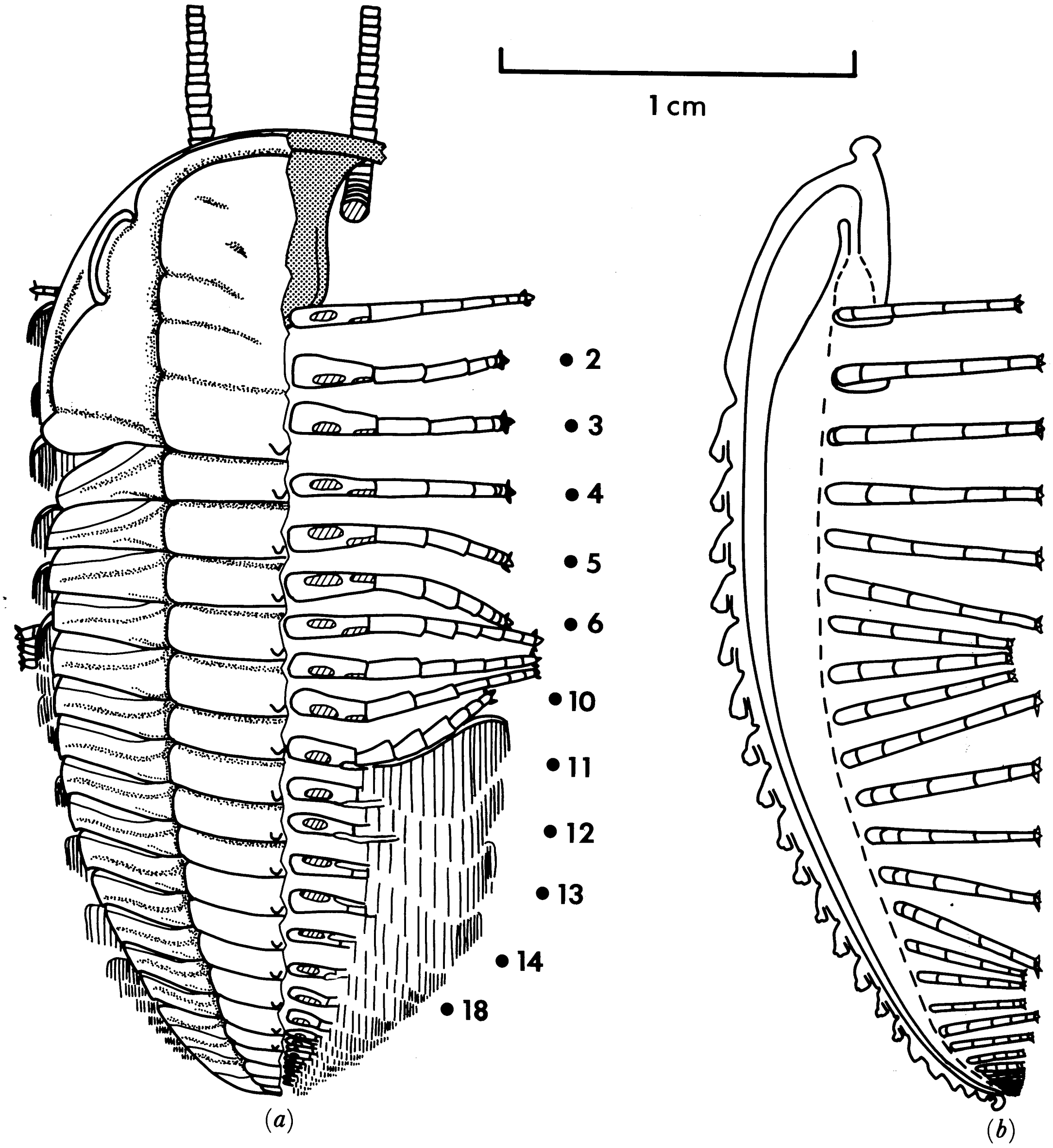


FIGURE 38. Restoration of *Triarthrus eatoni*. (*a*) Dorsal view, in 'still' position of gait (§6*j*), exoskeleton of right side removed to show hypostome and appendages (antennae incomplete). Exite of right biramous limbs 1–9 removed to show attitudes of leg branches. Solid circles and numbers opposite tips of leg branches on substrate, diagonal shading on coxa–body junction and at base of exites where removed. (*b*) Right lateral view of sagittal section combined with right leg branches. Coxae except those of limbs 1 and 2 not shown. Dashed line indicates ventral cuticle, alimentary canal in solid outline.

measured over the surface is also less than that of the axial ring. There was a narrow, rolled doublure along the abaxial and posterior margins of the outer portion of each pleura, that was pyrite-filled and so preserved in some specimens (figures 6, 11, 14, 26, 28, 36). At about the mid-length (exs.) this ridge projects, and immediately behind is recessed, thus forming a stop to limit overlap between successive pleurae in enrolment. All the structures associated with enrolment are thus shown by *T. eatoni*, in specimens of length (sag.) 7 mm upward, and a vincular notch in the posterolateral cephalic doublure of larger specimens (figure 23).

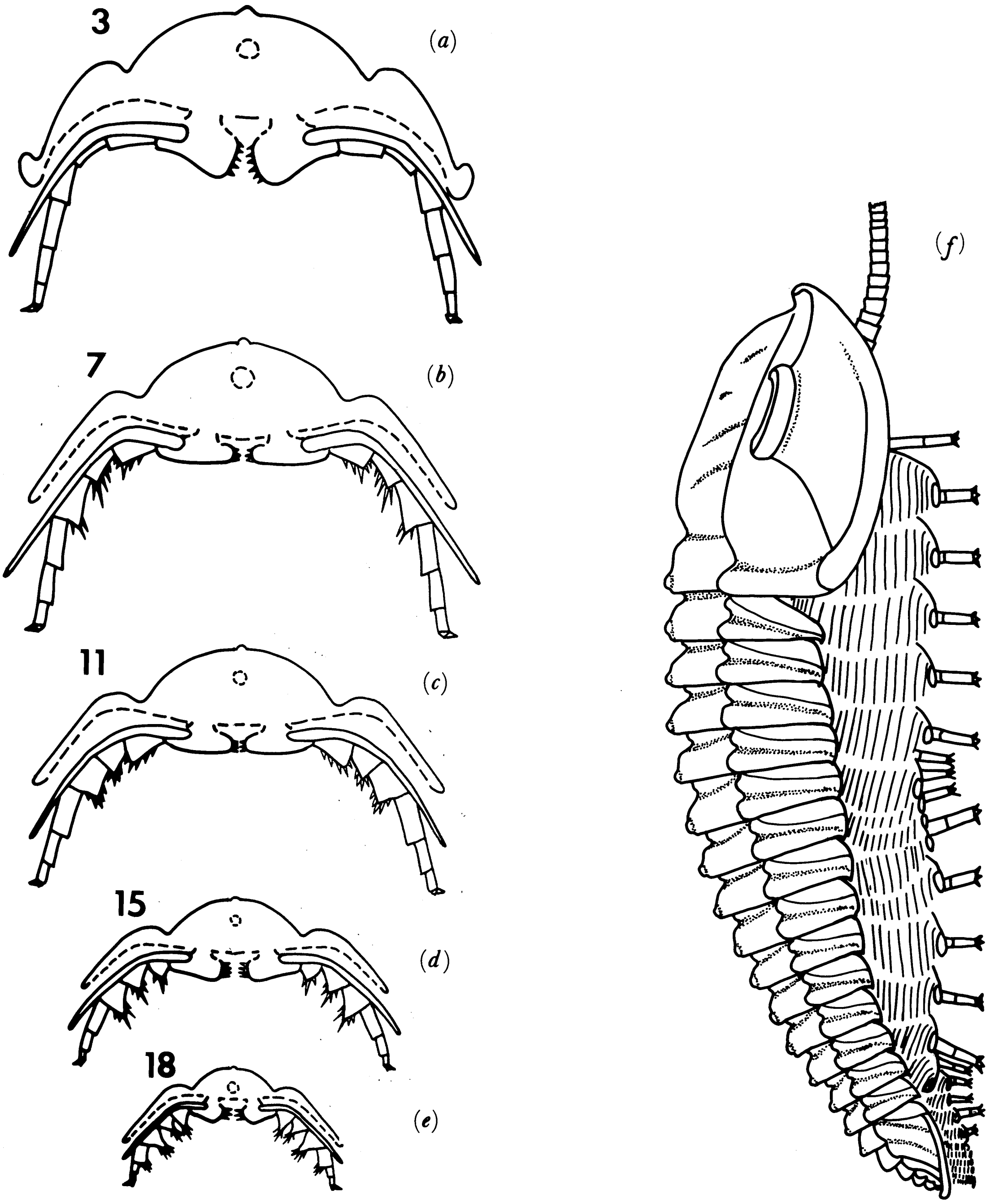


Figure 39 (*a–e*) Restoration of *Triarthrus eatoni*. Cross sections through exoskeleton, showing biramous limbs of series, as numbered, in posterior view, leg branches are vertical. Dashed lines indicate ventral cuticle and section through alimentary canal, filaments and division of exites omitted. (*f*) Restoration of figure 38 in right lateral view, exoskeleton complete and all exites shown diagrammatically.

Ross (1979, plate 1, figures 1–13) described uncompressed, enrolled specimens of *Triarthrus* (the species *T. beckii* according to Ludvigsen & Tuffnell (1983, p. 571)), similar in size to the originals of our figures 7, 8. The species *T. eatoni* and *T. beckii* are similar, and hence we model the form and convexity of the exoskeleton of *T. eatoni* accordingly, particularly the lateral and anterior profiles of the cephalon (figures 39*f*, 40), the form of the pleurae and the outline of

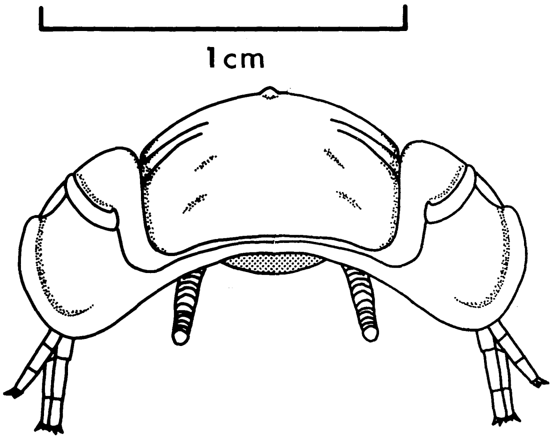


Figure 40. Restoration of *Triarthrus eatoni*, anterior view, hypostome shaded, antennae incomplete, leg branches 1–3 only shown.

thorax and pygidium posteriorly, to fit against the inner margin of the cephalic doublure. The thickness of the body of the pleural regions (between exoskeleton and ventral cuticle) is much less in our reconstruction (figure 39*a*–*e*) than in that of Cisne (1981, text-figure 6), but similar beneath the axial region. This means that there is more space within the capsule of the enrolled animal to accommodate all the appendages, including the antennae. The fit of the exoskeleton in enrolled *T. beckii* (Ross 1979, plate 1, figures 1–13) shows no anterior gap through which antennae might have been protruded; only partial enrolment would have allowed this.

The hypostome of *Triarthrus* is inadequately known. It is not shown clearly by specimens figured herein, or earlier photographs (Whittington 1957*a*, plate 116, figure 13, the species now attributed to *T. beckii* by Ludvigsen & Tuffnell 1983, p. 571; Ludvigsen 1979, figure 38, of a slab showing many specimens of *T. eatoni*, an enlargement of part of which was kindly supplied by Dr R. Ludvigsen). It appears to have had a length (sag.) about three-fifths that of the cephalon, and its position in the present specimens as well as earlier photographs suggest that it was attached along a hypostomal suture to the narrow anterior cephalic doublure. The posterior portion was subquadrangular in outline and had narrow lateral and posterior borders (figures 20, 23), anteriorly the hypostome became wider (tr.) as it merged into the anterior wing. The general form of the alimentary canal is suggested (figure 38*b*), the mouth region having been above the posterior portion of the hypostome, the anus below the border of the pygidium.

The most anterior appendages preserved are the single pair of antennae (figure 35; see also Raymond 1920, plate 2, figures 2, 3, 6; plate 4, figures 3, 4). Each tapers distally and is annulated, the annulations increasing in length (exs.) distally, the broad, basal section longer than the adjacent annulations. In many specimens (figures 6, 21, 28, 36) the pair of antennae are symmetrically placed beneath the most anterior portion of the glabella, and proximally converge forward, pass close together beneath the anterior cephalic doublure, then diverge forward and outward. The basal portions are separated by a distance that is slightly more than half the width (tr.) of the glabella at that point, so that each lies some distance inward from the axial furrow, and beside the anterior portion of the hypostome where it widens forward presumably to the anterior wing (figures 23, 24). If this characteristic position of the antenna is indicative of its point of insertion in the ventral cuticle, this position lay immediately behind the anterior wing of the hypostome, inward from the axial furrow, as Raymond (1920, pp. 43–44) recognized.

Our views on the morphology of the biramous appendages are summarized in figure 41; this morphology is similar along the entire biramous series. These appendages are least well revealed beneath the cephalon, where they have been rotated about the coxa–body junction and brought to lie close beneath the inner surface of the exoskeleton. In some examples (figures 8, 9, 23, 30) the rotation has been forward so that the posterior side of the coxa and proximal portion of the leg branch faces ventrally, in one (figure 24) the rotation has been backward. These specimens all support the conclusion that there were three pairs of biramous appendages on the cephalon, the third attached beneath the occipital ring, in agreement with Cisne (1981, pp. 108–110). The thorax, in specimens from 7 mm (figure 9) in length (sag.) upwards to 28 mm (figure 36), has 14 segments and one pair of biramous appendages associated with each segment. On the pygidium (figures 1, 31, 33) there appears to have been 8–12 pairs of biramous appendages. In specimens exposed from the ventral side (figures 2, 7, 8, 24, 27) appendages of thorax and pygidium have been rotated backward about a transverse axis so that the anterior face of the leg branch is directed ventrally, the branch gently curved and directed outward, or flexed to varying degrees.

