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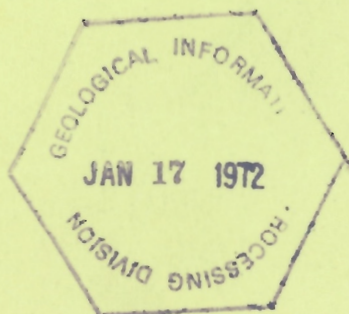
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BULLETIN 209

**REDESCRIPTION OF
MARRELLA SPLENDENS (TRILOBITOIDEA)
FROM THE BURGESS SHALE, MIDDLE CAMBRIAN,
BRITISH COLUMBIA**

H. B. Whittington



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Ottawa
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1971

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FROM THE BURGESS SHALE,
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BRITISH COLUMBIA

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Ottawa, 1971

PREFACE

The Burgess Shale of Yoho National Park, British Columbia, is world famous and unique. It was from these fossiliferous Cambrian beds that Charles D. Walcott, before the first World War, collected and subsequently described, according to the state of paleontological knowledge of that time, a remarkable and diversified group of fossils that represent the primitive ancestors of nearly every Class of arthropod as well as several other animal Phyla.

Because of its importance to geology, zoology, and its significance in the chronology of events in the Cambrian Period, a complete revision of this pioneer work has long been overdue and in 1966 and 1967 the small quarry excavated by Dr. Walcott high on the mountain-side above Emerald Lake was re-opened. New collections were essential because details of the occurrence of various forms present in the fauna were not recorded previously and were necessary for an understanding of the death assemblages to reconstruct the ecology of the time. Experts on many groups of invertebrates have been invited to collaborate, and the fauna and geology of the occurrence will be fully interpreted in modern terms based on present knowledge and techniques. This report describes and illustrates in detail one of the unique soft-bodied forms so remarkably preserved in the Burgess Shale.

Research in systematic paleontology is one of the means by which the Geological Survey of Canada provides data for the calibration of the geological time scale so necessary for precise chronology and correlation of the rocks that make up the geological framework of Canada.

Y. O. FORTIER,

Director, Geological Survey of Canada

OTTAWA, April 27, 1971

BULLETIN 209 — Neue Beschreibung der *Marrella splendens* (Trilobitoidea) aus dem Burgess-Schieferton des Mittelkambriums, British-Columbia
H. B. Whittington

БЮЛЛЕТЕНЬ 209 — Новое описание *Marella splendens* (Trilobitoidea) из бурджесского сланца, средне-кембрийский период, Британская Колумбия.
Г. Б. Уиттингтон

CONTENTS

	PAGE
INTRODUCTION.....	1
SYSTEMATIC DESCRIPTION.....	4
Family Marrellidae— <i>Marrella splendens</i> Walcott, 1912	
General description and summary.....	5
Detailed description and discussion.....	7
REFERENCES.....	22
Table I. Direction of slope of gill branches in specimens from five samples....	14
II. Analysis of amino acids from 0.4 g of fragments of <i>Marrella splendens</i> with 6 <i>N</i> hydrochloric acid.....	17

Illustrations

Text-figures 1–9. Diagrammatic descriptions of fossils.....	25
Plates I–XXVI and Text-figures 10–33. Photographs and explanatory diagrammatic descriptions of fossils.....	31

REDESCRIPTION OF *MARRELLA SPLENDENS*
(TRILOBITOIDEA)
FROM THE BURGESS SHALE, MIDDLE CAMBRIAN,
BRITISH COLUMBIA

Abstract

Previously studied specimens and additional material from old and new collections have been prepared with attention to those oriented obliquely, laterally, and vertically, as well as approximately parallel, to the bedding. New photographs accompanied by explanatory line drawings are given, as well as reconstructions of the animal in various aspects. The cephalic shield was wedge shaped, and bore two large pairs of spines; no compound eye or facial suture of trilobite type has been observed; the presence of a pair of projections on the posteroventral edge of the shield is demonstrated, these projections being part of the labrum. The first two appendages, the anterior of thirty segments, the second six-segmented with the distal five setose, are thought to represent first and second antennae and to have been attached to the body in the posterolateral region of the cephalic shield. The post-cephalic body, of twenty-four to twenty-six somites, ended in a minute telson and lacked pleurae; each somite bore a pair of biramous appendages. The basal segment was long, sub-cylindrical; five additional segments formed what was presumably a walking leg; a branch bearing filaments was attached to the proximal part of the basal segment. This flexible branch may have been in life swung backward and forward and rotated through an arc of some 140 degrees; it may have functioned as a gill. Moulded exoskeletons of the cephalic shield are found extremely rarely; most individuals were complete when entombed. The associated dark stain in the rock, in many places surrounding the posterior part of the body, has yielded by acid extraction nearly a full suite of protein amino acids, suggesting that soft parts had not decayed before burial. These observations support the view that the fossils are of individuals of a living population that was catastrophically buried.

Résumé

Des spécimens étudiés précédemment et de nouveaux spécimens provenant de collections anciennes et récentes, ont été préparés en tenant compte des orientations obliques, latérales et verticales, ainsi que pratiquement parallèles à la stratification. De nouvelles photographies, accompagnées de dessins explicatifs, sont présentées, ainsi que des reconstitutions de l'animal sous divers aspects. La carapace céphalique avait une forme triangulaire et présentait deux longues paires d'épines; on n'observe ni oeil composé, ni suture faciale du type trilobite. On démontre la présence d'une paire de saillies sur le côté postéroventral de la carapace; ces saillies font partie du labre. Les deux premiers appendices, l'appendice antérieur constitué de 30 segments,

et le second appendice composé de six segments avec le cinquième distal sétueux, sont supposés représenter la première et la deuxième antennes, et avoir été rattachés au corps dans la zone postérolatérale de la carapace céphalique. Le corps post-céphalique, composé de 24 à 26 somites, se terminait en un minuscule telson et ne possédait pas de plèvres; chaque somite portait une paire d'appendices à deux branches. Le segment basal était long, légèrement cylindrique, et cinq segments supplémentaires formaient ce que l'on suppose avoir été un membre pour la marche; une antenne portant des filaments était attachée à l'extrémité du segment basal. Cette antenne flexible peut, du vivant de l'animal, avoir été douée de mouvements d'avant en arrière et rotatifs suivant un arc d'environ 140°; elle peut avoir fonctionné comme un appareil respiratoire. On trouve très rarement des exosquelettes résultant de mues de la carapace céphalique, la plupart des animaux étaient complets lorsqu'ils ont été ensevelis. La tache foncée que l'on trouve sur la roche à côté de ces animaux, dans de nombreux cas autour de la partie postérieure du corps, a produit par extraction acide une suite complète d'acides aminés protéinés, ce qui donne à penser que les parties tendres n'étaient pas détruites lors de l'ensevelissement. Ces observations corroborent l'opinion selon laquelle les fossiles proviennent d'individus d'une population en vie qui a été ensevelie lors d'un cataclysme.

INTRODUCTION

A new investigation of the Burgess Shale was begun in 1966 by the Geological Survey of Canada (Aitken, Fritz, and Whittington, 1967; Aitken and Fritz, 1968). The geological setting of the shale has been described by Fritz (1971), and in the same volume the history of paleontological research is reviewed (Whittington, 1971) and the mode of preservation of the fossils considered with reference to *Marrella splendens*. It is the intention of the new investigation that a series of papers should be devoted to a detailed restudy of the fauna and flora of the shale, based on the new collection and earlier material obtained by Charles D. Walcott. This paper is the first of the proposed series, and is devoted to the commonest non-trilobite arthropod in the shale, a species about which much has been written. These earlier accounts differ widely in their interpretations and were based partly on Walcott's original illustrations and partly on examination of additional material. However, the specimens were not completely prepared, and Walcott's illustrations were made in a manner that revealed certain details more clearly than others. I have re-examined and prepared where necessary all the previously studied material, as well as more than a hundred additional specimens, and examined more rapidly the thousands of others. This work showed that an individual specimen is not compressed flat in a single bedding plane, but lies within a thin layer of rock so that, for example, each branch of an appendage, and successive appendages, may lie at differing levels. Further, the individual may not have been entombed morphologically parallel to the bedding, but at any angle to it. Thus when the rock is split parallel to the bedding, an individual may be revealed not only in dorsal or ventral aspect, but in an oblique, lateral or anterior aspect. Since parts of the body lie at slightly different levels in the rock, it is important to examine both part and counterpart of a specimen, for different parts of the body lie on either side of the planes along which the rock has split (Pl. XXI, figs. 1-4). Walcott (and subsequent authors) did not recognize fully the implications of such a mode of preservation for interpretation of original shape, and he retained very few counterparts.

There is no detailed record of how Walcott's photographs were taken, but whether daylight or artificial light was used, it is clear they were made in a manner here defined as 'reflected.' The fossils are preserved as a thin, dark, apparently carbonaceous film, and the surface of this film reflects light since it bears a dense scatter of minute reflective particles. Certain areas of the fossils are more intensely reflective than others, particularly the sites of originally fluid filled canals. If the light source is at an angle of, say, 30 degrees to the axis of the camera, and the specimen placed in a plane at right angles to the plane bisecting this angle, a photograph will show the maximum effect of this reflectivity. Examples of such reflected photographs, taken using ultraviolet radiation, may be compared with Walcott's (e.g., compare Pl. III, fig. 2, with Walcott, 1912, Pl. 25, fig. 4; and compare Pl. IV, fig. 4, with Walcott, 1931, Pl. 22, fig. 7). Most of the photographs used here have been taken in ultraviolet radiation directed at a low angle to the plane of the specimen; such photographs bring out the different levels at which parts of the fossil are preserved, and show features that are

faintly or not at all displayed by reflected photographs. Examples of pairs of the two types of photographs are given in Plates VI to IX, XIII, XIX, XX, XXIII to XXV. Ultraviolet radiation was selected, after experimentation with different types of light source and filters, to give the best definition and detail.

Walcott labelled some features on his earlier photographs (1912), but those of 1931 were not labelled and were considerably retouched, as comparison with the present photographs will show. Other authors have not attempted to show in detail their interpretation of a particular specimen. The present camera-lucida drawings reproduced as text-figures attempt to show the parts of each appendage, the position of joints, setae, filaments, etc., that I observed. They are placed opposite the relevant photographs to facilitate comparison. For simplicity, all the details (e.g., the exact number of filaments on a gill branch), are not shown in the drawing. Further, before making a drawing the specimen was studied in light directed at a variety of angles, so that features such as joints between segments may be shown in a drawing but be difficult to see in a particular photograph. This difficulty is inevitable and doubts about my interpretation of a specimen, as shown in a drawing, may only be resolved by studying the specimen. In interpreting the evidence of a particular specimen, the level at which a particular part of the body—cephalic spine, antenna, appendage or branch of an appendage—lies in the rock is critical. For example, in lateral (Pl. XVII, figs. 1, 2, Text-fig. 26) and oblique (Pl. XXI, figs. 1–4, Text-figs. 28, 29) specimens the right and left first and second antennae lie on either side of the flattened cephalic shield. To show these changes of level and thus relative levels, hachures are used, these being directed down-slope from a solid line which runs along the upper edge of a break in slope. These breaks in slope are minute scarps, produced either when the rock split or by excavation of the specimen, and are revealed by shadows in the photographs. The direction of the radiation in each photograph is given, and has been varied to emphasize these changes in slope.

A considerable amount of new information has come to light, hence the detailed description is lengthy because it includes arguments for and against particular interpretations. I have therefore preceded it with a short general description and summary, which omits detailed references to the literature or figures of particular specimens, but is illustrated by reconstructions of the animal in various aspects.

In the paper discussing the preservation of *Marrella splendens* at various angles in the rock (Whittington, 1971), terms were defined to describe the attitude in the rock of individual specimens: *parallel*, *oblique*, *lateral*, and *vertical*, referring to their approximate attitude to the bedding planes. The parallel, oblique, and vertical positions are further qualified as *backward* or *forward* tilted, backward meaning rotated so that the posterior portion was moved morphologically ventrally; forward, that the rotation was in the opposite sense. Vertical backward means a rotation from the vertical plane so that the animal was tending toward a position lying on its dorsal side, vertical forward the opposite rotation.

Descriptive terminology follows that of Størmer (*in* Moore, 1959, Fig. 15) in the use of 'first antenna' and 'second antenna', and in referring to the biramous appendage as consisting of a 'walking leg' and 'gill branch'. While these terms presume the function, they have the merit of not being the same as terms applied to the biramous appendage of either trilobites or crustaceans, and so not carrying any implication of relationship. Certain terms have been used as defined by Moore and McCormick (*in* Moore, 1969, p. 90–103), such as 'somite' for a division of the body, and 'segment' for an individual component of a limb, connected by a movable 'joint' with the adjoining segment. Sagittal (sag.) refers to the median line, exsagittal (exs.) to a line parallel to the sagittal line, and transverse (tr.) to the direction at right angles. Symbols used on text-figures and plates are explained below; these symbols have also been used in the text.

I am indebted to many friends for help with this work: Drs. C.P. Hughes, D.L. Bruton, and W.D.I. Rolfe have critically discussed the manuscript and illustrations; Dr. Porter M. Kier, U.S. National Museum (abbreviated below as USNM), afforded every facility for study of the Walcott collection; Dr. Donald W. Fisher loaned material for study from the New York State Museum (abbreviated as NYSM); officers of the Geological Survey of Canada (abbreviated as GSC) invited me to take part in collecting and to undertake study of the fossils; Professor Frederick M. Swain, University of Minnesota, and Dr. G.C. Speers, British Petroleum, kindly agreed to undertake the geochemical studies. This study is supported by NERC grant GR3/285, my pencil drawings have been redrawn by John Lewis, and photographs enlarged by David Bursill and Dr. Hughes.

Explanation of Symbols on Text-figures and Plates

- a₁ = first antenna
- a₂ = second antenna
- b = gill branch, suffix denotes somite number following a₂
- ds = dark stain
- f = frontal slope of cephalic shield
- l = lateral cephalic spine; also as prefix indicates left side
- m = median cephalic spine
- mp = median projection in parallel backward specimens
- o = ovate area, probably an ostracode shell, supposed by Walcott to be the labrum
- p = anterodorsal angle of cephalic shield projecting above lateral spine
- pr = paired projection at posteroventral angle of cephalic shield
- r = prefix denoting right side
- t = telson
- v = ventral surface of cephalic shield
- w = walking leg, suffix denotes somite number following a₂
- 1—n = number of somite following a₂, used as suffix to b and w; also as number of joints in a₂.

Hachures show breaks in slope, the solid line at the upper edge of the break, the hachures directed downslope from this line.

SYSTEMATIC DESCRIPTION
Class TRILOBITOIDEA Størmer, 1959

Family MARRELLIDAE Walcott, 1912
Genus *Marrella* Walcott, 1912

Type Species. *Marrella splendens* Walcott, 1912

Diagnosis. Wedge-shaped cephalic shield bearing one pair of lateral spines, one pair of median spines; no compound eye; one pair of projections from posteroventral corners of shield; first antenna long, of some thirty segments, attached at side of posterior half of shield below base of second antenna; latter of six segments, the basal long, the distal five bearing numerous setae. Post-cephalic body of some twenty-six somites and a minute telson, somites subcircular in cross-section, lacking pleurae; each somite bearing a pair of biramous appendages, the basal segment long and subcylindrical, one branch of five additional segments, the other branch tapering and bearing many long, slim filaments.

Geological Horizon. Middle Cambrian, Stephen Formation, *Bathyriscus-Elrathina* Zone, British Columbia.

Marrella splendens Walcott, 1912

Plates I-XXVI, Text-figures 1-33

- 1912 Walcott, p. 193-194, Pl. 25, figs. 1-6; Pl. 26, figs. 1-6.
1918 Walcott, p. 140, 170.
1920 Raymond, p. 115-116, 143, 148, Text-fig. 32.
1921 Walcott, p. 375-376.
1925 Fedotov, p. 387-388, 390-391.
1928 Henriksen, p. 3-6.
1930 Beurlen, p. 502-503, Text-fig. 75.
1931 Walcott, p. 28-37, Pl. 22, figs. 1-9.
1931 Ruedemann, p. 9-16, Text-figs. 4, 5; Pl. 3, figs. 1, 2; Pl. 6, figs. 1-3, Pl. 7; figs. 1-4.
1932 Richter, p. 855, Text-fig. 44A.
1939 Størmer, p. 232-234, Text-fig. 30a.
1944 Størmer, p. 95-98, Text-figs. 19, 5, 6.
1958 Tiegs and Manton, p. 313-314, Text-fig. 6b
1959 Størmer, in Moore, 1959, p. O29, Figs. 14, 3; 15, 1-4.
1962 Simonetta, p. 172-185, Text-figs. 1, 2, Pls. 14-17.
1971 Whittington, p. 1170-1201, Text-figs. 4-24.

Lectotype. USNM 57674, Pl. III, fig. 1, Text-fig. 13, original of Walcott, 1912, Pl. 26, fig. 5, designated Simonetta, 1962, p. 183.

Other material. USNM 57664–57673, 57675, originals of Walcott, 1912, Pls. 25, 26 (57667, 57668, 57670, originals of Ruedemann, 1931, Pl. 7, figs. 3, 4; Pl. 6, fig. 1 respectively; 57666, 57668, originals of Whittington, 1971, Figs. 10, 15); USNM 83486 a–i, originals of Walcott, 1931, Pl. 22, figs. 1–9 (83486b, d, originals of Ruedemann, 1931, Pl. 6, fig. 3; Pl. 7, fig. 2, respectively; 83486e, original of Whittington, 1971, Fig. 8); USNM 83486, original of Ruedemann, 1931, Pl. 7, fig. 1; USNM 166574, original of Ruedemann, 1931, Pl. 6, fig. 2; NYSM 9781, original of Ruedemann, 1931, Pl. 3, figs. 1, 2; USNM 139622–33, originals of Simonetta, 1962, Pls. 14–17; USNM 139634–139673; 139696–139700, studied by Simonetta; GSC 25429–25435, originals of Whittington, 1971, Figs. 6, 7, 9, 12, 14, 16, 22; USNM 165847–8, originals of Whittington, 1971, Figs. 18, 20.

Major additional collections in USNM and GSC, latter including material figured and measured in Whittington, 1971, and herein. The non-trilobite arthropods in the Museum of Comparative Zoology, Harvard University, collected by P.E. Raymond (Rolfe, 1962) include two hundred and two specimens of *M. splendens*.

Locality, Stratigraphical Horizon, Numbers of Specimens. Middle Cambrian, Stephen Formation, Burgess Shale section, *Pagetia bootes* faunule of *Bathyriscus–Elrathina* Zone, situated on the ridge between Wapta Mountain and Mount Field at an elevation of approximately 7,500 feet; longitude 116° 28' 30", latitude 51° 26' 50", 3 miles north of Field, southern British Columbia (see Fritz, 1971, for geology and stratigraphy of the shale).

The part of the Burgess Shale in question is that which Walcott (1912) called the "Phyllopod bed", 7 feet 7 inches thick, and the overlying few feet of beds. The Walcott quarry and the positions of the levels given in Text-figure 1 are shown in Whittington, 1971, Figures 2, 3. Text-figure 1 shows numbers of specimens collected in 1966, and Figure 5 of Whittington, 1971, shows numbers collected in 1967. The peaks are at similar levels in each graph, and the big samples come from thin layers—one hundred and thirty-seven specimens from 5 inches (8 ft. 7 ins. to 9 ft. 0 ins.) in 1966, more than two hundred specimens from 3 inches (6 ft. 11 ins. to 7 ft. 2 ins.) in 1967. There are an estimated twelve thousand specimens in the U.S. National Museum, collected by Walcott, all labelled '35k', i.e., the 'Phyllopod bed' in the Walcott quarry. There is no indication from which particular layer they came.