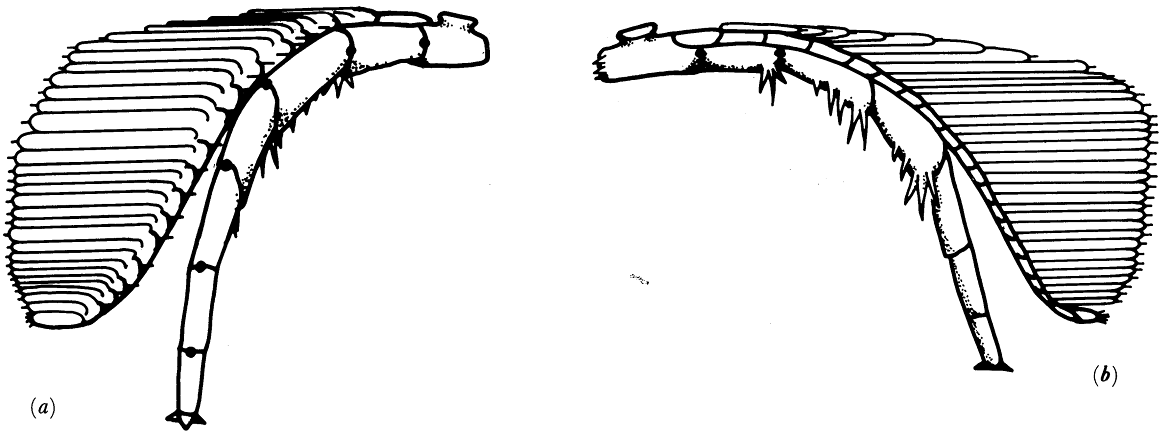


FIGURE 41. Restoration of biramous limb of anterior thorax of *Triarthrus eatoni*, in (*a*) oblique anterolateral view and (*b*) seen obliquely from behind in the midline. Solid circles show positions of pivot joints between coxa and podomere 1, between podomeres 1 and 2, and of hinge joints between more distal podomeres.

The leg branches and shafts of the outer branches of the limbs are revealed in the parallel specimens more clearly than other portions of the limbs, because of the relatively robust pyrite infilling and because preparation from the ventral side reached them first and was halted. The delicate filaments of the outer branch are rarely seen, and the coxae are poorly preserved in most examples, either as thick, transverse ridges or irregular areas. The coxae of the thorax were transversely elongate (figures 7, 9, 10, 15, 30, 37), seemingly subrectangular in outline (figures 8, 24), becoming less deep adaxially (figures 34, 35). Beneath the cephalon (figures 9, 23) the coxae appear to have been deeper, so that the adaxial portion projected downwards; this feature suggests some specialization of coxae of limbs 1–3 adjacent to the mouth, contrasting with the more rectangular coxae of the thorax. As the coxae became shorter transversely on the posterior portion of the thorax and the pygidium, they became triangular in outline (figures 1, 2, 14) and downward-projecting, resembling endites of the leg branch. Setae on the mesial edge of the coxa are shown following Cisne (1981, p. 108; plate 18, figure 3; text-figure 13), but have not been seen in the present specimens. The leg branch is least well preserved beneath the cephalon, but it appears that the first was the slimmest and shortest (tr.), and that there was a progressive increase in size in limbs 2–4 (figures 6, 11, 24, 29, 30), and not a marked change in size between the posterior cephalic and first thoracic limb, as shown by Beecher (1895, plate viii), Raymond (1920, figure 10) and Cisne (1981, text-figures 1, 2). The podomeres of the cephalic leg branches were sub-oval or sub-circular in cross section, endites not developed. Leg branches of the thorax (figures 2, 7, 8, 15, 24) consist of six podomeres that become shorter (tr.) and less deep distally, so that while podomeres 1–4 were elongate-oval in cross section, podomeres 5 and 6 were cylindrical. The relative lengths of the leg branches of limbs 4–17 (thorax and first of the pygidium), and the changing outline in lateral view of podomeres 1–4, are shown by these specimens. Podomere 1 of limb 4 or 5 is triangular in outline, deepest distally, the lower, distal margin bearing a group of spines. Podomeres 2 and 3 of the leg branch become triangular in outline, and spinose in limb 7 podomeres 1–3 become progressively more triangular in form along the series. Thus posterior thoracic limbs (13–17 in the series) have podomeres 1–3 extended as endites, stout inward projections, that bore spines (figures 2, 31). On the pygidium the pairs of limbs were progressively more closely spaced and diminished in size rapidly posteriorly, so that the hindmost pairs were tiny and difficult to see clearly (figures 1, 32, 33). Up to ten pairs have been observed, and there may have been one or two more. Not only were podomeres 1–3 of the posterior leg branches extended inward as long spines, but podomere 4 developed this form and was spinose at the tip. From specimens such as shown in figures 2, 24, a rough measurement may be made of width (tr.) of each axial ring of the thorax, and of length of coxa and leg branch of the corresponding limb. These two measurements have a ratio of about 1:1.5, and this ratio is used in the reconstruction to determine length of limbs in relation to the exoskeleton.

On the thorax and pygidium (figures 2, 7, 8, 15, 16), and rarely on the cephalon (figures 7, 29, 30), the shaft of the exite is visible. The shaft is broad proximally, tapering distally, and appears proximally on the upper, posterior side of the leg branch. It is closely aligned proximally with the leg branch, and emerges (in anterior view of the limb) from behind podomeres 1–3 of that branch. It was attached to the posterior side, apparently of the coxa, as suggested by right exite 10 of 400933 (figure 7), right exites 4 and 5 of 400934 (figure 8), and exites x and y of 400938 (figure 16). As the invariable alignment of the branches proximally shows, the attachment was rigid. The tapering shaft was, on limbs 3–9 (figures 2, 24, 29), approximately the same length as the leg branch, behind there it was longer than the leg branch, especially on the limbs of the pygidium (figures 1, 33). When viewed from what is apparently the inner side (figures 2, 8), the shaft shows a series of short divisions that run transversely or obliquely across it. There may be a median longitudinal groove dividing the shaft into a section that shows the divisions, and one that does not (figure 7), or the divisions may be seen on each side of the groove (figures 2, 15). In a lateral specimen (figure 16) that shows the outer, upper side of the shaft, it is divided by a change in level between an anterior side showing the well-spaced divisions, and a posterior side showing much more closely spaced (about three times as numerous) divisions. Exite y in 400938 (figures 16, 17) shows that these close-spaced divisions are the most proximal portions of the filaments, some of which are more complete in the uppermost exposed portion, and are directed backward. The shaft is thus interpreted as having transverse (or oblique) divisions that permitted flexibility, and to have had the filaments attached to the upper, posterior surface. The filaments extended directly back beneath the ventral cuticle, and adjacent to the mid-length of the shaft were long enough to overlap those of the succeeding limb. Beecher's photographs (Raymond 1920, plate 3, figure 6; plate 5, figures 5, 6) show that these filaments were longest medially on the shaft, and were progressively reduced in length distally. In 400938 (figures 17, 19) the filaments appear as thin, flat slats, projecting outward and downward from the matrix, and resembling the slats of a partly closed Venetian blind. On the outer side of the tip of the exite shaft was a small, oval lobe (figures 1, 2, 14, 29), spinose around the margin. The lobe is less well seen on exites of the thorax, seemingly because they were aligned edge-on in ventral view. We portray the exite shaft as curving back distally (figures 39*f*, 41), so that the lobe lies parallel to, and immediately outside, the outermost filament. Thus the filaments are directed back at 90° to the inner portion of the exite shaft, but at an increasingly acute angle to it distally. In specimens exposed from the ventral side the acute angle between parallel filaments and shaft distally is characteristic. We follow Størmer (1939, figure 22) in showing setae projecting from the lines of division along the anterior margin of the shaft, and at the tips of the filaments.

While many morphological features of the limbs may be observed, the nature and position of the coxa–body junction is not preserved. In many specimens (figures 7, 8, 24, 30, 37) it appears that the inner ends of the coxae were quite close together in life. Such a position is shown in the reconstruction, as part of a particular stance and mode of walking. Arguments for these are from presumed function, and are given in §6*j*.

6. Discussion

(*a*) *Summary of distinctive features of the restoration*

When compared with that of Cisne (1981, text figures 1–7) our reconstruction (figures 38–41, 43) differs in:

(i) the greater depth of the exoskeleton resulting from the slightly wider (tr.) genal regions and pleurae, and in many details of the exoskeleton such as absence of connective sutures, presence of 3S and 4S glabellar furrows, and structures associated with enrolment;

(ii) that the pair of antennae are not shown as lyriform in attitude, the metastome is omitted;

(iii) the form of the coxa and its variation along the series, the inner branch of the limb inserted into the full depth of the outer edge of the coxa, and the outer branch to the upper, posterior edge; no transverse furrows are shown, and the coxa–body junction is conjectural in form and situated well inward from the axial furrow;

(iv) the more robust, obliquely subdivided shaft of the exite;

(v) showing a progressive gradation in dimensions of the anterior limbs, and not a relatively abrupt change between those of the cephalon and the first pair of the thorax;

(vi) showing the progressive posterior development of spinose endites on the leg branches, as demonstrated by Beecher;

(vii) the absence of a 'post-pygidial abdomen';

(viii) showing a 'hanging stance' of the limbs and a suggested mode of walking. Because of the steeper inclination of the limb branches distally, both project well below the exoskeleton in lateral aspect, but only the tips are seen in dorsal view.

From his study of X-ray stereographs, Cisne (1981, pp. 115–126) considered that traces of various muscles, of endoskeletal bars, and of features of the digestive system were preserved. We have not observed any such traces in studying specimens in reflected light, so make no comment on the skeletomusculature proposed by him.

(*b*) *Exoskeleton*

The greater depth and convexity we give to the exoskeleton is a major distinction between our reconstruction and earlier ones (Walcott 1918, plate 34, figures 4–7; Størmer 1939, figure 23), while from that of Cisne (1981, text-figures 6, 8) it differs in the slightly greater width (tr.) of the pleurae. It is based on the assumption (see §5) that the exoskeleton of *T. eatoni* was alike in convexity to that of uncompressed, enrolled *T. beckii*. This assumption, together with the view that the body was relatively thin beneath the pleurae, has considerable implications for a plausible reconstruction of stance of the animal (see §6*j*). The result is a dorsal reconstruction (figure 38*a*) that, compared with earlier versions (Beecher 1896, plate viii; Cisne 1981, text-figure 1), shows only the tips of the biramous appendages.

Cisne (1981, pp. 113–114, text-figure 7) discussed enrolment and the associated structures, but did not describe either the vincular depression in the posterolateral cephalic doublure, the fulcral process and socket, or the facet and stop of the doublure of the pleura (§5). Cisne considered that complete enrolment in *Triarthrus* was not possible, but that the pygidium could have been brought beneath the anterior portion of the thorax. The structures we describe strongly suggest that complete enrolment was possible in *T. eatoni*, as in *T. beckii* (Ross 1979). When enrolled the pygidium would have lain against the inner side of the cephalic doublure, and there would have been no opening in the exoskeletal capsule; all the appendages must have been enclosed within it.

(*c*) *Antenna and hypostome*

We portray the antennae as directed forward from a point of attachment adjacent to the hypostome (figures 38*a*, 40), and do not give them the pronounced lyriform curvature (figure 35) that leads to the pair crossing close together beneath the anterior cephalic border before they diverge forward. Enrolment (see §6*b*) required that the antennae were highly flexible, and we suggest that the curvature may not be original, but an effect of preservation. Collapse of the body in the earliest stages of decay, so that appendages were brought to lie close to the exoskeleton, and early stages of compaction, may have brought the antennae close together beneath the apex of the frontal arch of the border. We do not accept Raymond's (1920, p. 98) suggestion that the antennae may have acted as claspers, based on the hypothesis that variations in antennal configurations reflected sexual dimorphism.

In trilobites in which there is an anterior pit at the junction of the axial and anterior glabellar furrows, the hypostome may be braced against the corresponding boss on the inner surface by a process directed up from the anterior wing (Whittington & Evitt 1954, pp. 19–20, and references). The antenna is thought to have been linked by muscles to the anterior boss, and to have emerged via the lateral notch of the hypostome. In *T. eatoni* there is no anterior pit, and the antenna (§5) may have been attached beneath the anterolateral area of the glabella, approximately beneath the most anterior glabellar furrow. The hypostome is poorly known, but it appears to have widened forward and been linked by a hypostomal suture to the anterior ephalic doublure. If the anterior wing was similar to that in the olenid *Parabolinella* (Ludvigsen

1982, figure 48*u*), it would have curved upward and outward so that the tip lay close beneath the junction of the axial and preglabellar furrows. Such a large wing is not incorporated into our reconstruction (figure 38*a*) because of the uncertainty.

(*d*) *Supposed metastome*

The metastome was first recognized by Beecher (1895, p. 97, plate iv, figure; plate v, figures 8–11) as a small, arcuate plate a short distance behind the hypostome. Subsequent authors have followed Beecher, including Cisne (1981). The latter author, however, does not offer evidence that we find convincing (Cisne 1981, plate 18, figure 4; plate 20, figures 1, 2; plate 21, figure 2; plate 22, figure 3) for the existence of this plate as a structure separate from the convex posterior border of the hypostome. Cisne (1981, p. 130) also draws attention to the peculiarities of the specimen used as evidence for the metastome by Raymond. We conclude that the presence of such a plate in trilobites is questionable, for there appears to be no specimen showing the metastome in *Olenoides serratus* (Whittington 1975, p. 122) or any other trilobite.