One slab in the U.S. National Museum, from the *Ogygopsis klotzi* faunule in the Stephen Formation, west side of Mount Stephen (Fritz, 1971, Fig. 1), contains *Olenoides serratus* and a poorly preserved *Marrella* sp.. This is the only specimen of this genus known from other than the Burgess Shale section.

As Text-figure 1 and Figure 5 of Whittington, 1971, indicate, *M. splendens* is present throughout the lower 4½ feet of the Phyllopod bed, and occasionally in 6½ feet of overlying beds; it has not been found higher. It has been found in the same bedding planes as most of the other non-trilobite arthropods.

General Description and Summary

Marrella splendens, the commonest non-trilobite arthropod in the Burgess Shale, has attracted much attention, and the five different reconstructions (Raymond, Walcott, Richter, Størmer, and Simonetta), epitomize progress in understanding of the morphology. Both Walcott and Simonetta realised that the fossils were oriented in different directions in the rock, Simonetta recognizing vertical specimens. Neither author prepared specimens or used counterparts, nor exploited the information offered by lateral and oblique specimens. The new investigation has enabled more closely reasoned reconstructions of the animal (Text-figs. 2–5), but has by no means solved all the problems.

The cephalic shield was subquadrangular in dorsal aspect and bore two pairs of long stout spines; one curved outward and backward from the side, just below the anterior part of the dorsal surface, the other curved upward and backward from the posterolateral corner. Walcott thought that a compound eye was present at the anterolateral margin of the cephalic shield, at the base of the lateral spine, but like *Simonetta* I have been unable to see any evidence of it. The cephalic shield appears to have been wedge shaped, the frontal slope flat and directed downward and slightly backward, the shield tapering to the narrow, flattened ventral surface, the apparently flat sides sloping downward and inward. Both oblique and vertical specimens suggest that the transverse section was triangular, while laterally compressed specimens show a rectangular outline. Walcott believed that there was a labrum on the ventral surface, rectangular in outline, attached to a broad (tr.) flat doublure about half as long (sag. and exs.) as the cephalic shield. However, the shape of the cephalic shield precludes there having been a doublure of such dimensions. A pointed process projects backward and outward from each posteroventral angle of the shield, and is part of the labrum; from between the bases of these processes the posterior wall of the cephalic shield ran steeply upward.

The axial region of the animal is so compacted in all specimens that little is revealed of the ventral side of the cephalic shield, body, and proximal parts of the appendages. The body behind the cephalic shield was apparently subcircular in cross-section, tapering backward, divided into some twenty-four to twenty-six somites, and ending in a minute telson, always obscurely preserved but apparently semicircular in dorsal aspect. Walcott did not consider that pleurae were present; they were introduced by Ruedemann, based upon a misinterpretation of one of Walcott's original illustrations. Subsequent authors have retained them, but I find no evidence of them.

The first appendage projected forward and slightly outward, was flexible and composed of some thirty segments. The segments became longer distally, those immediately in front of the cephalic shield had setae projecting from the joints between them. This appendage was inserted low down on the side of the cephalic shield, behind the mid-length. The second appendage was apparently inserted immediately above and behind the first, and was shorter and stouter, the appearance plumose because of the fine setae closely spaced along the distal five segments. The basal portion is here considered to have been a single, long proximal segment, lacking setae, which projected forward or outward. These two appendages have been referred to as the first and second antennae, but the exact manner of their attachment cannot be seen, and they may have been branches of a single appendage.

Behind these appendages were some twenty-four to twenty-six pairs of similar, biramous appendages, progressively diminishing in size posteriorly. The basal segment is elongated, subcylindrical in form, and articulated with it were five similar segments, the distal bearing three bristles. The second branch was attached to the most proximal part of the basal segment, and consisted of an elongate, cone-shaped rod which bore many fine filaments, longest proximally. The first eight to nine of the five-segmented branches diminish slightly in length posteriorly, the remainder show a more rapid diminution, and segments one to four display a progressively increasing distal expansion. The first eight or nine branches functioned as walking legs. The remainder, when curved downward and inward, formed a net because of the expansions and may have functioned in food trapping and filtering. The filament-bearing branches were flexible, and are preserved sloping downward and forward or backward. In life the branch could have been swung forward and backward and rotated (Text-fig. 9), allowing a rowing-like motion. The branch could have functioned as a gill and the movements may have helped in swimming and in catching and sweeping food particles to the ventral side of the body. In many parallel specimens the first walking leg may be preserved

projecting outward and forward between the first and second antennae. In parallel backward specimens as many as six legs may be in this position. Such specimens led Simonetta to consider that the second appendage was biramous, one branch a walking leg, the other the second antenna. Reasons for rejecting this interpretation are given here.

As Walcott observed, the position of the alimentary canal and of fluid-filled canals in the spines of the cephalic shield and the appendages, are shown by bands or areas of high reflectivity. In oblique specimens, such areas suggest that the mouth was situated on the posterior wall of the cephalic shield and that the alimentary canal within the cephalic shield was U-shaped, posteriorly extending along the axis of the body. Canals which traversed the cephalic spines appear to have been connected proximally to the alimentary canal. Characteristic of specimens of *M. splendens* is a dark stain surrounding the posterior part of the body and extending outward for some distance. The stain may extend around the entire body or even in front of it. Geochemical investigations show that the stained area contains organic material different from that in the bulk rock, probably representing protein residues. This organic material may have been squeezed out of the body during compaction of the sediment after burial.

Nearly all specimens are of complete individuals with traces of soft parts and the dark stain, which argues strongly for their having been whole animals when buried, and not empty, moulted exoskeletons. Measurements of sagittal length of individuals showed a range from 2.5 to 19 mm, and in five samples a bimodal distribution was evident (Whittington, 1971, Fig. 23). This distribution may reflect sexual dimorphism, though no other morphological evidence for such dimorphism was observed. The separation between the two peaks was 5 to 7 mm, an amount apparently too great to be that between successive instars. The implication of these observations is that a particular layer containing abundant *M. splendens* is a biocoenosis, the population having suffered a catastrophic death. The mode of preservation at all angles in the fine sediment suggests that the animals were overwhelmed by a moving cloud of sediment travelling along the sea bottom, and were buried as it settled. If these deductions are correct, then *M. splendens* must have inhabited the basal water layers of the benthonic environment, walking on the bottom or drifting and swimming close to it. The absence of individuals smaller than 2.5 mm long suggests that the early developmental stages may have been passed in a different environment, perhaps the surface waters.

The present investigation supports Simonetta's claim that no compound eye, or suture of trilobite type, is present in *Marrella*, and finds no evidence of pleurae; a labrum was present, but not attached to a broad doublure as in trilobites. It is debatable whether or not the presence of supposed first and second antennae indicates crustacean affinities. The succeeding biramous appendages are alike, and of general trilobite type in that there is a walking leg from the most proximal part of the basal segment out of which arises a filament-bearing branch. Neither branch is like that of any known trilobite, the walking leg having one (or two?) segments less than known in trilobites, the filament-bearing branch being differently constructed.

Detailed Description and Discussion

Cephalic Shield

The subrectangular outline of this shield in dorsal view has been known since Walcott's first description, but Simonetta (1962, Pl. 16, upper right figure, Text-fig. 1b, *see* this paper, Pl. IV, figs. 2, 3) was the first to attempt an anterior view, based on his recognition of a vertical-backward specimen. Simonetta did not, however, consider laterally compressed

specimens or the effects of compression on oblique specimens. The present restorations (Text-figs. 2–5) are based on such considerations, and show a wedge-shaped cephalic shield, subtriangular in cross-section, with the lateral spine coming off the anterior part of the side closer to the dorsal than to the ventral surface. The anterolateral corner of the cephalic shield, rounded and slightly inflated, is shown to project above the base of the lateral spine by lateral (Pl. XVII, figs. 1, 2) and oblique (Pl. VI, fig. 3; Pl. VIII, fig. 3; Pl. XVI, fig. 1; Pl. XXI, figs. 1, 2; Whittington, 1971, Fig. 15), specimens. In parallel specimens (Pl. III, fig. 1; Pl. IV, fig. 1; Pl. XXVI, fig. 1) compaction resulted in the slope above the base of the spine being flattened, thus giving a line or change of level that was first interpreted by Walcott (1912) as the junction between ‘antennule’ and cephalon; later (1931, p. 30) as a suture separating the spine (‘free cheek’) from the median part of the cephalon (i.e., the ‘cranidium’). I agree with Simonetta that this line represents the position of a sharp change in slope. Walcott (1912, Pl. 25, fig. 5; *see* Whittington, 1971, Fig. 15) labelled the anterolateral angle of the cephalic shield as the eye. He also labelled a semicircular area on a lateral specimen (1912, Pl. 25, fig. 4; Pl. I, fig. 4; Pl. III, fig. 2) as the eye. Judging by its position, and that of the right lateral spine, this area may well be the proximal part of the left lateral spine. The specimens that indicated the visual surface of the eye to Walcott (1931, p. 30) have not been traced, and I agree with Simonetta that compound eyes were absent for I have seen no structure, or area showing facets, that indicates their presence. The lateral spine was stated by Walcott (1931, p. 28) to have, and portrayed by Simonetta as having, a median dorsal ridge. It is difficult to be sure which side of the spine is being observed in a particular specimen, but many (Pl. II, fig. 1; Pl. IV, fig. 1; Pl. IX, fig. 1; Pl. XIV, fig. 1) suggest the presence of a groove in the dorsal surface, situated closer to the inner than the outer side. The appearance of a jagged inner edge claimed by Ruedemann (1931, p. 11–12) is merely that of an incomplete or unprepared specimen. However, minute serrations may be observed in some specimens (Pl. V, fig. 3; Pl. XXI, fig. 3) on the outer edge of the distal part of the lateral spine; such serrations are indicated in Walcott’s (1931) Text-figure 9. Lateral (Pl. XVII, figs. 1, 2; Pl. XXV, fig. 1), oblique (Pl. XXI, figs. 1, 3), and vertical (Whittington, 1971, Figs. 20, 21) specimens show that the pair of median spines of the cephalic shield curved upward as well as backward, and distally curved down; in dorsal aspect the curvature was convex outward, distally becoming straight with a slight turning out at the tip (Pl. I, fig. 2; Pl. XII, fig. 2; Pl. XX, fig. 1). Small spines along the edges were largest proximally on the outer side, smaller medially and present on both edges (Pl. X, fig. 2; Pl. XIV, fig. 2), diminishing in size progressively distally. Simonetta claimed that the spine was triangular in cross-section, the median ridge bearing small spines like the lateral margins, but I cannot confirm such a structure.

Lateral specimens (Pl. XVII, figs. 1, 2; Pl. XXV, fig. 1) show in profile the steep, slightly backwardly inclined frontal slope of the cephalic shield, the sharp, downward-projecting anteroventral angle, and the slightly undulating but approximately horizontal ventral surface. Oblique, backward-tilted specimens (Pl. XVI, fig. 1; Whittington, 1971, Figs. 10–13) exhibit a triangular median projection at the anterior edge of the cephalic shield. One side of this projection is continuous with the anterior, dorsal margin of the cephalic shield (*f in* Text-fig. 25, cf. Pl. XVI, fig. 1) and is the obliquely crushed frontal slope; the other side (*v in* Text-fig. 25; cf. Pl. XVI, fig. 1) runs back from the tip to pass ventrally beneath the base of the opposite lateral cephalic spine and is the crushed ventral margin of the shield. The position in which the antennae are preserved in this specimen, la_1 lying above *f* and ra_1 lying below *v* (Pl. XVI, fig. 1; Text-fig. 25) that is on either side of the ventral part of the shield, confirms this interpretation. A triangular projection, the point truncated, at the median, anterior margin of the cephalic shield, may also be observed in parallel, back-

ward-tilted specimens (Pl. XII, fig. 1; Pl. XV, figs. 1, 2). This projection suggests that the sides of the shield sloped inward, and that there was a narrow, flat ventral surface. Thus the cephalic shield appears to have been wedge shaped in cross-section, the ventral surface being the narrow end of the wedge. Vertical-backward specimens (Pl. XIII, figs. 2, 3) also show this triangular cross-sectional shape. The tip of the projection, in parallel-backward specimens, may be expanded to give a blunt arrowhead appearance (Pl. XV, figs. 1, 2), suggesting that the sides of the shield turned out just before meeting the ventral surface, at least at the anteroventral tip of the shield. Simonetta (1962, p. 178, Pls. 15, 17) interpreted the projection in backward-tilted specimens as being the labrum (hypostome) pushed in front of the remainder of the shield, and described the apex as denticulate, possibly because he interpreted the arrowhead appearance as denticles.

The claim that a labrum was present, attached along an anterior sutural margin as in the hypostome of trilobites, was made by Walcott (1912, Pl. 26, fig. 2; 1931, p. 29, Text-fig. 9), who stated that there were two spines on the posterior margin and one at the posterolateral angle. Walcott regarded the labrum as being attached to a broad doublure of the cephalic shield, this doublure being of length (sag. and exs.) equal to the width of the lateral cephalic spine, the width (tr.) equal to that of the median anterior part of the cephalic shield. No detailed evidence for these statements was offered, and Raymond's (1920, Text-fig. 32) restoration of the labrum is based on Walcott's 1912, Plate 26, figure 2 (*see* Pl. 1, fig. 1). Størmer (1944, Text-fig. 19, 6; *in* Moore, 1959, Text-fig. 15, 4) followed Walcott, but Simonetta (1962, Text-fig. 2, p. 178) shows a narrower (tr.) plate, which tapers back and has spines along the posterior margin. My interpretation of the wedge shape of the cephalic shield is like that of Simonetta's, and implies that there can be no broad (tr.) doublure of the shield as assumed by Walcott. As explained above, I interpret the triangular projection in backward-tilted specimens as the crushed anteroventral part of the shield, and not as the labrum. Details of the ventral surface of the shield are obscured by compaction in parallel specimens; certain examples (Pl. VII, figs. 1-3; Pl. XVIII, fig. 4; Pl. XXVI, figs. 1, 2) suggest the narrow, elongate shape of the ventral part of the shield. Other specimens (Text-fig. 6; Pl. III, fig. 1; Pl. XX, fig. 1) suggest that the posteroventral margin of the shield may have been transverse and less than half as wide (tr.) as the dorsal width of the shield. This transverse line lies anterior to the dorsal margin of the shield (between the bases of the median spines) and is not an impression of the dorsal margin resulting from compaction.

Lateral (Pl. XVII, fig. 1; Pl. XXV, fig. 1) and oblique (Pl. VI, fig. 3; Pl. XXIV, figs. 1-4) specimens show a curved, elongated, backwardly directed projection from the posteroventral edge of the cephalic shield. A unique parallel specimen (Pl. XXIII, figs. 1, 2) shows that there is not a single projection but a pair, arising from the ventral, posterior corners of the shield. The posterior wall of the shield appears to have curved upward between the bases of the projections; the transverse posteroventral margin referred to in the previous paragraph may be the impression of this wall. The two projections appear to be parts of a labrum that projected back below the mouth (presumably situated in the posterior wall) and between the proximal parts of the first two biramous appendages. The original of Walcott's 1912, Plate 26, figure 2 (Pl. 1, fig. 1), is an incomplete, oblique specimen, exposed from the ventral side, poorly preserved, and his illustration was retouched. An oval plate with a broad border and convex median area, is not clearly outlined in the manner shown by Walcott and Raymond. An irregularly ovate area on the shield is visible and may result from the compaction of the shield over one of the small, ostracode-like shells (Archaeocopida?) occurring in the fauna. Other specimens (Pl. 1, figs. 2, 3) show such shells more clearly, lying in a similar position.

Post-cephalic Body

This projects beyond the posterior margin of the cephalic shield, is narrower (tr.) than the shield, and tapers gently posteriorly. Commencing to count at the somite bearing the first walking leg, some twenty-six or twenty-seven somites (Pl. III, fig. 1; Pl. XIII, fig. 1) have been observed. In parallel specimens (Pl. III, fig. 1; Pl. VII, figs. 1–3) the body is extended straight back between the median spines, in some instances (Pl. VIII, figs. 1, 2; Pl. IX, figs. 1–3) showing a slight curvature posteriorly. In lateral specimens (Whittington, 1971, Figs. 16, 17; Pl. XVII, figs. 1, 2; Pl. XXV, fig. 1) the body is straight or curves slightly posteriorly. In oblique specimens (Pl. XXI, figs. 1–4; Pl. XXIV, figs. 1–4) the maximum curvature observed (Pl. XVII, fig. 3) is not more than 30 degrees. There is no evidence of the body having been capable of more than such limited curvature in any direction. Presumably the cross-section was circular or oval in outline; lateral and oblique specimens show that the appendages were attached on the ventral side. The body rings, flattened by compaction, are shown by parallel specimens exposed from the dorsal (Pl. III, fig. 1; Pl. IX, fig. 1) or ventral (Pl. VIII, figs. 1, 2; Pl. XVIII, fig. 4) side, a shallow step downward posteriorly delineating the posterior margin. Oblique specimens (Whittington, 1971, Figs. 16, 17; Pl. XXI, figs. 1, 3) show the tergites in sublateral aspect after compaction. In no specimen are the sternites or the way in which the appendages are inserted clearly seen. The most posterior somites and the telson are small and difficult to see; the better-preserved specimens (Pl. XIII, fig. 1; Pl. XVIII, fig. 1; Pl. XX, fig. 1) suggest that the telson is short (sag.) and rounded posterolaterally. In reflected light (Pl. XIX, fig. 2; Pl. XX, fig. 3; Pl. XXIV, fig. 2) certain specimens show an irregular, subcircular, reflective patch at the posterior end of the body that is considerably wider than the last few somites. Walcott (1912, Pl. 26, figs. 1, 6) termed this patch the 'abdomen'. In low-angle illumination (Pl. XII, fig. 2; Pl. XIX, fig. 1; Pl. XX, fig. 2; Pl. XXIV, fig. 1) this patch is not preserved in the same manner as the body rings in front of it, and specimens with a well-preserved tip do not show it. The patch appears to be rather a part of the dark stain (*see* below). The lateral margin of the tergite is not clearly defined and there is no evidence of a pleura, particularly not a pleura of the trilobite type separated from the axial ring by an axial furrow (Pl. 1, fig. 2; Pl. III, fig. 1; Pl. VIII, fig. 1; Pl. XVI, fig. 2; Pl. XVIII, fig. 1; Pl. XX, fig. 1).

The number of somites bearing biramous appendages is more than shown by Simonetta (1962, Text-fig. 1). Neither Walcott (1912, 1931) nor Raymond (1920) claimed that pleurae were present. Ruedemann (1931, p. 13–14, Text-figs. 4, 5), as part of his interpretation of *Marrella splendens* as a freshly moulted trilobite, suggested that the proximal parts of the pleural exoskeleton were represented in the originals of Walcott's 1912, Plate 26, figures 1 (Pl. XII, fig. 2), 4, 6, and particularly in the first of these. This latter specimen is exposed from the ventral side, and between the median cephalic spines the body rings and proximal parts of the gill branches are preserved. The striations across these branches are visible, the branches being broken off at the line of the inner edge of the median spine. In the originals of Walcott's figures 4 and 6 the structures referred to are either gill branches or walking legs. Størmer (1944, p. 95, Text-fig. 19, 5; *in* Moore, 1959, p. O 29, Text-fig. 15, 3) believed that pleurae were present on the basis of Ruedemann's and Beurlen's (1930, Text-fig. 75) sketches, but both these drawings are based on misinterpretations of Walcott's figures. Simonetta was uncertain of the existence of pleurae and unable to see them clearly, but nevertheless portrayed narrow (tr.) pleurae. I am unable to see any structures that I can accept as pleurae.