(*e*) *Coxa*

This basal segment of the limb is poorly and incompletely preserved, and the nature of its junction with the body unknown. Hence the restorations of figures 39*a–e*, 41 and 43 are tentative, and the size and position of the coxa–body junction is an assumption, as is the distance between the adaxial ends of the coxa. We find no evidence for the 'precoxal segment' of Størmer (1939, figure 23), and site the coxa–body junction far inward from the axial furrow, not beneath it as Walcott 1918, plate 34, figures 4–7, or immediately inside it as in Cisne 1981, text-figure 8*c*. Such a position is a necessity if the limbs are to be given a hanging stance.

A quite different restoration of the coxa was given by Cisne (1981, pp. 107, 109, text-figures 4, 5, 8), that appears to be based (figure 42) on the outline of the supposed coxa of his text-figure 16, which in turn is based on his interpretation of the X-ray stereographic pair of his plate 19, figure 3. This specimen is shown in its entirety in Cisne's plate 19, figure 1, and leg branches are visible beneath, and extending beyond, the thoracic pleural regions. Counting podomeres of leg branches shows that podomeres 1–3 in the series lie beneath the pleurae, and that the coxae (obscurely visible because of dark shadowing) lie largely beneath the axial region but distally extend across the axial furrow. The disposition of the coxae and leg branches beneath the exoskeleton of the anterior thorax is similar to Cisne's plate 17; plate 22, figure 4; and that on the right side of 400942 (figures 27, 31). Thus we do not think that the coxa lies beneath the mid-portion of the pleura as in Cisne's interpretation (1981, text-figure 16; plate 19, figures 1, 3). Figure 42*a* is a copy of Cisne's text-figure 16, beside our interpretation (figure 42*b*) of what is to be seen in his stereographic pair of X-ray photographs of a portion of the specimen. It has been prepared from the ventral side, the limbs of the thorax and pygidium having been rotated backward so that the anterior side faces ventrally. In such preparations, where the pyritized limb lies against the tip of the pleurae, the portion of the leg branch that crosses the edge of the exoskeleton is readily removed, as it has been in some of the leg branches of such specimens as the originals of figures 4, 11, and 26. Thus we interpret the leg branch in Cisne's specimen, that underlies right thoracic pleurae 10 and 11, as showing a typical gap between the incomplete podomeres 3 and 4, where it lay against the doublure of right pleura 11. The missing portion was removed in preparation, and the branch was not

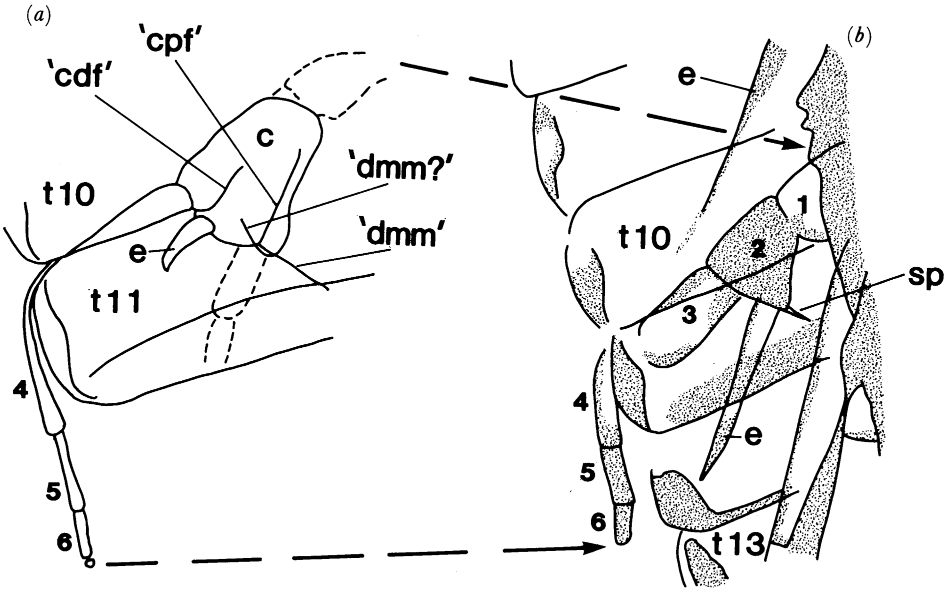


FIGURE 42. (a) Copy (re-oriented) of text-figure 16 of Cisne (1981, p. 136), abbreviations in quotation marks from Cisne: 'cdf', coxal distal furrow; 'cpf', coxal proximal furrow; 'dmm', dorsomedial extrinsic limb muscle; other abbreviations as used herein. (b) Our interpretation of X-ray stereograph of Cisne (1981, plate 19, figure 3), darker areas stippled, abbreviations as used herein, arrows indicate area to which Cisne's text-figure 16 relates. See §6*e* for discussion.

'squeezed through the small space separating' right pleurae 10 and 11, as Cisne (1981, p. 109) claimed. Much more importantly, however, the area of the X-ray stereograph that Cisne portrays as the coxa with its furrows (dorsal side facing inward and backward in figure 42*a* as oriented here), we regard as podomere 2 of the walking leg, dorsal side facing forward and outward in our figure. The dashed, unlabelled outline to the right of the 'coxa' in Cisne's figure we interpret as part of podomere 1 of the leg branch, the unlabelled, dashed outline below and to the left of his 'coxa' as the exite shaft of the limb, curving out from below podomere 2. The short, tapering shaft that Cisne labels as the 'exite' in his figure appears to us to correspond with the ventral margin of podomere 3 of the leg branch. The thick line that Cisne labels 'dmm', the 'dorsomedial extrinsic limb muscle', appears to be probably a spine at the tip of the endite of podomere 2. Thus we do not consider that the portion of the specimen 7190/15, shown in Cisne's (1981) plate 19, figure 3, reveals the coxa, but the curved, outer portion of a leg branch and underlying exite, as seen in many specimens prepared from the ventral side, and illustrated here. It follows that there is no basis for a restoration showing the leg branch and exite shaft as slim proximally, and as inserted into the lower, abaxial margin of the coxa. On the contrary, many specimens (figures 7, 8, 24, 34, 35) show a dorsoventrally broad podomere 1 of the leg branch inserted into the full depth of the abaxial edge of the coxa. The form and attachment of the outer branch is discussed in §6*h*. No specimen is known that shows the outline and form of the coxa, with supposed distal and proximal furrows, as depicted by Cisne.

(*f*) *Biramous limbs on the cephalon*

Beecher (1895, 1896) considered there were four pairs of biramous limbs on the cephalon, basing his conclusion largely on specimen number 220 (original of his 1895, plate iv; also figured by Raymond 1920, plate 3, figure 2, and Cisne 1981, plate 23, figure 2). Three pairs of coxae lie below the cephalon, behind the hypostome, but how these are connected to leg branches or exites, or both, is not shown clearly by any of the illustrations. Beecher (1895, plate v, figures 8, 9, 10) also figured three additional specimens, all showing three (or as Beecher thought, four) pairs of coxae on the cephalon behind the hypostome, but only proximal fragments of some of the leg branches or exites. One of Beecher's specimens may be number 211, figured by Raymond (1920, plate 2, figure 5) and Walcott (1921, plate 104, figure 15). One of our specimens (figure 28) is like those of Beecher (particularly his plate v, figures 9 and 10) in showing the coxae as plates sloping upward (ventrally) and forward out of the matrix, the anterior edge curved convexly forward. In our specimen (figure 30) the connection between coxae and leg branches may be seen, and the coxa of right limb 2 apparently has a double ridge on the ventral side. The similar structure in Beecher's (1895) figures 9 and 10 of plate v he interpreted (plate v, figure 11) as a separate coxa and restored a leg branch attached to it. The problems in interpreting these specimens as seen in reflected light are obvious, but if coxa and one or both branches can be traced, difficulties are lessened. Thus we consider that the interpretations (figures 8, 9, 23, 24) we have made of additional specimens, in which coxae and leg branches are preserved in the cephalon, support the view that it bore three pairs of biramous limbs.

Raymond (1920) and Størmer (1951, p. 130) followed Beecher in regarding the cephalon as bearing four pairs of biramous appendages. The claim that there were only three such pairs was first made by Cisne (1974) and reinforced later by additional X-ray stereographs (Cisne 1981, pp. 108–110). Of those referred to by Cisne (1981) his plate 18, figures 3, 4; text-figures 13, 15; plate 20, figures 1, 2, are the most convincing, showing coxae and attached leg branches. The coxae, as in our drawings, appear deeper (ventrally extended) at the inner end, that is, the edge curves convexly forward in the posterior view given by the specimens; an additional ridge may be present on the posterior face of the coxa. This different form of the cephalic coxae was noted by Raymond (1920, p. 42, figure 10), but regarded by Størmer (1951, pp. 130–131), as resulting from a different orientation of these coxae after burial, as compared to those of the thorax. Cisne (1981, p. 127, text-figures 8, 10) considered that the cephalic limbs were modified as mouth parts, and suggests a ventrally projecting inner portion of the coxae.

(*g*) *Inner or leg branch*

This branch was relatively slim in dorsal view (figure 37), but the development of endites on podomeres 1–4 of thorax and pygidium means that these podomeres were deep (in dorsoventral dimension), the cross-section elongate-oval. Thus in anterior view (w 4–6 in figure 24) podomere 1 of the anterior thoracic leg branch was sub-triangular in form, and deep where it was inserted into the coxa. These endites, shown by Beecher (1896, plate viii) and Raymond (1920, figure 10) were minimized or omitted by Cisne (1981, text-figures 4, 5). Their reality is evident in the present specimens, which also support the view that the leg branch consisted of six podomeres, progressively shorter distally, and that two, probably three (for example, a thoracic limb on the left side of Cisne 1981, plate 17) spines at the tip of podomere 6 formed a foot.

(*h*) *Outer branch or exite*

In Cisne's (1981, text-figure 4) restoration a slim, circular shaft of the exite is inserted into the outer end of the coxa above the leg branch. However, as shown above (§6*e*), we consider this based on a misapprehension, and have argued in §5 that the shaft was attached to the outer, posterior side of the coxa. The shaft (figures 2, 10, 16, 24, 37) was stout proximally, tapered and divided by some 15 oblique grooves, the filaments having been attached to the upper side of the shaft. These filaments (figures 14, 16, 18, 33, 36) appear fine and numerous, and each shaft may have borne some 50 of them. Our restoration (figure 41) shows fewer filaments, in the interests of clarity. Cisne (1982, pp. 81–83, figures 6, 7) has argued from cross-sections that the filaments were elongate-cylindrical in form, arranged along the shaft without intervening gaps. As described in §4*g*, the filaments may be preserved as flattened strips, separated by narrow gaps, projecting out of the plane of compression of the specimen. Such a form can hardly result from compression of originally cylindrical, juxtaposed filaments. The appearance of the filaments in figure 36 as fine, evenly spaced, parallel structures also suggests an original blade-like form. The problem of the original form of the filaments needs further investigation.

In Cisne's dorsal and ventral restorations (1981, text-figures 1, 2), there is an abrupt change in dimensions between the posterior exite of the cephalon and the anterior of the thorax. Further, the thoracic exites of limb pairs 4–12 are shown extending far out beyond the tips of the leg branches, behind limb pair 12 becoming progressively shorter (tr.) so that posteriorly on the pygidium they do not extend out as far as the leg branches. As pointed out in §5, the present specimens show a gradation in size and form between cephalic and thoracic limbs, and that on limb pairs 3–9 (figures 4, 29) the exites were similar in length (tr.) to the leg branches, but posteriorly became longer (figures 3, 33). The lobe at the tip of the pygidial exites is relatively far larger than in more anterior limbs. These changes in relative dimensions along the limb series indicate differences in growth rates: the tiny, first formed posterior leg branches increased in size more rapidly than the exites; the shaft of the exite increased in length (tr.) more rapidly than the terminal lobe.

(*i*) *Posterior limbs and 'post-pygidial abdomen'*

Lateral and lateral-obliquely compressed specimens (figures 10, 15, 16) have rarely been illustrated previously, and the significance of the features they show hardly appreciated. For example, they show the relation of the posterior limbs to each other and to the exoskeleton. Beneath the pygidium the pairs of limbs are rapidly and progressively posteriorly reduced in size and packed more closely together. This arrangement results from their ontogenetic development, the smallest and most posterior belonging to the last-formed somite at the anterior margin of the telson, successively earlier-formed somites with their appendages being progressively larger. Thus the first four pairs of limbs (18–21) on the pygidium lie beneath the four axial rings and corresponding pleural regions, which become progressively shorter (sag. and exs.); the remaining pairs of limbs are packed together beneath the tip of the axis and posterior pleural regions. Such an arrangement is typical in trilobites, shown by the packing together of serially paired muscle scars in the posterior axial region (see, for example, Whittington 1959, plate 25, figures 5, 6; plate 32, figure 21).

In figures 1, 3, 31–33, this arrangement of the appendages is seen from the ventral side, the limbs rotated back and curved posteriorly, and the body collapsed, so that they lie close below the exoskeleton. Thus several tiny posterior pairs lie overlapping one another on the pygidial doublure medially and project backward beyond it. These limbs are biramous and similar in morphology throughout their range in size; because the specimens were prepared from the ventral side, leg branches are better exposed than exites. Similar specimens were illustrated by Walcott (1918, plate 29, figures 4–6; 1921, pp. 415–416), who suggested that the 'anal plate' of Beecher and Raymond was a misinterpretation of these tiny limbs, which may as a result of compression during preservation have been brought to lie on or immediately behind the pygidial border. We endorse this view, as did Størmer (1939, p. 204), and the lateral compressions point most clearly to the original position of these posterior limbs.

Cisne (1981, pp. 107, 109, 111, text-figures 1–3, 9), on the other hand, regarded this 'anal plate' as part of a cone-shaped series of limb-bearing segments, ending in the telson that bore the anus, that projected beyond the posterior margin of the pygidium. His evidence for this so-called 'post-pygidial abdomen' is apparently his plate 19, figures 1, 2; plate 22, figure 4 and text-figure 28; plate 23, figure 1. The latter illustration is dark and difficult to interpret, but the other two stereographs show specimens very like those of figures 3, 32 and 33, in which the overlapping series of posterior leg branches curve progressively more strongly inward, the deep endites of podomeres 1–4 directed transversely as blunt, tapering, triangular processes. We consider that in his text-figure 28, Cisne appears to have portrayed these overlapping endites and interpreted them as the segments of his 'post-pygidial abdomen'. We therefore reject the arguments advanced for this supposed structure. Lateral-obliquely compressed specimens show (figures 12, 19) the tiny, posterior limbs hanging down below the posterior portion of the pygidium, and no evidence of such a structure, and neither does Cisne's (1981, plate 23, figure 3) X-ray stereograph of an oblique specimen.

Rare specimens (figures 7, 14) show the length of the posterior exite filaments. These overlapping sheets of filaments must have formed a curtain, that hung down outside the diminutive leg branches (figure 39*f*) to conceal them beneath the border of the pygidium. All these structures must have been enclosed within the enrolled exoskeleton.

(*j*) *Locomotion, respiration and feeding*

(i) *Stance and walking*

Our reconstruction incorporates a hanging stance (figure 39*a*–*e*) of the paired limbs (cf. Manton 1977, p. 200), the spinose, mesial margins of the coxae closely apposed, the proximal portion of the limb slightly upwardly curved, the distal portion steeply inclined. Given the exoskeletal convexity adopted here, such a stance appears reasonable. It requires that the coxa–body junction be situated well inward beneath the axial region, and that the body was thin beneath the pleural regions. The reconstruction provides limited space for the overlapping layers of filaments borne by the successive outer limb branches, and for the appendages to be accommodated within the enrolled body. If the joints between podomeres of the leg branch and between branch and coxa (figure 41), were like those proposed for *Olenoides serratus*, then the mode of walking may have been similar (Whittington 1980, pp. 190–194, text-figures 9–11, following Manton 1977, pp. 39–49). This mode (figure 38*a*, *b*) was basic and generalized, and assumes a promotor–remotor swing of the coxa, at the coxa–body junction, about an approximately horizontal, transverse axis; pairs of limbs would have swung in concert, and slight fanning of the transverse axes would have occurred anteriorly and posteriorly. The action of intrinsic leg branch muscles would have kept the tip of the limb firmly on the substrate, and provided a major component of the propulsive force, as suggested in Whittington (1980, text-figure 10). The joints of the leg branch would have allowed the stance suggested here, and the amount of flexure seen in leg branches in figure 5, for example. The above assumptions immediately raise a problem compared with *O. serratus*, in that from limb 8 onward length (tr.) is successively reduced. To suggest *T. eatoni* walking (figure 39*f*) using the maximum possible number of pairs of limbs, 1–18 (the latter the first on the pygidium), the body must be curved down posteriorly; this brings the tip of the pygidium close to the substrate. The tiny, crowded limbs behind pair 18 (figures 1, 16, 31) could not have been used in walking. Slightly fewer pairs of limbs, pairs 1–14, for example, could also have been used, but walking on many fewer pairs of limbs would appear to have been unstable. As a result of our assumptions, the reconstruction differs from all previous drawings most obviously in that only the curved tips of the exites, and the tips of longer leg branches in the recovery stroke, project beyond the margins of the exoskeleton in dorsal view (compare figure 38*a* with Beecher (1896, plate viii), and Cisne (1981, text-figure 1)). In lateral view (figure 39*f*) not only the leg branch, but also a large portion of the exite of each limb, projects below the exoskeleton. This is in sharp contrast to the condition in *O. serratus* (Whittington 1975, figures 25, 26*e*), in which the outer branch is relatively much shorter (tr.), and consequently concealed beneath the pleural region in dorsal or lateral aspect. Because the tips of the walking legs would have sunk into the substrate, the extremities of the exites would have been close to, posteriorly possibly touching, its surface.

(ii) *Exite movement and function*

Figures 39 and 41 reconstruct the exite as having curved downward behind the leg branch close below the body, and curved back distally, the filaments in an overlapping series that lay outside the leg branches. There must have been intrinsic musculature within the exite shaft, that held it in this position while walking, and also flexed the exite strongly to enable it to be tucked within the exoskeleton during enrolment, given the rigid junction between exite and coxa. During walking, the distal curvature of the exite held it just clear of the substrate, and it would have swung to and fro with the metachronal movements of the limbs, as suggested by the varying directions of the filaments in the lateral view (figure 39*f*). We have given reasons (§6*h*) for considering that these filaments were in the form of long, thin blades, the flat sides of the blades possibly vertical (figure 41). During the up or down movement of the exite water would have been forced or drawn between the filaments, but a considerable volume of water could hardly have been drawn in (on the down stroke) or forced out (on the up stroke) between the exite and the ventral integument, unless the blades were inclined to the vertical. Thus the action of the exites as a particle filtering device, or to create currents to promote swimming (Størmer 1939, pp. 223–227; Bergström 1969, pp. 407–408, 410; Whittington 1975, p. 132) seems improbable. In the case of a filtering device, how particles trapped by the filaments could have been collected and carried to the mouth is highly problematical.

The length and parallel arrangement of the filaments of the exite, their occurrence in overlapping sheets dorsal to the leg branch, and the rigid attachment of exite to coxa, all argue, as in the case of *Olenoides serratus* (Whittington 1980, pp. 188–189), that the function of the outer branch was primarily respiratory. There is no evidence from this or other species (Whittington 1980, pp. 189–190) to suggest that the exite could have been rotated, and the filaments brought to extend vertically (between adjacent leg branches) to sweep or scrape sediment. In *T. eatoni*, in contrast to *O. serratus*, the exites were long enough to be exposed below the pleural regions for a considerable distance (figure 39*f*), perhaps an aid in respiration. If so, it is unlikely that *T. eatoni* would have dug or ploughed to any depth in the substrate, because the fine sediment would probably have inhibited respiration by clogging the filaments.

It was acknowledged above (§6*j* i) that the reconstruction provides very little space for the limb branches beneath the ventral integument of the pleural regions. This is so particularly for the filaments of the overlapping series of exites during walking, but also for the leg branch when raised and extended in the forward swing. More space could have been provided by deepening the body in the axial region, but this would have raised the animal higher above the substrate and reduced stability, as well as reducing space within the enrolled exoskeleton into which limbs could have been packed.

(iii) *Drifting, excavating in substrate*

A backward swing by a group of leg branches, in the manner suggested for *Olenoides serratus* (Whittington 1980, p. 195, text-figure 13), would have enabled *T. eatoni* to launch itself off the bottom and drift in a current. As indicated in §6*j* ii, it is unlikely that the exites as we reconstruct them could have created a backwardly directed current to enable even feeble swimming. The leg branches could not have been used as oars because they could not have been 'feathered' on the recovery stroke.

Scraping away the substrate by flexure of pairs of limbs, perhaps alternate pairs, seems a likely activity, in the manner suggested for *Olenoides serratus* (Whittington 1980, p. 195, text-figure 14). *T. eatoni* may also have been able to plough shallowly in the surface sediment (cf. Whittington 1980, text-figure 15) by tilting the cephalon downward as it walked, and thus reducing the height of the anterior arch (figure 40). The strength of any such ploughing would depend on how the work of the legs was transferred to the cephalic exoskeleton. The coxa–body junction was not an articulation with the mineralized exoskeleton, but with the sclerotized ventral cuticle, and the coxa was presumably held in place and moved by extrinsic muscles attached to the exoskeleton. The ability to push into sediment would have been limited by the strength of these extrinsic limb muscles. The ventral cuticle was apparently not as heavily sclerotized as the limbs, but was sufficiently so to resist decay and hold the series of limbs in position during the early stages of pyritization. Thus shallow ploughing, but not burrowing to any depth in the substrate, was possible for *T. eatoni*; the exposed distal portions of the exites (figure 39*f*) would have prohibited such burrowing.

(iv) *Manner of feeding, function of endites*

Cisne (1981, pp. 126–127) envisaged *T. eatoni* as feeding on fine particles from the substrate, passed forward along the ventral midline by the interaction of the spiny inner edges of successive pairs of coxae (cf. Whittington (1980, pp. 192–193, text-figure 9) for a similar mechanism in *Olenoides serratus*). Cisne suggested that the food material was scooped up by the trunk limbs, presumably the leg branches, and conveyed to the food groove, but exactly how fine particles were so conveyed is problematical. As discussed in §6*j* ii, a mechanism for such transport involving the trapping and sorting of fine particles by the exites, and carrying them forward to the mouth by currents created by exite movements, is regarded as unlikely (cf. Cisne 1981, p. 127).

A striking feature of the leg branches in *T. eatoni* is the development of endites that are progressively more numerous, relatively shorter (tr.) and more prolonged inward (deeper) backward along the series (figure 43). These endites all bear a group of setae around the tip, and constitute a formidable armature beneath the body. 'Progressively backward', however, is the reverse of their direction of growth. In the last-formed limb branch (28 in figure 43), and adjacent branches, both coxa and podomeres 1–4 of the leg branch are short (tr.) and deep, acutely triangular in anterior–posterior outline (figures 3, 32, 33). In larger, earlier-formed leg branches (7 in figure 43) the podomeres (like the coxae) become progressively longer (tr.) and relatively less deep, less acutely triangular in outline. Anteriorly the endite on podomere 4 disappears (15 in figure 43), and endites on podomeres 1–3 are progressively reduced in more anterior limb pairs than those shown in figure 43. Thus, as a result of differential growth rates, the armature of endites is most formidable in the mid and posterior thoracic region of the body. The downward curvature of the body necessitated by our reconstruction (figure 39*f*) concentrated this armature around the midline below the body, and surrounded it posteriorly (figure 43). This enclosed region was open to the anterior below the body (figure 40). The armature thus appears to have been part of an apparatus for catching and sorting food particles of varied size, and small, soft-bodied animals. Such fragments and prey could have been brought by currents, or scraped up by the leg branches, captured and squeezed by flexure of pairs of branches. Such flexure could also have pushed food particles into the mid-line, to be further shredded and passed forward by pairs of coxae. The larger, more triangular coxae of the cephalon may have been used to push food into the mouth at the posterior margin of the hypostome, a process perhaps helped by suction. We suggest that *T. eatoni*, while able to trap particles in suspension, was predominantly a benthic deposit feeder, scavenger and predator,

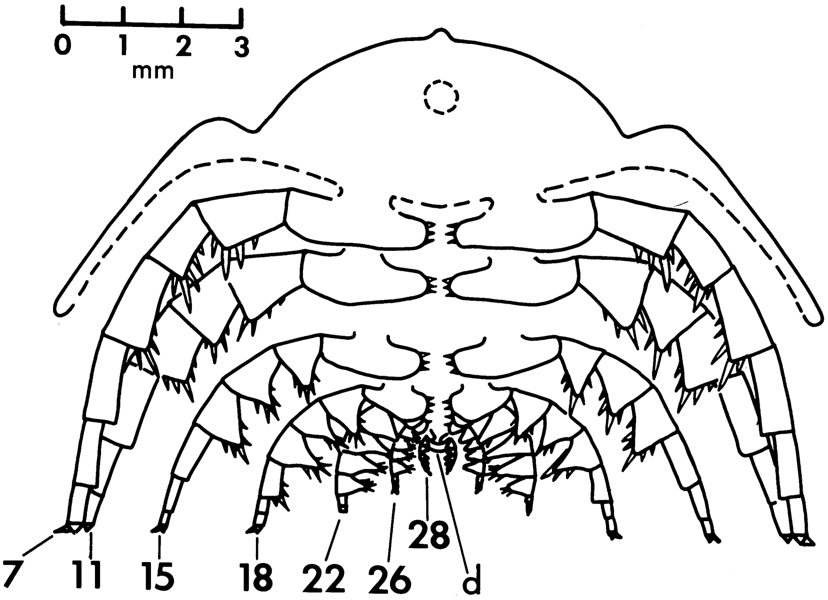


Figure 43. Restoration of coxae and leg branches of *Triarthrus eatoni* as numbered, each pair vertical, looking posteriorly from cross-section of body at fourth thoracic segment, stance as in figure 39*f*. For clarity, only selected coxae and leg branches are shown, exites are omitted, d is median portion of doublure of pygidium. See §6*j* iv.

that dug into the mud using particularly the larger anterior and middle thoracic leg branches in search of food. We interpret the limbs as specialized for such activities by differential development of coxae and endites of the leg branches. The outer branches formed an overlapping sheet of filaments, a curtain hanging above and outside the leg branches. No specimen shows exite filaments and leg branches alternating, that is, there is no evidence that the exite shaft could have been rotated, and the filaments of the outer branches could not have been directed downward between the leg branches. Consequently the setose endites of the leg branch cannot have been used to scrape filtered food particles off the exites.

It is not readily evident how currents to assist in the collection and transport of food particles could be created by *T. eatoni*. The broad anterior and posterior faces of the endites of the more posterior leg branches can hardly have been used to assist in swimming, since they could not have been sufficiently 'feathered' in the return stroke. During metachronal movements of the limbs, however, water would have been squeezed out as branches swung toward each other, and drawn in as they separated. Possibly the leg branches beneath the pygidium may have been used in this manner to produce such a current, either to draw water backward beneath the body or direct it forward along the mid-ventral region.