Two Anterior Appendages (a_1 and a_2)

The first of these, as seen in dorsal aspect in parallel specimens (Pl. X, fig. 3; Pl. XI, fig. 1; Pl. XVIII, fig. 6; Whittington, 1971, Fig. 9), projects in front of the cephalic shield at 15 to 30 degrees to the sagittal line, is variously curved and was clearly flexible. The segments are longer and slimmer distally (Pl. XII, fig. 1), some twenty to twenty-two being visible, the eight to ten adjacent to the cephalic shield having setae inserted at the articulations. These setae are longest proximally, may be double on the inner side, and when seen on the outer side (Pl. XVIII, fig. 6) are shorter and single. The proximal part of a_1 , which lay beneath the cephalic shield, is incompletely preserved in one example (Pl. XI, fig. 1); some seven additional segments are visible, suggesting a total of about thirty. Simonetta describes, but does not portray (1962, Figs. 1, 2) the longer distal segments, and I have not observed setae at the articulations beyond the position described.

The appendage lying next is that described by Walcott as the mandible, by Størmer as the second antenna, and by Simonetta as the exopod of the first biramous appendage. Walcott (1912, Pl. 25, fig. 3; see Whittington, 1971, Figs. 10, 11; Walcott, 1912, Pl. 26, fig. 3; see Pl. II, figs. 1, 2) described the nature of this appendage, but his restoration (1931, Text-fig. 9) is at variance with his description, for it does not show the plumose appearance. Richter and Størmer portrayed it more correctly, as did Simonetta, but I cannot accept the details of any of these versions. I consider it to have been a six-segmented appendage, the basal segment long and lacking setae, the distal five segments of approximately equal length (about one quarter that of the basal segment) and setose. The basal segment is preserved directed at between 45 and 110 degrees to the sagittal line, straight or slightly curved (Pl. XIV, figs. 1, 2; Pl. XV, fig. 2; Pl. XVIII, fig. 4; Pl. XIX, figs. 1, 2). It has not been observed to be flexed in these specimens, or in others in a wide variety of orientations (Pl. XXI, figs. 1-4; Pl. XXII, figs. 1, 2; Pl. XXVI, figs. 1, 2), as might be expected if it had been divided by joints. Walcott (1931, p. 31), considered that this portion was divided into four segments, but his illustrations (1931, Pl. 22, figs. 2, 3, 6, 7) were retouched. Study of the originals, in low-angle illumination and reflected (Text-fig. 6, Pl. IV, figs. 1, 4; Pl. VI, figs. 1, 2; Pl. VIII, figs. 1, 2) does not convince me of the presence of joints in this basal portion of the appendage nor of setae inserted at these joints. Some of the irregular lines apparently taken by Walcott as indicating the position of the joints may be observed, for example, in ra_2 of the original of Plate VI, figures 1, 2. However, this specimen shows folds and wrinkles in the integument, running north-northeast, resulting from compaction, and I consider that the irregular lines are these wrinkles, and not the indication of original joints. The latter, present in the distal part of the appendage, are more distinct (Pl. VI, figs. 1, 2, Text-fig. 16). Simonetta shows a basal and three additional segments making up this proximal part of the appendage, but of the specimens he refers to, only the original of Plate X, figure 1, shows this portion. I consider the part extending outward and forward as far as the lateral spine to be a single segment, for it is not clearly divided by articulations, as is the distal portion which is visible outside the lateral spine.

The most difficult questions regarding these two anterior appendages concern their mutual relationship. Does each belong to a separate somite (Walcott, Størmer), or are they branches of the biramous appendage of one somite? Does the many-jointed one (a_1) belong to a separate somite while the other (a_2) is one branch of a biramous appendage, the other branch being the first walking leg (Simonetta)? The preservation of the specimens, and especially the compaction of the cephalic shield and appendages below it, is such that it is difficult to distinguish details (cf. Walcott, 1931, p. 36). Thus unequivocal answers to these questions cannot be given, the varied opinions being an expression of the difficulties. Among the relevant points are the following:

1. Many parallel specimens show, as the proximal parts of a_1 and a_2 are followed from inside the lateral cephalic spine toward the margin of the cephalic shield, that a_1 goes ventrally beneath the most proximal part of a_2 (Pl. III, fig. 1; Pl. V, fig. 1; Pl. IX, fig. 1; Pl. XIII, fig. 1; Pl. XX, fig. 1). An extremely thin layer of rock may separate them. Vertical specimens (Pl. XIII, figs. 2, 3; Whittington, 1971, Figs. 18–21) show the base of a_2 situated high up on the side of the cephalic shield. Oblique specimens (Pl. XXI, figs. 3, 4; Whittington, 1971, figs. 14, 16, 17) show also that the most proximal part of a_1 lay ventral to the base of a_2 , and that the bases of the two appendages were situated close together, at the side of the cephalic shield below the base of the median spine. Simonetta (1962, Text-fig. 2a) portrays a_1 as emerging from the side of the shield well in front of a_2 , but the specimens referred to, and the original of Plate XI, figure 1, lead me to reject this view.

2. No specimen shows clearly the most basal parts of a_1 and a_2 , and whether a_1 was a branch from the ventral side of the most proximal part of a_2 , or whether it was a separate appendage that emerged from the cephalic shield at a point immediately anteroventral to the base of a_2 . I have adopted the latter view (Text-figs. 3, 5). In no specimen have a_1 and a_2 been observed lying approximately parallel to one another, and one below the other, as might be expected if they were branches of a biramous appendage. Rather, in parallel specimens, a_1 and a_2 , even if both extend forward, lie at an angle of at least 20 degrees to each other (Pl. XIII, fig. 1; Pl. XIV, figs. 1, 2) and more usually a_2 is directed sideways and there is an angle of 45 to 80 degrees between the two (Pl. III, fig. 1; Pl. V, figs. 1, 2; Pl. XV, fig. 2). These positions suggest that a_1 and a_2 may have belonged to separate somites, and if this is assumed they may be called first and second antennae (Størmer, *in* Moore, 1959, Figs. 15, 3).

3. In many parallel specimens (Pl. III, fig. 1; Pl. IV, figs. 1, 4; Pl. V, figs. 1, 2; Pl. VII, figs. 1, 3; Pl. VIII, fig. 1; Pl. XI, fig. 1; Pl. XIV, figs. 1, 2; Pl. XXVI, figs. 1, 2) one walking leg may be preserved with the distal part projecting forward and outward between a_1 and a_2 . In other parallel specimens (Pl. II, fig. 1; Pl. X, fig. 3) two legs may be in this position, and in some parallel backward-tilted specimens as many as three (Pl. XV, fig. 1) or four (Pl. XII, fig. 1) legs. Because of compaction it is difficult to trace the position of the proximal parts of these walking legs. Thus in the original of Plate XXII, figures 1, 2, the most anterior walking leg (w_1) on either side may be regarded as being attached to the same segment as a_2 , or, as I consider more likely, to the following segment. Simonetta (1962, Text-figs. 1a, 2a, p. 179) interpreted such specimens (Pl. XI, fig. 1; Pl. XII, fig. 1) in the former manner (i.e., as showing that a_2 was a branch attached to the basal joint of the first walking leg). Examination of these and other specimens does not convince me that this interpretation is correct. For example, in the original of Plate XXVI, figures 1, 2, in which the first walking leg extends forward and outward between a_1 and a_2 , it has been shown by preparation that it crosses proximally beneath the basal part of a_2 , as it does in other specimens (Pl. II, figs. 1, 2; Pl. III, fig. 1; Pl. V, figs. 1, 2; Pl. VII, figs. 1–3). In certain parallel specimens (Pl. VI, figs. 1, 2; Pl. IX, figs. 1–3; Pl. X, fig. 1; Pl. XX, fig. 1; Pl. XXIII, figs. 1, 2) the first walking leg appears to be attached to the somite behind that bearing a_2 ; oblique and vertical specimens (Pl. XXI, figs. 3, 4; Whittington, 1971, Figs. 16–19) support this interpretation. This combination of evidence from specimens in a variety of orientations leads me to reject Simonetta's view and consider that the first walking leg (w_1) is attached to the somite following that bearing the second appendage (a_2).

Succeeding Biramous Appendages

All authors are agreed that each somite behind that bearing the second antenna (a_2), bears a pair of biramous appendages, each half consisting of a walking leg and a gill branch.

Some twenty-four to twenty-six somites are behind that bearing a_2 ; the original Plate XVIII, figure 1, shows that walking legs were on the posterior somites; while the original of Plate XIII, figure 1, shows that gill branches were also present. The twenty-six pairs of appendages shown in the restoration is the same number as Walcott (1931, Text-fig. 9) showed, but more than Simonetta (1962; 21 *in* Text-fig. 2a).