(v) *Comparisons with other arthropods*

It is suggested herein that in manner of walking, digging in the substrate, capturing prey, and conveying food forward along the midventral line, *Triarthrus eatoni* and the Middle Cambrian *Olenoides serratus* (Whittington 1975, 1980) were similar. However, *T. eatoni* differs from *O. serratus* not only in the lack of posterior cerci, but in the presence of a large number of limbs on the pygidium that diminish rapidly in size backward. The latter type of pygidial appendages are known in *Cryptolithus* (Raymond 1920, figure 20) and probably in *Rhenops* (Bergström & Brassel 1984, p. 70, figures 1–3) and *Phacops* (Stürmer & Bergström 1973, pp. 118–119), trilobites of very different morphology from *Triarthrus*. In all endites are deeper and more numerous on the proximal podomeres of the posterior leg branches. Bergström & Brassel (1984, p. 71) suggested that these pygidial limbs in *Rhenops* and *Phacops* may have aided in catching prey, which may have been brought toward the mouth by partial enrolment. It would seem that neither *Triarthrus*, *Phacops* nor *Rhenops* could stand on the more anterior limbs while so enrolling, these limbs not being long enough. In the non-trilobite arthropod *Marrella* (Whittington 1971), that had increasingly large endites on the more posterior leg branches, a similar behaviour in catching prey and bringing it to the mouth has been suggested (Briggs & Whittington 1985, pp. 155–156, figure 3); *Marrella* has the anterior leg branches sufficiently long for it to have remained standing on them while the posterior portion of the body enrolled. It was also argued that the posterior endites in *Marrella* acted to trap and filter food particles that were swept back beneath the body by the brush-like second appendages. A similar action seems likely in *Triarthrus*, but how particles were carried back towards the trap is not clear. In both animals the filamentous outer branch lay outside the region concerned in feeding, and appears to have been respiratory in function.

It appears that the trilobites discussed above may have been generalized in feeding habits, predators and scavengers, as well as deposit feeders; such habits characterized certain contemporaneous non-trilobite arthropods. Other trilobites (including *Olenoides*) and non-trilobite arthropods appear to have been more specialized as benthic scavengers and predators (Briggs & Whittington 1985, pp. 153–154).

(*k*) *Environment*

Cisne (1973) listed the 29 species of benthic organisms that accompany *T. eatoni* in the dark grey, graded siltstone of Beecher's trilobite bed. Numerically the assemblage is dominated by trilobites (mostly *T. eatoni*), brachiopods and graptolites. The more general study of the strata in which the bed occurs (Cisne *et al.* 1980) indicates that *Triarthrus* is present in a sloping, dark shale facies intermediate between shallow-water limestones with thin, interbedded shales and deeper-water graptolitic shales. The exact distribution of *T. eatoni* is uncertain, because Cisne *et al.* (1980, p. 53) regarded *T. eatoni* and *T. beckii* as one species, whereas Ludvigsen & Tuffnell (1983) argued that they are separate species. These latter authors record *T. eatoni* as present in New York State, Ontario and Quebec, and as having a long stratigraphical range, Upper Caradoc to Ashgill (Shermanian to Maysvillian); these occurrences appear to be in dark shales. The evidence indicates that *T. eatoni* was a benthic species characteristic of off-shore muds containing abundant organic matter. There is no certainty that this environment was low in oxygen, as the characteristic environment for olenid trilobites is thought to have been (Fortey 1985, pp. 228–229). The exites in *Triarthrus* are exceptionally long (tr.), and hang well below the pleural regions (unlike the condition in the very different trilobites *Olenoides*, *Cryptolithus*, *Phacops* or *Rhenops*, for example). This condition might be regarded as an adaptation for respiration in environments low in oxygen. The rock in which the uncompressed, enrolled specimens of *T. beckii* (Ross 1979) were enclosed is not recorded, but presumably it was a limestone rather than a shale.

We are indebted to Mr Frederick J. Collier, Department of Paleobiology, U.S. National Museum of Natural History, for loan of the specimens. Mr Collier informs us that these specimens were first catalogued in 1903, with the statement that they had been collected by C. D. Walcott. Hence the probability that they, and the specimens numbered 65523–531 (figured by Walcott (1918)), were all collected by him in 1893. Dr R. J. Ross, Jr, kindly sent us a photographic copy of the original of his 1979, plate 1, and Dr R. Ludvigsen a photograph of *T. eatoni* from Ontario showing an incomplete outline of the hypostome. Miss Sheila Ripper has converted pencil drawings into the figures. The gift to H.B.W. by the late Mrs William M. Hunt, daughter of Professor C. E. Beecher, of a bronze original of his model, acted as an inspiration for this work; H.B.W. is indebted to the Leverhulme Trust for their support. J.E.A. is grateful for the award of a Natural Environment Research Council studentship (GT4/81/65/15), during which this work was undertaken. Comments on the manuscript by Dr C. P. Hughes and the referee have been most helpful. This is Cambridge Earth Sciences Publication number 753.

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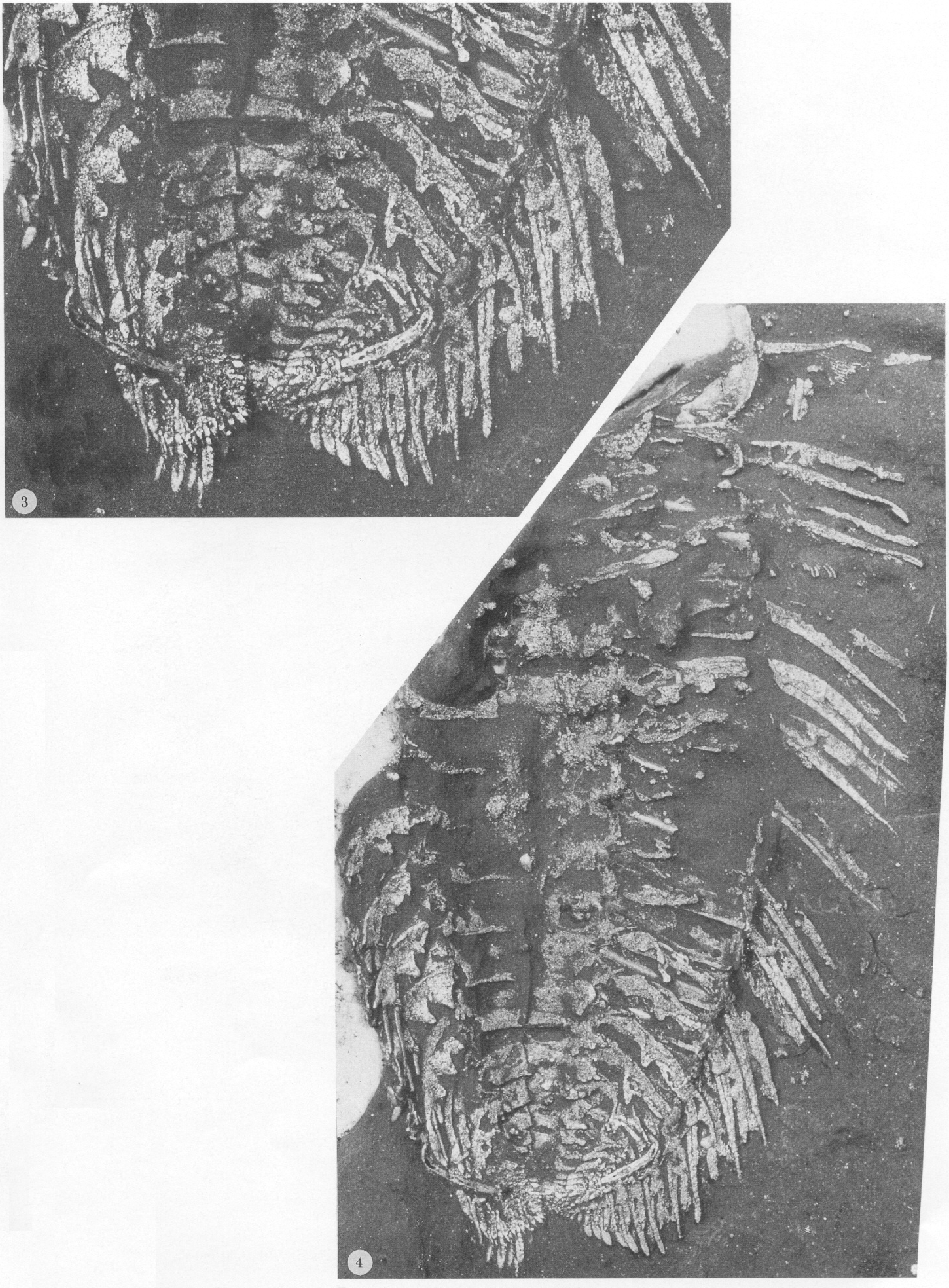
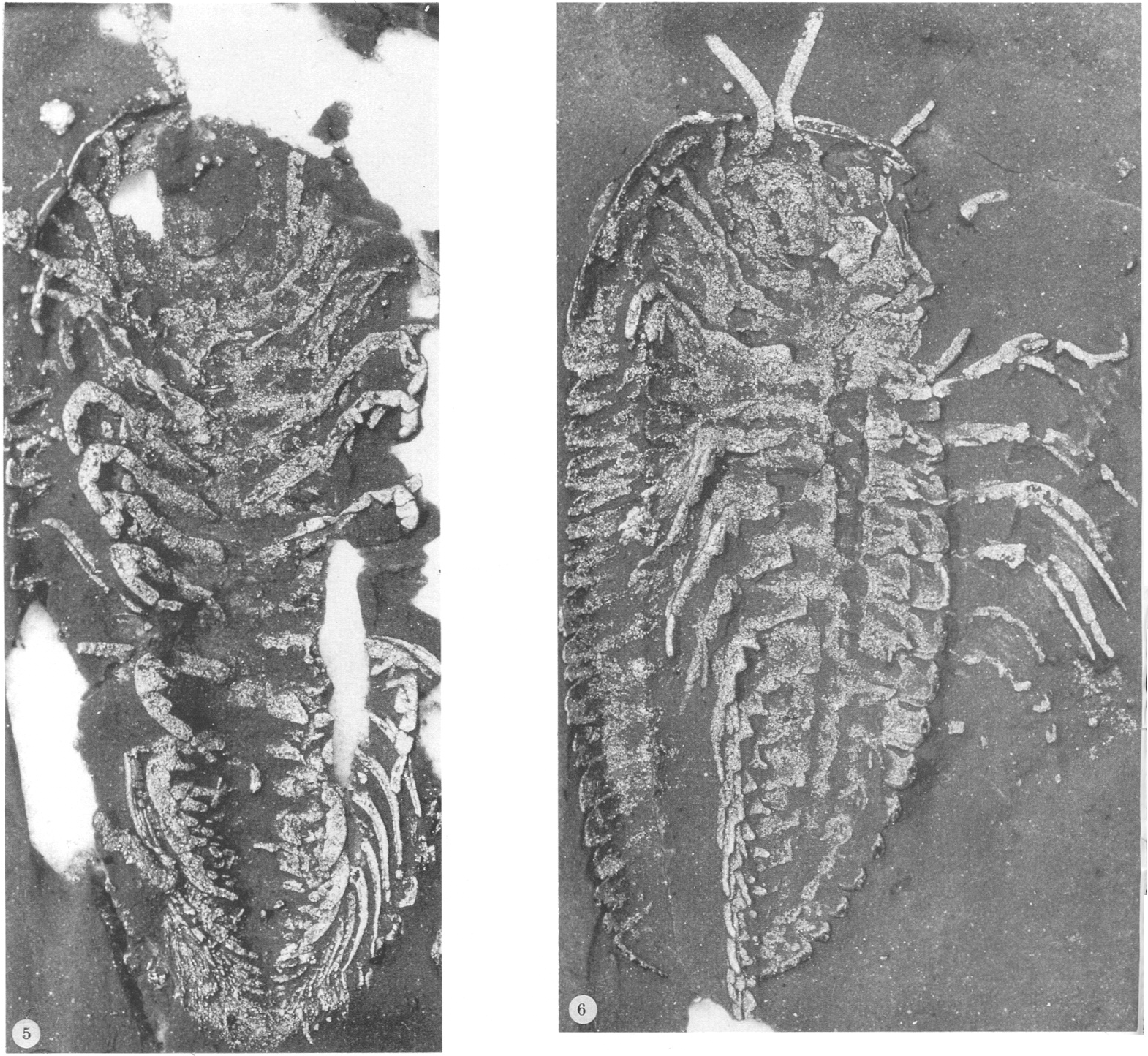
LIST OF ABBREVIATIONS

a	antenna
ahr	articulating half-ring
axf	axial furrow
a–z	serial lettering of limb branches when anterior branches on body are not preserved
c	coxa
ce	cephalon
ced	doublure of cephalon
cepb	posterior border of cephalon
cpm	posterior margin of cephalon
c st	curved structures
d	doublure
dpb	doublure of posterior border of cephalon
e	exite
el	lobe at tip of exite
es	exite shaft
ex.	exsagittal, a line parallel to, but outside the sagittal line
ey	furrow at outer margin of eye lobe
fil	filaments of exite
fr	fracture
gr	longitudinal groove in exite shaft
gs	genal spine
h	hypostome
l	limb
lbf	lateral border furrow
L	prefix denoting left side of animal
or	occipital ring
os	ostracod valve
pbf	posterior border furrow
pl	pleura
plf	pleural furrow
pm	posterior margin
pyg	pygidium
R	prefix denoting right side of animal
S	glabellar furrow, numbered 1S, 2S etc. anteriorly from 1S, the furrow next to the occipital furrow
sag.	sagittal, a median longitudinal line in the body
sp	spine
st	step in level
stp	stop in enrolment
t	thoracic segment
tr.	transverse, a direction at right angles to the sagittal line, used also for the direction along the axis of a limb branch
to	trough
U.S.N.M.	United States National Museum of Natural History
v	vincular depression
w	walking leg
1–*n*	serial numbering of thoracic segments, pleurae or pleural furrows, coxae, branches of limbs when first in body is known, and podomeres of leg branch

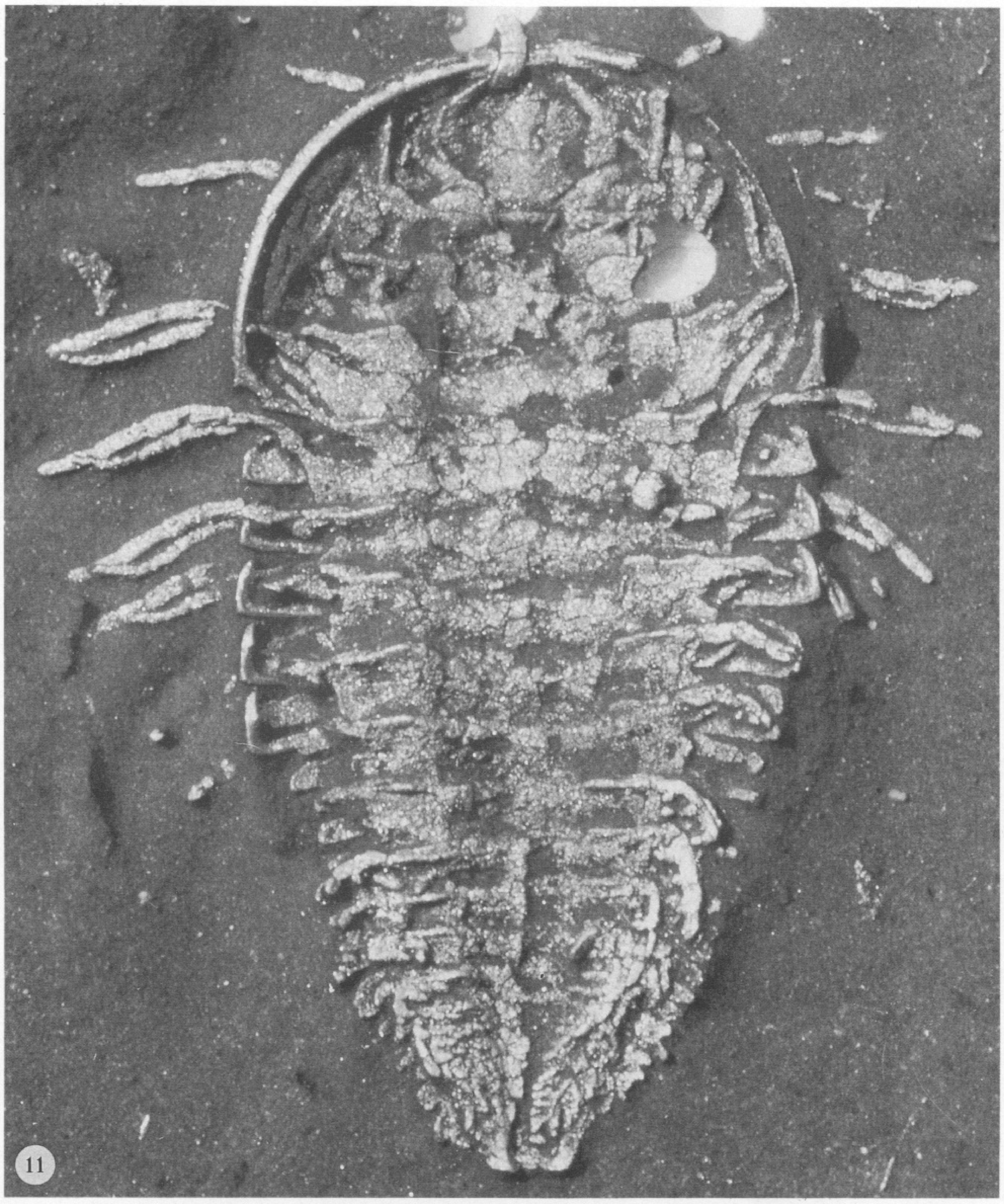
Stipple in the explanatory drawings is used along broken edges or to show holes through the specimen, which are white in the photographs.



FIGURES 3, 4. For description see opposite.



FIGURES 5, 6. For description see opposite.



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Figures 11, 12. For description see opposite.

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FIGURES 13, 14. For description see opposite.

FIGURES 18, 19. For description see opposite.

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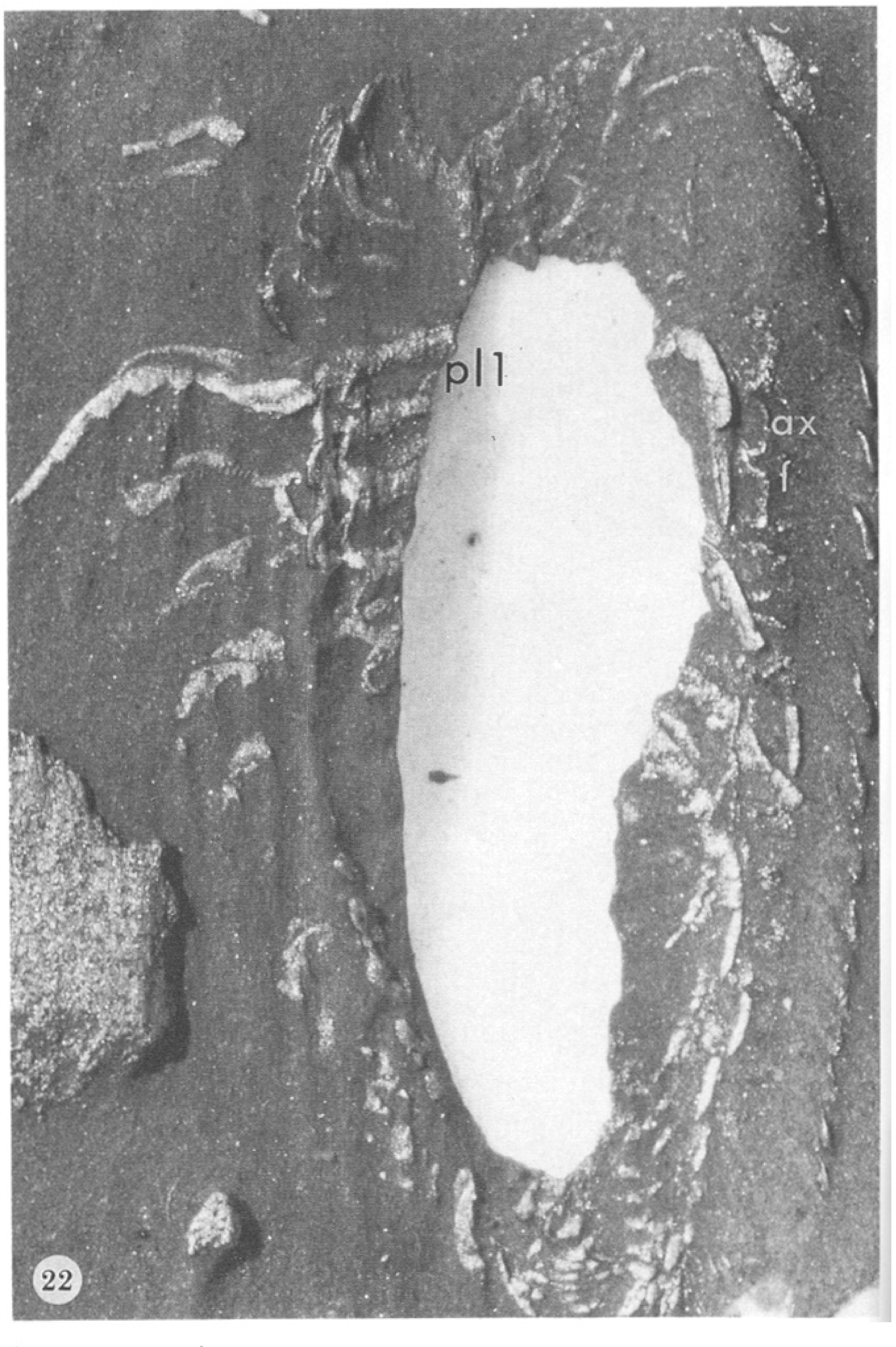

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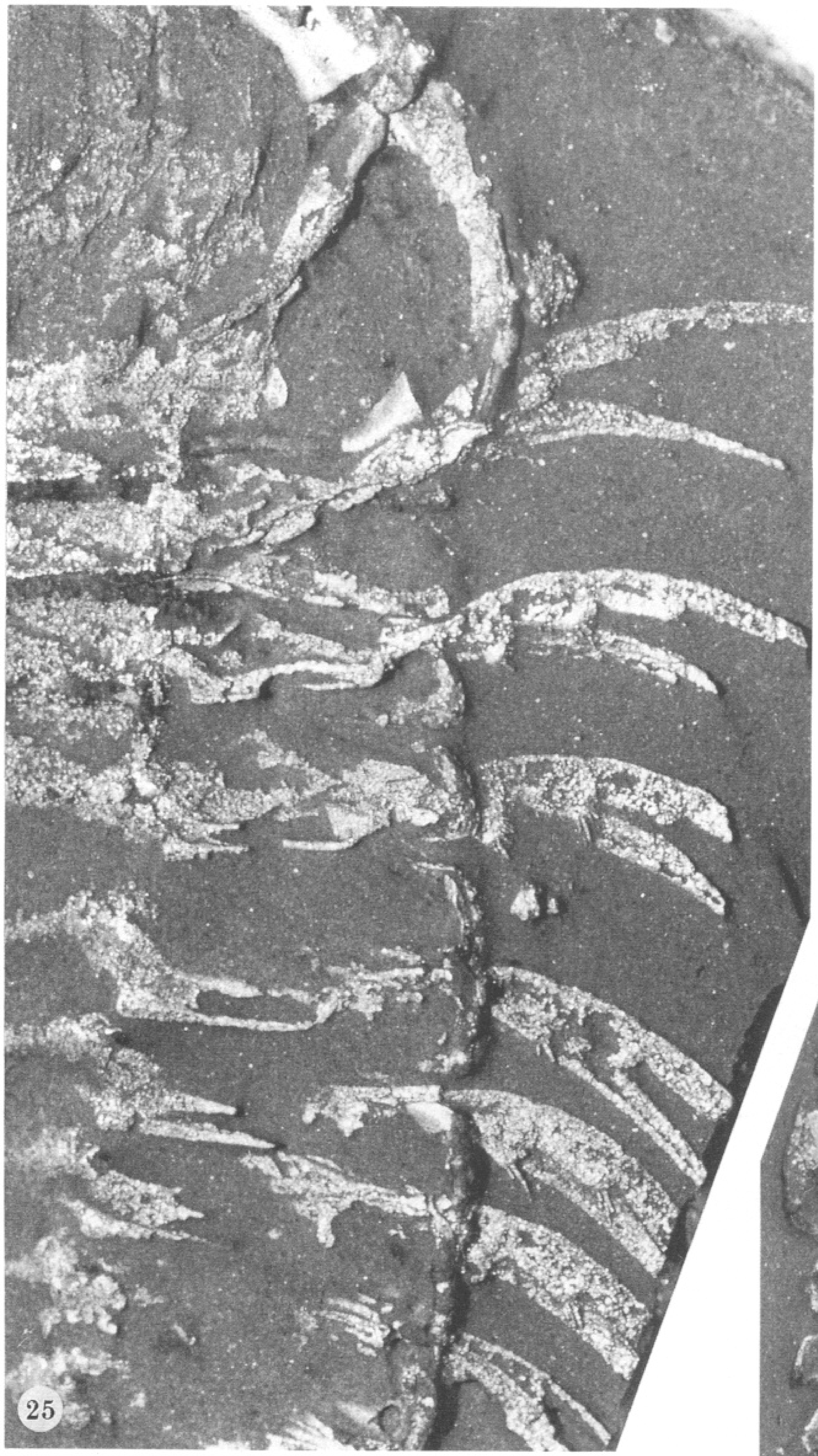
FIGURES 20–22. For description see opposite.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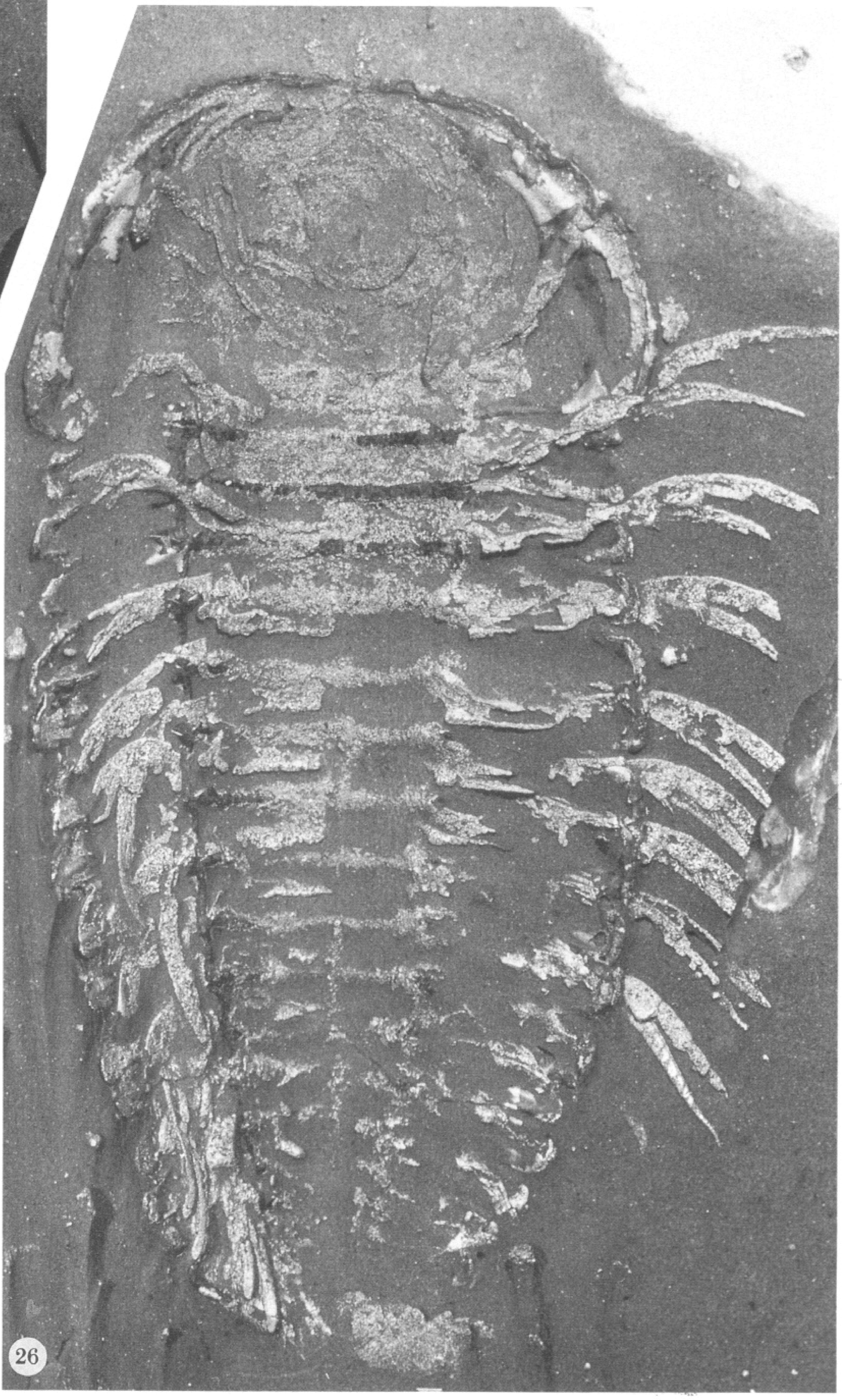
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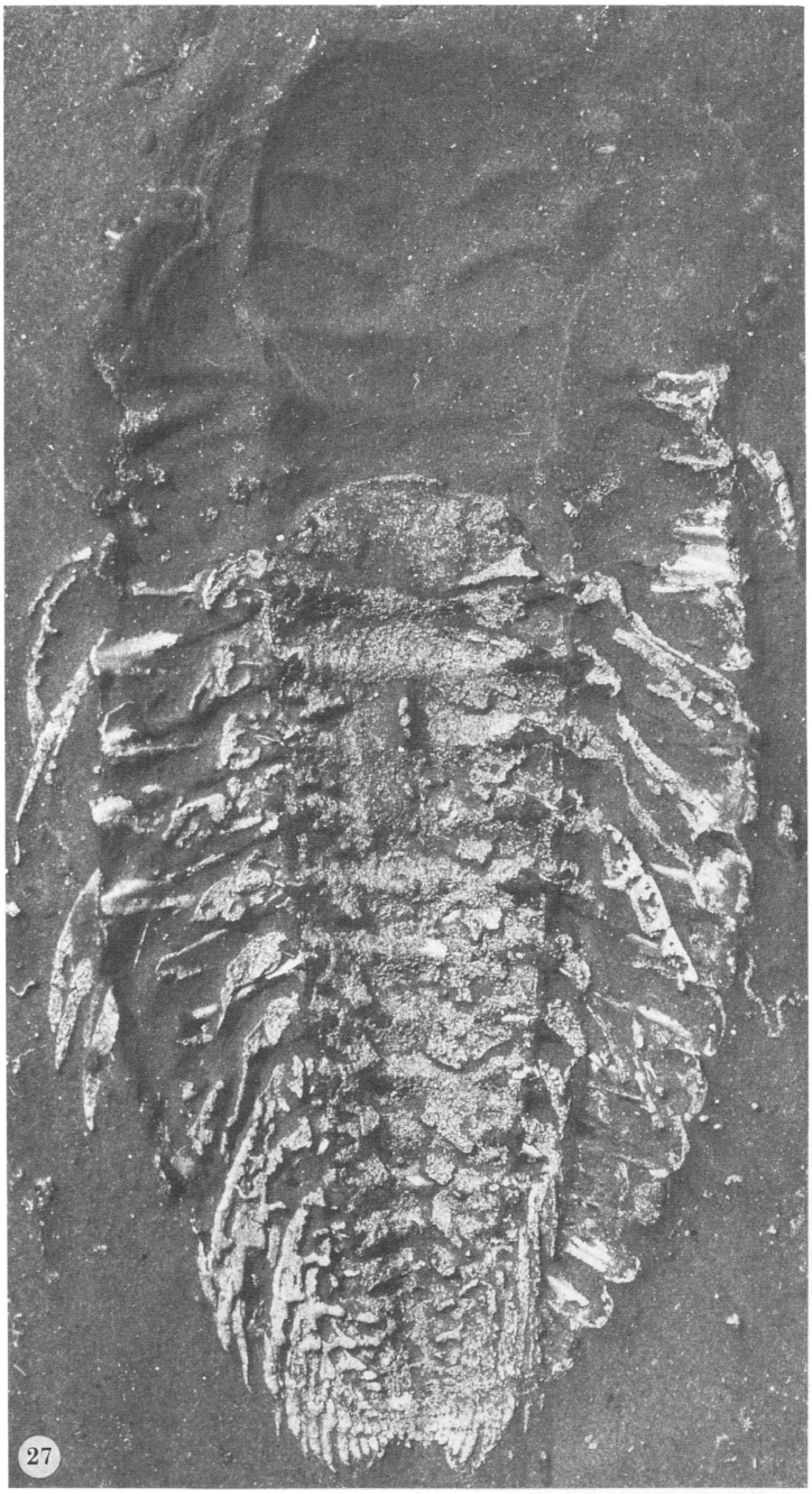
FIGURES 25, 26. For description see opposite.