The basal segment of the appendage, 'protopodite' of Walcott (1931, p. 32, Text-figs. 9, 10), was described by this author as more or less cylindrical in form, tapering to a point at the proximal end. Størmer (1944¹, Text-fig. 19, 6; *in* Moore, 1959, Text-figs. 14, 3; 15, 4) accepted this view, but Simonetta (1962, p. 179, Text-figs. 2a, b) introduced an admittedly conjectural reconstruction of a short, broad basal segment bearing denticles. He cites no specimens in support of this view, and I have been unable to find any evidence for it. The basal segment (Pl. IX, figs. 1–3; Pl. X, fig. 1; Pl. XV, fig. 2; Pl. XX, fig. 1; Pl. XXI, figs. 3, 4) appears to be as broad (*exs.*) as the somite proximally, and to taper evenly distally in dorsal or ventral view; in lateral specimens the proximal portion is broad, then tapers rapidly to a narrower distal portion. The walking leg (Pl. II, figs. 1, 2; Pl. VII, figs. 1–3; Pl. IX, figs. 1–3; Plate X, fig. 1) consists of five additional segments (two to six) that are successively shorter and slimmer; in the anterior six legs segments three to five widen slightly distally, particularly on the inner side, before insertion of the following segment. One or two setae projected inward from the distal end of the third to fifth segments. These expansions and setae appear to be only on the inner side, and not on both sides as Walcott showed (1931, Text-figs. 9, 10). Simonetta (1962, p. 179, Text-fig. 2a) stated that these setae were artifacts of preservation, and showed a corona of fine hairs at the distal end of each segment, but I have observed no evidence for such a claim. I can find no evidence either for Simonetta's view that there is a short, seventh segment in the walking leg, which bears two long setae, but I have observed that at the tip of the leg there are two (Pl. II, fig. 2; Pl. XI, fig. 3), and most probably three, spines (Pl. XXII, fig. 1) much as Walcott showed.

The first walking leg is the longest, and the succeeding eight legs show a regular diminution in length posteriorly (Pl. II, figs. 1, 2; Pl. VIII, figs. 1, 2; Pl. IX, figs. 1–3; Pl. XXV, fig. 1); four or five were long enough when extended horizontally to reach out beyond the lateral cephalic spine (Pl. X, fig. 1; Pl. XXII, fig. 1). There is a more rapid diminution in length from the ninth leg posteriorly (Pl. XI, fig. 3; Pl. XXV, fig. 1; Whittington, 1971, Figs. 18, 19). Walcott (1931, p. 31–32, Text-fig. 9, Pl. 22, figs. 1, 2) portrayed the first two 'endopodites' behind a_2 (his maxillula and maxilla) as considerably shorter and slimmer than the walking leg of the succeeding somite. The originals (Pl. VII, figs. 1–3; Pl. VIII, figs. 1, 2) show that his illustrations were considerably retouched; only the proximal parts of the first two walking legs are preserved in these specimens, as comparison with more complete examples (Pl. IX, figs. 1–3; Pl. X, fig. 1) shows. A feature of the walking legs, described only by Walcott (1912, Pl. 26, fig. 6; 1931, p. 33, Text-fig. 9), is the expansion of the segments distally, the expansion being most conspicuous posteriorly (Pl. IX, figs. 1–3; Pl. XI, fig. 3; Pl. XVIII, fig. 1; Pl. XIX, figs. 1, 2; Pl. XX, figs. 2, 3), where it gives the appearance of a network. Walcott described the expansion as being medial, on proximal segments of more anterior (w_{4-8} of present reconstruction) legs, and on all but the distal segment of the tenth and successive legs. Such distal expansions of the segments in the first six legs have been noted above, and the expansions become greater on successive legs. It is difficult, beyond the sixth or seventh leg, to be sure where on the joint the expansions occur, but they appear to be distal rather than medial (Pl. XI, fig. 3).

The gill branch of the appendage (Pl. X, fig. 3; Pl. XV, figs. 1, 2; Pl. XXII, figs. 1, 2; Whittington, 1971, Fig. 8) is attached to the most proximal part of the basal segment of the

¹ And 1939, Text-fig. 30a.

appendage, on the dorsal side. The shaft tapers gradually distally in the form of an elongated cone, and is divided into some fifty short rings. From each ring a filament projects on the lower side, the filaments being of maximum length at about one quarter the length of the shaft, the length diminishing progressively distally. Simonetta (1962, Text-fig. 2b) appears to have based his reconstruction of the length of the filaments on the gill branch on Walcott's (1931) Plate 22, figure 8. These filaments, however, are those of several successive overlapping gill branches on the left side of the specimen, but the shafts are not preserved. The filaments in a single shaft (Pl. X, figs. 2, 3; Pl. XV, figs. 1, 2; Whittington, 1971, Figs. 10, 11) appear to be of the relative length shown in Text-figures 2, 3, and not exactly as by Simonetta or by Walcott (1931, p. 34, Text-fig. 10), who regarded them as longest distally. The most proximal part of the shaft is not shown by any specimen, and it is not known whether it was undivided and lacking in filaments (Text-figs. 2, 3), or whether it was divided and bore short filaments, as suggested in Text-figure 8. The filaments were described by Walcott (1931, p. 35) as rounded in section, by Simonetta as laminar, but the preservation does not allow of any certainty. On an anterior gill branch there are some fifteen to eighteen filaments in 1 mm, suggesting that the diameter of a filament was about 0.06 mm. Simonetta (1962, p. 179, Text-fig. 2b) states that each ring of the shaft bears a second filament, short and upwardly directed. The upper filament is preserved on the anterior shaft in the original of Plate X, figure 2, but other specimens do not show them, perhaps because of their shortness and fragility. In the reconstructions they are shown only on the anterior shaft in Text-figure 3.

The gill branch with its filaments has been shown in restorations in a variety of positions—filaments directed forward and slightly upward (Raymond, 1920, Text-fig. 32), backward and slightly upward (Walcott, 1931, Text-fig. 9; Størmer, 1944, Text-fig. 19, 5, 6; *in* Moore, 1959, Text-fig. 15, 3, 4), and downward and slightly forward (Simonetta, 1962, Text-figs. 1a, 2a). However, in parallel specimens the filaments of each branch are disposed on a surface that may be inclined forward and slightly downward (Pl. II, figs. 1, 2; Pl. X, fig. 3; Pl. XI, fig. 1; Pl. XII, fig. 1; Pl. XV, figs. 1, 2; Pl. XXII, figs. 1, 2), or backward and slightly downward (Pl. VI, fig. 1; Pl. IX, figs. 1–3; Pl. XIII, fig. 1). Successive gill branches and filaments overlap one another, and have a thin layer of rock between them. Table I shows the directions of slope of gill branches in specimens from five intervals in the Phyllopod bed. Those that slope forward and downward are most abundant in four of the samples. In most specimens the inclination of all the gill branches is the same, but there are exceptions. In the original of Plate XIX, figures 1, 2; Plate XX, figures 2, 3, they are inclined anteroventrally on the left side, posteroventrally on the right. In the original of Plate XXVI, figure 3, the inclination is posteroventral on the left side and in the anterior three on the right side, the remainder on the right being anteroventrally inclined. The sets of filaments have not been observed to slope upward, either forwardly or backwardly directed. The shafts of the gill

TABLE I

*Direction of slope of gill branches in specimens from five samples at different levels in the Phyllopod bed*¹

Level of sample	Number of specimens	Anteroventral	Posteroventral
5'1" – 5'5"	11	7	4
6'7½" – 7'3"	54	40	14
6'10" – 7'0"	63	44	19
8'7" – 8'9"	20	9	11
8'7" – 9'0"	21	15	6

¹These samples are the same as those used for measurements of sagittal length (Whittington, 1971, Fig. 7).

branches were evidently flexible, are curved back distally, and the branch may curve through 90 degrees or more, as seen in the horizontal plane (Pl. XII, fig. 1; Pl. XV, fig. 2). The proximal parts of the shafts are directed in a progression, the anterior may be directed forward and the posterior slightly backward (Pl. XI, fig. 1; Pl. XIII, fig. 1), or the proximal parts of the shafts may be subparallel, directed outward (Pl. XIV, figs. 1, 2) or posterolaterally (Pl. XIX, figs. 1, 2). Lateral (Whittington, 1971, Fig. 6) and oblique (Pl. XXI, figs. 3, 4; Whittington, 1971, Figs. 16, 17) specimens show that the distal parts of the shaft curved not only backward but upward, and as a result in the original of Plate XVIII, figure 1, the compacted shaft shows a sharp flexure, as it may do in a parallel specimen (Pl. XXV, figs. 2, 3). In some specimens (Pl. XI, fig. 1; Pl. XIV, figs. 1, 2; Pl. XXII, fig. 1; Pl. XXVI, figs. 1, 2) the proximal segments of the walking leg of the first one to three somites are directed forward and outward, at an angle of as much as 80 degrees to the proximal part of the shaft of the gill branch. This divergence between the two branches is achieved without disruption, and appears to be indicative of the great flexibility of the shaft. In these specimens the walking leg extends anteriorly to the gill branch; in only one example (Pl. IX, figs. 1–3) is it behind the gill branch.

In considering an unusually well preserved specimen Walcott (1912, Pl. 26, fig. 4) termed the structure on the left side a 'large gill lobe' or 'epipodite', but later (1931, p. 34) concluded it was formed by gill branches matted together, an interpretation with which I agree. He continued to maintain in 1931 that an 'epipodite', a "small oval flattened lobe attached to the dorsal side of the protopodite", was probably present, but did not consider the evidence warranted showing it in his restoration (1931, Text-fig. 10). Like Simonetta (1962, p. 180), I have not found a specimen showing such a lobe.