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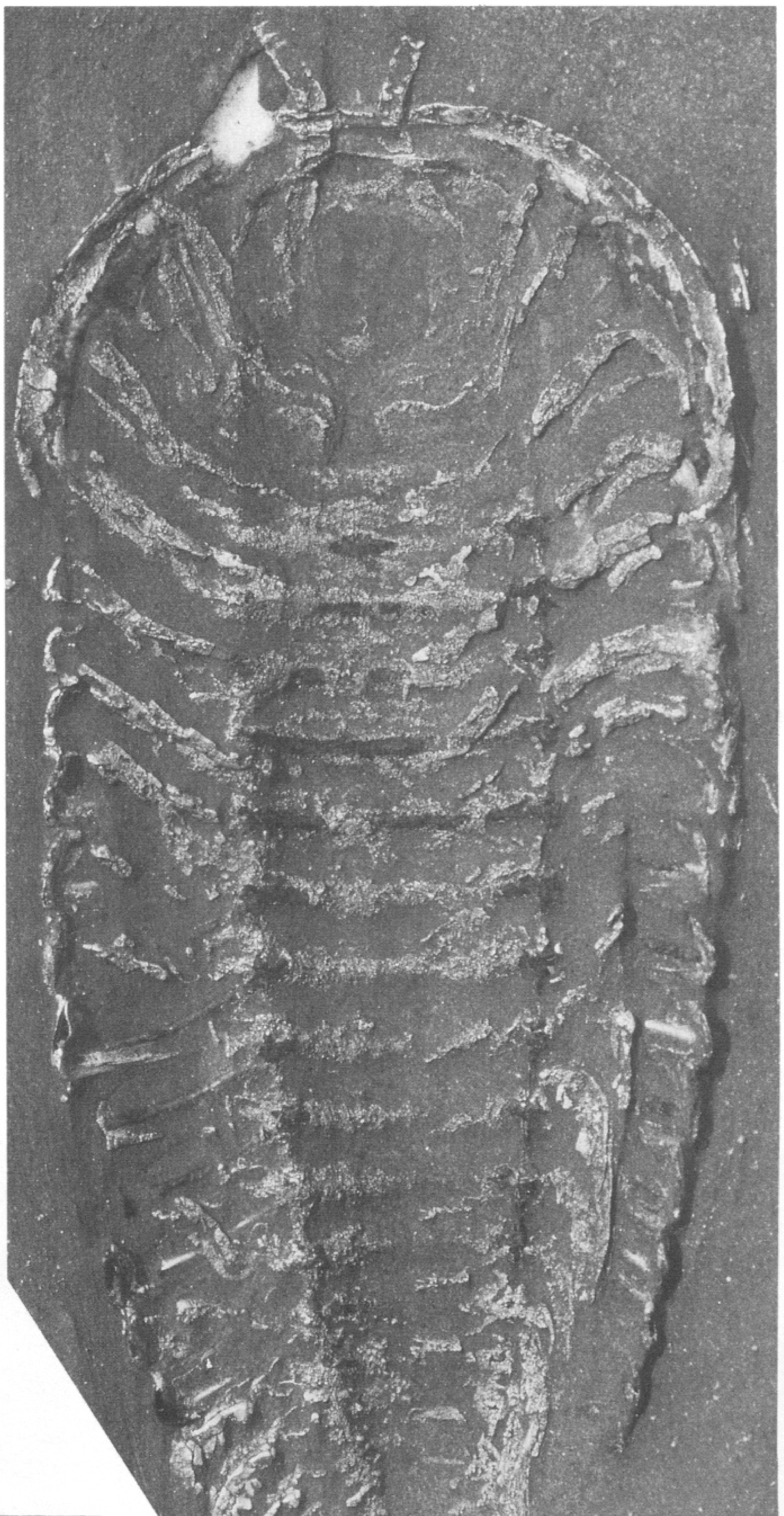

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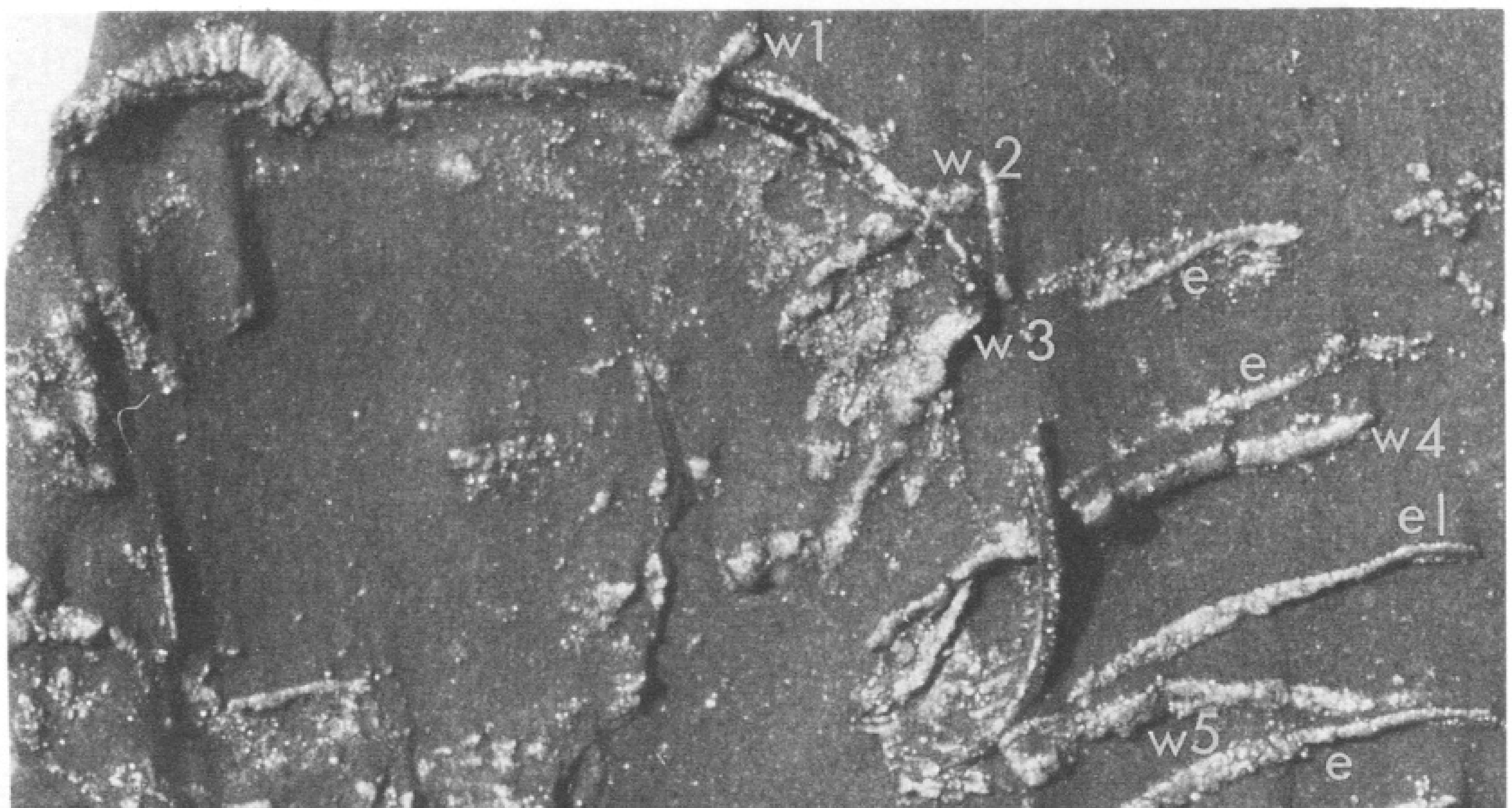