Internal Features

Walcott (1912, p. 193–4, Pl. 26, figs. 3, 6; 1931, p. 30, Pl. 22, figs. 6, 7, 9) described the alimentary canal as extending from the posterior margin of the labrum to the telson, contracting a little at the junction between successive somites, and stated that anteriorly the intestine widened out beneath the median part of the cephalic shield into what may have been the stomach. He also noted that canals, probably connecting with the stomach, traversed the lateral and median spines of the cephalic shield. His interpretations were based on reflected photographs that revealed these features as highly reflective areas. Parallel (Pl. IX, figs. 2, 3; Pl. XXIII, fig. 2), oblique (Pl. XXIV, figs. 2, 3), and lateral (Whittington, 1971, Fig. 6) specimens show such areas. There is a large, in some cases ill-defined, area in the cephalic shield, into which run highly reflective bands that traverse the lateral and median spines. The band on the lateral spine is closer to the inner than the outer edge, corresponding in position and width to the supposed groove on the external surface. The area in the cephalic shield may be subrectangular in parallel specimens (Pl. IX, figs. 2, 3); in an oblique specimen (Pl. XXIV, fig. 3) it is an ovate area with an extension tapering and running back to the posteroventral wall of the cephalic shield. It is joined to the sagittal band along the body, and bands on the right lateral and median spines. The appendages, including their branches, are traversed by narrow, reflective bands that proximally join the sagittal band. The conclusion of Walcott that these areas and bands are in the position of the alimentary and other originally fluid-filled canals in the animal appears reasonable, and is accepted also by Simonetta. The lateral and oblique specimens suggest that the mouth was situated in the ventral wall of the cephalic shield, above the lateral processes, and that the stomodaeum leads forward into the large, U-shaped stomach within the shield.

Dark Stain

The position and nature of this stain was discussed previously (Whittington, 1971, p. 1188–1190, Figs. 6, 7, 9, 16), and arguments advanced for considering that it was made by original organic matter, possibly squeezed out of the body as the shale was compacted. The stain is revealed by almost all specimens (Pl. II, figs. 1, 2; Pl. VIII, fig. 3; Pl. XI, fig. 2; Pl. XIV, figs. 1, 2; Pl. XVI, fig. 2; Pl. XVII, figs. 1–3; Pl. XVIII, fig. 2; Pl. XIX, fig. 1; Pl. XX, fig. 2) in all attitudes and at varying sizes. It is situated dominantly around and behind the posterior part of the body, but also extends along the body (Pl. XX, fig. 2; Pl. XXIII, fig. 1) and in some examples in front of it (Pl. XX, fig. 1). It is not confined to one bedding plane, but may extend through about 1 mm of rock. Neither Walcott nor Simonetta commented on the stain. However Walcott (1931, p. 34; the footnote on this page is irrelevant) explained the original of his 1912, Plate 26, figure 4, as gill branches “macerated in the contents of the body which were squeezed out on that side”. The specimen has the dark stain covering the area in question. Ruedemann (1931, p. 14, Pl. 3, figs. 1, 2) noted a “fine carbonaceous film” associated with the posterior part of the body. This is undoubtedly the dark stain, and it is visible in his illustration, but in those made by Walcott and Simonetta it is inconspicuous or invisible.

A specimen figured previously (Whittington, 1971, Fig. 22), showed a twisted reflective strip extending from the posterior end of the body across the dark stain. It was suggested that this strip might represent the intestine, squeezed out during compaction. The original of Plate XVI, figure 2, shows a straight strip extending from the posterior end of the body across the dark stain, and may be interpreted in the same way.

Organic Matter in the Burgess Shale and the Dark Stain

Dr. G. C. Speers, British Petroleum Research Centre, has examined pieces of the shale, and reports that it “almost certainly contains indigenous organic matter present to the extent of 0.004 to 0.007 per cent weight. This material falls almost entirely in the carbon number range C₁₅–C₂₅ and contains a wide variety of organic compounds, including about 30 to 40 per cent hydrocarbons. Results for the alumina chromatography of the bulk shale extract are summarized in the table below:

Elution solvent	Fraction as percentage weight of total solubles	Carbon number range
n-heptane	33	C ₁₈ –C ₂₆
benzene	17	C ₁₉ –C ₂₅
ethanol	46	C ₂₀ –C ₂₅
carbon disulphide	4	C ₁₈ –C ₁₉

The last column gives the approximate carbon number distribution range of the fraction determined by column gas chromatography and indicates a slightly wider spread than that shown by the mixture as a whole.”

Three samples of shale fragments chipped out from the dark stain were examined. “Two of them appeared to be completely free of soluble organic matter . . . whilst the remaining sample clearly indicated the presence of organic matter in the carbon number range C₁₈–C₂₆ but with a markedly different distribution from that observed in the bulk shale extract.”

Professor Frederick M. Swain, University of Minnesota, has analyzed specimens of *M. splendens* for carbohydrates and amino acids. He reports that carbohydrate residues were almost nil, but that there appeared to be slight traces of glucose and galactose. The analyses for protein amino acids were more significant. Both free and acid-extractable amino acids were found, the former being about 10 per cent or less of the latter. The free amino acids determined by paper chromatography consisted of a few ppm of cystine, histidine, and lysine. Dr. Irvin Liener, Department of Biochemistry, University of Minnesota, made a quantitative analysis of amino acids extracted from 0.4gm of fragments of *M. splendens* with 6 N hydrochloric acid, following water extraction to eliminate free amino acids. His analysis is given in Table II. Professor Swain comments, "The analysis is really astonishing as nearly a full suite of protein amino acids is present. The fresh appearance of the samples and the care with which they were handled to avoid laboratory contamination certainly suggests the presence of protein residues." He remarks that the arthropod body would be a likely source of proteins; the associated matrix contained only traces of amino acids.

Professor Swain and his associates (Swain, Bratt, and Kirkwood, 1970) have also detected free sugars, possibly the degradation products of starch, in a small fragment of the Burgess Shale.

TABLE II

Analysis of amino acids extracted from 0.4g of fragments of Marella splendens with 6 N hydrochloric acid, by Dr. Irvin Liener, University of Minnesota

Amino acid	Total micro-moles in sample
Lysine	0.078
Histidine	0.030
Arginine	0.027
Aspartic acid	0.006
Threonine	0.015
Serine	0.039
Glutamic acid	0.027
Proline	0.048
Glycine	0.114
Alanine	0.084
Half-cystine	0.000
Valine	0.030
Methionine	trace
Isoleucine	0.030
Leucine	0.075
Tyrosine	0.039
Phenylalanine	0.084
Cysteic acid	0.024

Size

As previously discussed (Whittington, 1971, p. 1192-1197), sagittal length of *M. splendens* varies from 2.5 to 19.3 mm (Pl. II, figs. 1, 2), the maximum range observed in the USNM and GSC collections. Simonetta's (1962, p. 177) observations that the largest are 21 mm long appears to be based on an exsagittal measurement to the tip of the median cephalic spine, rather than a sagittal measurement. Small specimens (Pl. XVIII, fig. 2) appear to have five or six fewer somites in the body than larger specimens, but not to be otherwise morphologically distinct. Size-frequency distribution in five samples (Whittington, 1971, Fig. 23) shows a bimodality, the significance of which is discussed below.

Completeness of Individual Specimens

As the present illustrations show, with one exception each specimen is an entire individual with all the appendages preserved. Wrinkling, fracturing, and distortion result from compaction of the enclosing sediment (Whittington, 1971), and there is no evidence of partial decomposition or damage by predation. Further, traces of original organic matter appear to be associated with almost all specimens (*see above*), so that individuals appear to have been whole animals with the soft parts when entombed, and not moults of the exoskeleton. The GSC collection includes more than eight hundred individuals (Text-fig. 1; Whittington, 1971, Fig. 5). From the level 8 feet 0–7 inches came one specimen (Pl. XVIII, fig. 5) that appears to be the isolated exoskeleton of the cephalic shield. The Walcott collection in the U.S. National Museum contains some twelve thousand specimens, but only four similar isolated cephalic shields. These rare specimens may represent the more resistant part of moulted exoskeletons.

Malformed Individuals

One small, poorly preserved specimen (Pl. XVIII, fig. 3) shows a short, anterolateral branch from each lateral spine. This specimen comes from a level that yielded only nineteen other individuals, and is presumed to represent malformation. A further example of malformation was observed (Pl. XI, fig. 2) in the Walcott collection, in which the right median cephalic spine is bifurcated at the tip.

Function and Movements of Appendages

The first appendage was presumably sensory in function, extending in front of, and anterolaterally to, the cephalic shield. The second appendage was presumably also mainly sensory in function, laterally to the cephalic shield, and may also (cf. Walcott, 1931, p. 35) have assisted in swimming. The long, stout basal segment is perhaps suggestive of a strong backward and forward motion to assist in propulsion. The succeeding biramous appendages have been described as including a walking leg (*w*) and a gill branch (*b*). The first eight or nine of the walking legs are successively shorter posteriorly, and beyond this point these legs diminish rapidly in length and show the expanded segments. I suggest, therefore, that w_{1-8} or w_{1-9} were employed in walking, directed steeply downward (as in Text-figs. 5, 8, and perhaps more steeply than shown in Text-fig. 2). When walking straight forward, these legs may have been put down successively, from 8 (or 9) to 1, the footprints on each side being made in a line diverging from the sagittal forward, by a wave-motion of the body, as in Cambrian trilobites (Seilacher, 1959, p. 390–391, Fig. 2b). Thus in the reconstruction in dorsal view (Text-fig. 2) the animal is represented as standing on w_{6-8} , while w_{1-5} are extending forward; in the oblique-lateral view (Text-fig. 5), it is standing on w_{1-3} and the body is curved down posteriorly as w_{4-8} are curved and extending forward. The three setae at the tip of each leg would presumably act to support it on a soft mud surface. Legs 9 to 25 are short, the distally expanded segments 2 to 5 forming a network as the legs are curved in an arc (Text-figs. 4, 5, 8). Possibly this network acted as a trap and/or a filter for particles gathered under the body by currents in the manner suggested below.

The filament-bearing branches (*b*) have been termed here gill branches (cf. Walcott, 1931, p. 35), for the slimness (diameter ca. 0.06 mm) of the filaments suggests a thin integument through which oxygen could have been absorbed. The shaft of the branch was flexible, and could be swung backward (in dorsal aspect) relative to the walking leg (the original of Pl. XXVI, figs. 1, 2 shows an angle of 90 degrees between the branches) or exceptionally forward (the original of Pl. IX, figs. 1–3, shows an angle of 20 degrees between the branches).