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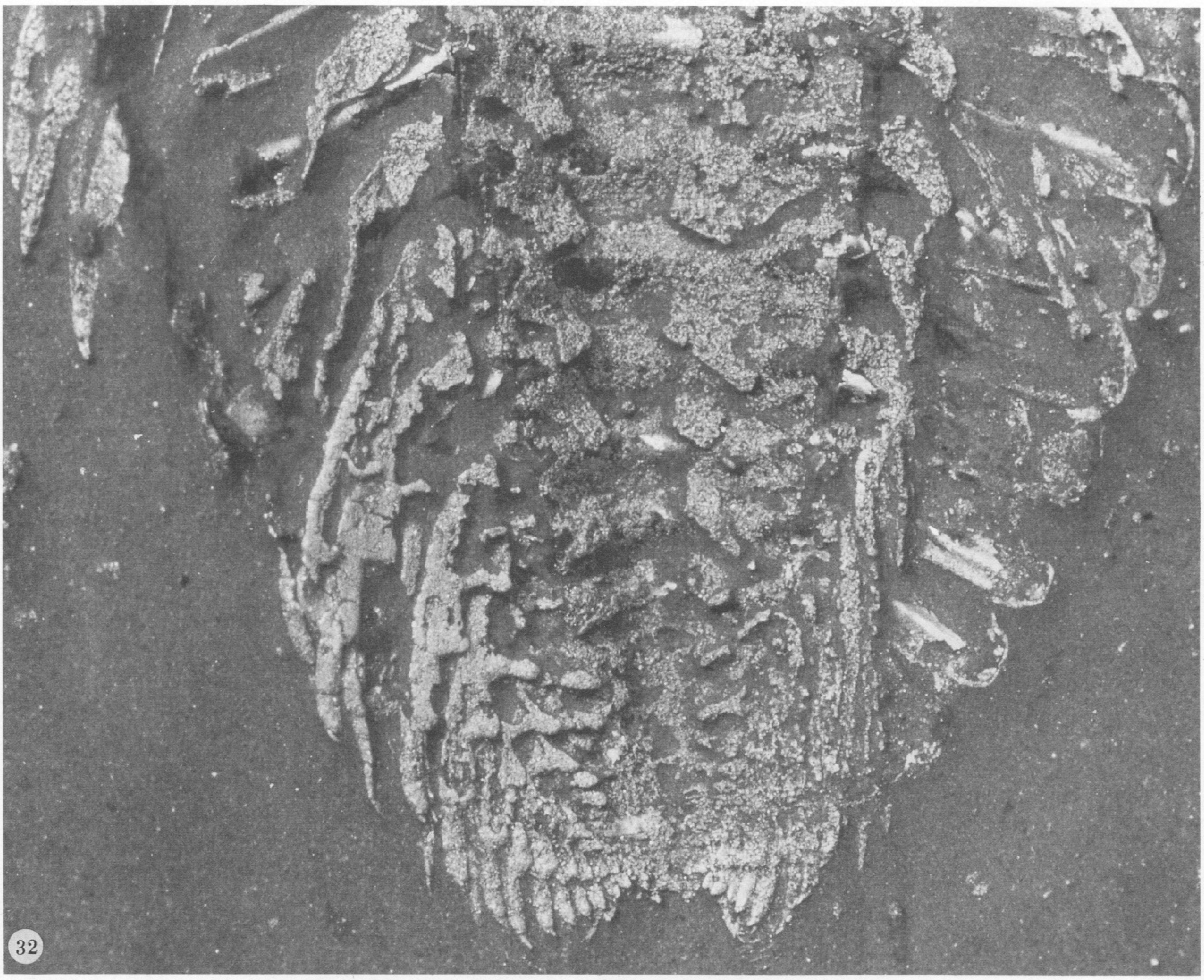
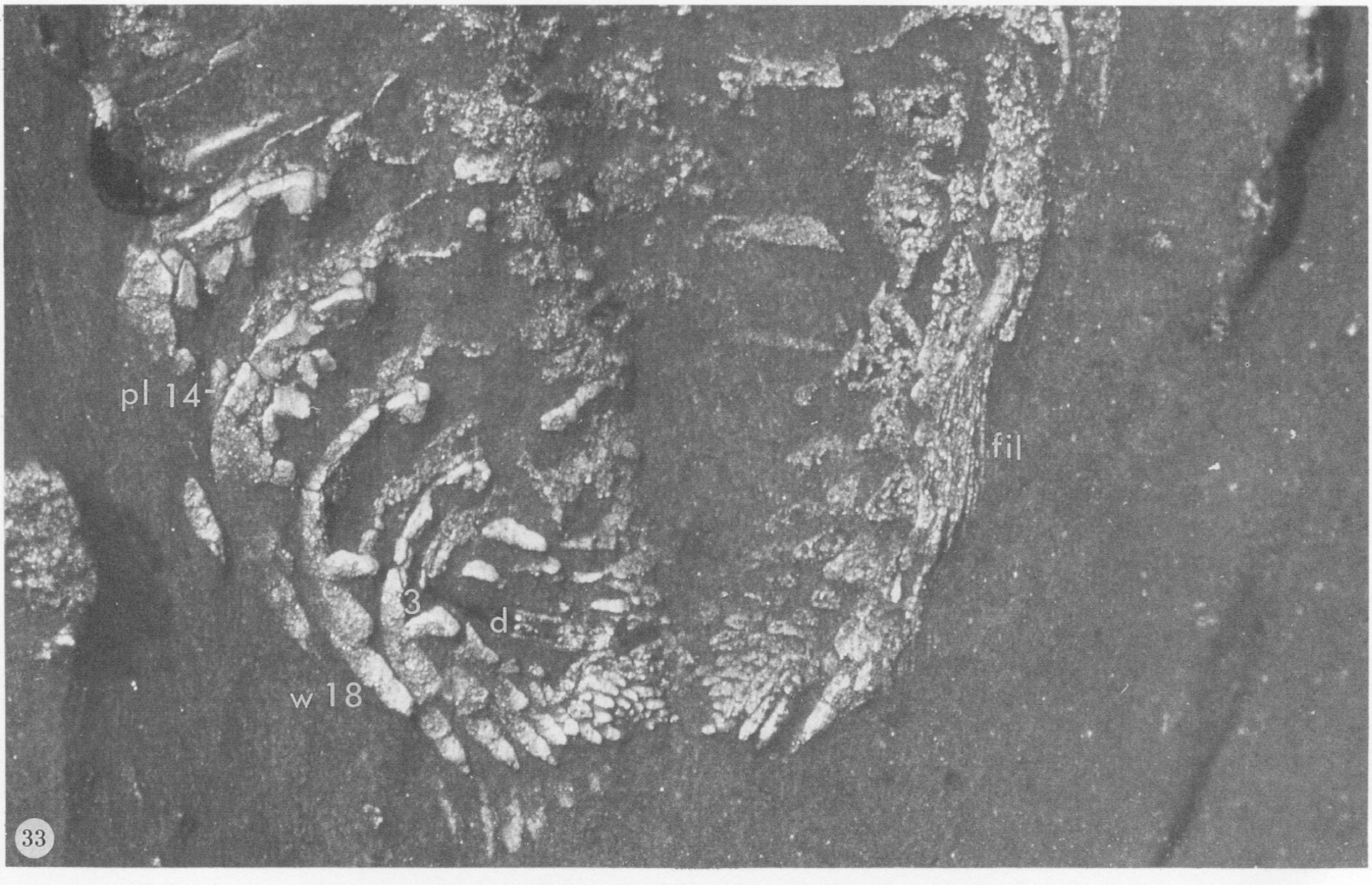
FIGURES 27–29. For description see opposite.





FIGURES 32, 33. For description see opposite.

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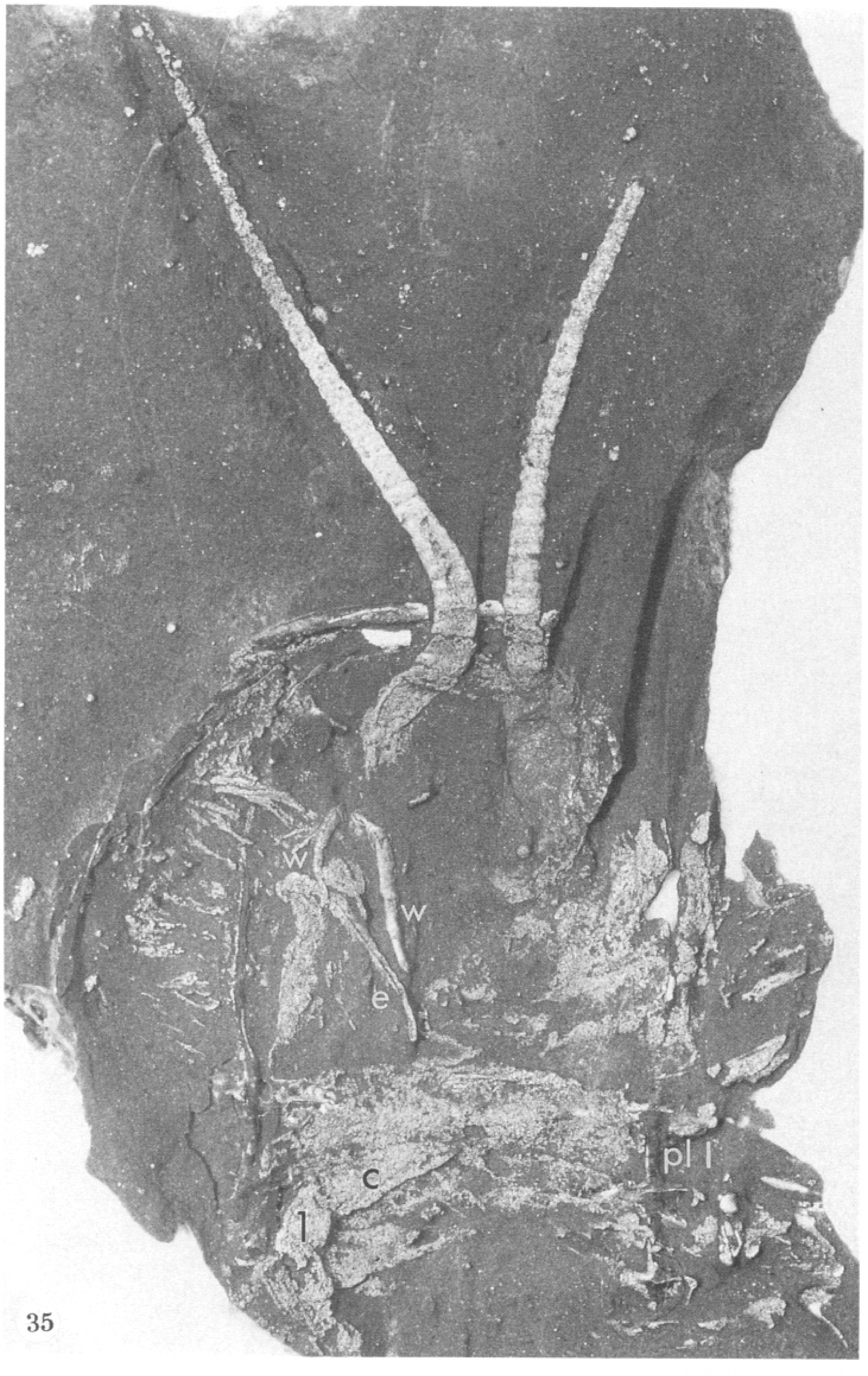

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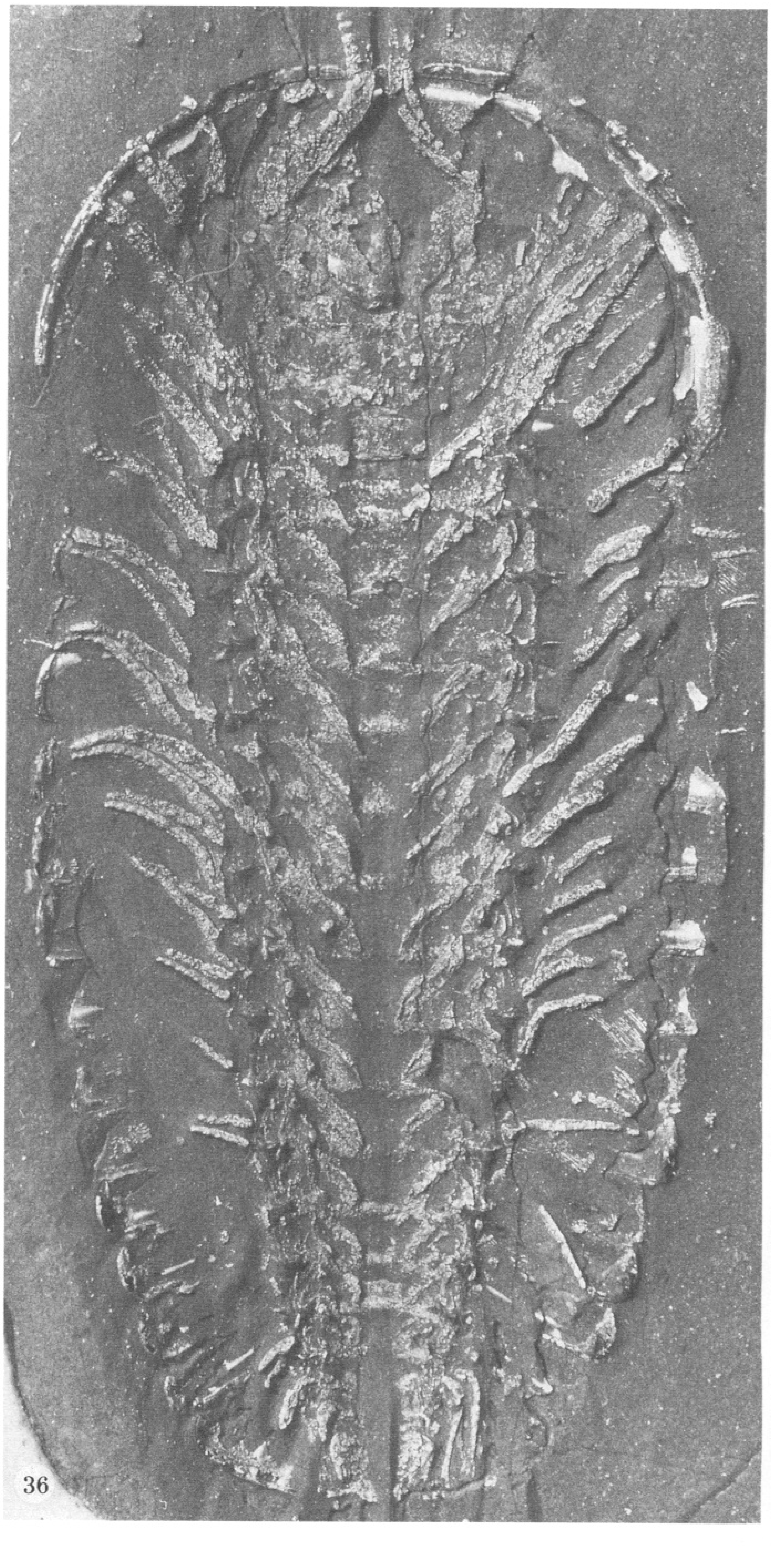

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Figures 34–36. For description see opposite.