The filaments are preserved sloping forward and downward or backward and downward, predominantly in the former direction (Table I). Compaction must have modified the post-burial positions of shaft and filaments. Text-figure 9 attempts to show diagrammatically some of the positions that shaft and filaments may have taken in life, and in which they were entombed. From these reconstructions it may be inferred that the gill branch could have been curved and swung forward or backward as well as rotated, these movements giving a rowing-like motion. The shaft is represented as moving forward with the filaments inclined downward and backward, the shaft curved backward and upward at the tip. At the beginning of the backward stroke the shaft would have been rotated so that the filaments sloped forward and downward, and during this stroke the shaft became more strongly curved. Although the movements of the shaft must have been effected by the muscles, the filaments were presumably stiff and almost straight in life, the curvature displayed (Pl. X, fig. 3; Pl. XX, fig. 1) being the result of compaction. Such movement of the gill branch is like that described for the second antenna of *Hutchinsoniella* by Sanders (1963, p. 12, Fig. 11b), and referred to as the typical 'sweep-net' movement of a crustacean nauplius. Sanders (1963, p. 9–12, Fig. 8) describes how metachronal movements of the trunk appendages of *Hutchinsoniella* induce currents that convey food particles to the median groove below the body. Such movements depend for their effectiveness in part on the pleurae acting as lateral valves, as they are thought to have done in trilobites (Størmer, 1939, p. 222–227, Fig. 28; cf. Bergström, 1969, p. 404–8, Figs. 4, 5). Since *Marrella* lacked pleurae, a similar mechanism was not possible, as Størmer (1939, p. 227) concluded. Presumably the gill branches functioned in the 'sweep-net' manner, and the movements would have assisted in swimming, and the filaments would have been continuously bathed in water. In this case, how the food particles caught and swept in were passed forward to the mouth is uncertain. The most proximal part of the basal segment of the appendage is poorly known, but has not been observed to bear bristles. It does not seem that the basal segments of the first and second antennae were used in mastication, as Walcott thought (1931, p. 34), since they are in front of the supposed position of the mouth, and none of the following appendages appears to be specialized for this purpose.

If such movement of the gill branches is accepted, then the walking legs (the first eight or nine biramous appendages) must have been steeply inclined to allow the filaments to sweep to and fro (Text-fig. 8). It has already been suggested that the remaining legs were steeply inclined and curved, and may have helped in trapping food particles. Text-figures 2, 5, are drawn with the walking legs so inclined, but Text-figures 3, 4, show the walking legs widely spread, as preserved in certain specimens (Pl. II, figs. 1, 2; Pl. IV, figs. 2, 3; Pl. VII, figs. 1–3; Whittington, 1971, Figs. 18, 19). These may not have been normal positions in life; in swimming the walking legs may have hung down steeply, curving back distally, as preserved in lateral specimens (Pl. XVII, fig. 1; Pl. XXV, fig. 1).

Mode of Preservation and Habitat

Both Walcott (1931, p. 34–35) and Simonetta (1962, p. 180–181) regarded *M. splendens* as nektonic, but as having used the legs for walking on the bottom, and the filamentous branches for swimming and food gathering. Størmer (1944, p. 95) and Tiegs and Manton (1958, p. 313) considered it to have drifted or swum in the ocean. If these suggestions were correct, the beds containing specimens could be expected to yield a sample that included moults and perhaps whole animals (if sufficiently rapidly buried), oriented parallel to the bedding and lying in one plane, and of random size distribution. None of these expectations is fulfilled—the overwhelming majority of specimens appear to have been whole animals when buried; and orientation in the rock is random, each individual not lying in a single plane. Further, the size distribution is bimodal (Whittington, 1971, Fig. 23), the sagittal

length of individuals ranging from 2.5 mm to 19 mm. Such a size distribution argues that the sample is of a biocoenosis, of a natural population catastrophically buried. I suggested (Whittington, 1971, p. 1197) that a suspended cloud of sediment, moving downslope, might have effected such rapid burial as it settled out; no great distance of transportation was envisaged. Such a mechanism would account for the random orientation and preservation of parts of the animal in different planes. The bimodal size difference in the sample may reflect sexual dimorphism, though no other morphological expression of this has been observed. The difference in sagittal length between the two peaks is approximately 5 to 7 mm, a difference which appears too large to be that between successive instars. In my previous discussion I used the analogy of year groups in molluscan shells to suggest that these size groups might represent year groups, but this analogy may be fallacious.

From the above considerations I conclude that *M. splendens* was benthic in habitat living on or near the bottom, for if it had lived in higher water layers it would have escaped being overwhelmed by moving, suspended sediment. The animal may have swum near the bottom in the zone of suspended particles immediately above the loosely packed sediment or walked on this sediment. Presumably it fed on organic particles, possibly stirring up the sediment with the walking legs. In the preceding section on function of appendages I discussed how they may have enabled particle feeding. In Plate I, figures 2, 3, are illustrated specimens showing an ostracode-like shell on the cephalic shield; Plate I, figure 1, is probably another example. Such specimens are less than 0.1 per cent of those in the Walcott collection. They may represent a random association, or be taken as evidence that the ostracodes were feeding on the decaying body of *M. splendens*, or that *M. splendens* could feed on such small animals. The second alternative may be the less likely in that evidence of predation, scavenging, and decay appears to be rare in the Burgess Shale fauna.

No specimen of sagittal length less than 2.5 mm has been found. This may be because the smaller, larval stages were planktonic, and thus not included in the biocoenosis of a benthonic population. This speculation begs the question as to whether *M. splendens* throughout its known size range was a larva, as hinted by Rolfe (*in* Moore, 1969, p. R 623).

Discussion

In the detailed description I have tried to explain why and how I differ from earlier authors, and have re-illustrated after preparation many of Walcott's and Simonetta's originals in the hope of clarifying some of the points of difference. Walcott's 1912 description was brief, the two plates of photographs taken in the reflected manner. Although his 1931 description is much more detailed, the photographs (taken in the same way) are poorer and several are heavily retouched to the point of falsification of certain features, notably the representation of the supposed mandible, maxilla, and maxillula. Størmer relied mainly on Walcott, but followed Henriksen (1928, p. 4) in recognizing first and second antennae, and like Richter (1932) did not recognize the supposed maxilla and maxillula. Størmer, with some question, added pleurae on the basis of sketches by Beurlen (1930, Text-fig. 75) and Ruedemann (1931, Text-fig. 4)—sketches which, as shown above, were based on misinterpretations of Walcott's photographs. Simonetta was the first to restudy not only Walcott's types but some of the thousands of additional specimens. He did not prepare any of these specimens, and his photographs are poorly reproduced. His reconstruction is striking, and includes for the first time an anterior view. He considered that the second appendage, a_2 , was one branch of a biramous appendage, the other branch being a walking leg. To this, and the succeeding biramous appendages, he added a basal segment, and terminal segments to the walking legs, for which I can find no reasons in his paper or the specimens. My reconstruction resembles his, but uncertainties continue regarding the shape of the cephalic shield, its

ventral surface, and the way the appendages are attached. A labrum bore at the posterolateral corner a relatively long, tapering projection, the presence of which is demonstrated for the first time. Whether the anterior two appendages, here regarded as first and second antennae, belong to separate segments, is problematical. I believe the weight of evidence, especially that from the lateral and oblique specimens not previously studied, shows that the first walking leg is attached to the segment behind the second antenna, and not to the same segment as Simonetta believed.

Ruedemann's interpretation of *M. splendens* as a freshly moulted trilobite verges on the fanciful, and cannot be taken seriously. It is based (Ruedemann, 1931, p. 11) on a misinterpretation of two of Walcott's figures (1912, Pl. 26, figs. 3, 5, respectively; Pl. II, fig. 1, and Pl. III, fig. 1) as showing the median cephalic spines in their supposed normal, outwardly directed position—Ruedemann was identifying the outwardly directed second antennae in these specimens as the median cephalic spines. He supported this view by claiming that the original of Walcott, 1912, Plate 25, figure 3 (Whittington, 1971, Figs. 10, 11) showed the left cheek in an area in which the proximal parts of the left lateral cephalic spine and second antenna are preserved. As noted, Ruedemann thought that the proximal parts of pleurae were present, and considered the dark stain to be the membrane of the moulted pygidium.

Henriksen (1928, p. 3) indicated that the cephalic shield of *M. splendens* is not a true carapace; it is impossible to decide how many segments may be fused to form this shield (cf. Størmer *in* Moore, 1959, p. O24).

Affinities of Marrella

This question has been debated by Walcott (1912, p. 162, 192; 1931, p. 36–37), Størmer (1944, p. 96–98; *in* Moore, 1959, p. O28–29), Tiegs and Manton (1958, p. 313–314) and Simonetta (1962, p. 181–183). It is claimed here (in agreement with Simonetta) that compound eyes are absent and there is no suture, like that of the trilobite, at the base of the lateral cephalic spine. A labrum was present, bearing the posterolateral process, but was not attached to a broad (tr.) cephalic doublure as in trilobites. The cephalic shield, as Størmer remarked, displays no trilobation and is not trilobite-like. I return to the view of Walcott that pleurae are lacking on the post-cephalic body. I follow Størmer and Henriksen (1928) in considering that the first two appendages belong to separate somites and call them the first and second antennae. The succeeding biramous appendages consist of a limb (termed here the walking leg) composed of six segments and the terminal spines; from the most proximal part of the basal segment of the appendage a filament-bearing branch arises. These appendages are “more or less trilobite-like” (Størmer, *in* Moore, 1959, p. O26) in the general sense that there is a segmented walking leg and a filament-bearing gill branch. However, I cannot find evidence of more than six segments and terminal spines in the walking leg of *Marrella*, whereas in trilobites there are seven (or eight if Størmer's pre-coxal segment is accepted) segments and terminal claws or spines. An expanded basal segment does not appear to be present in *Marrella*, though such a segment is known in trilobites. The gill branch in *Marrella* is like that of the trilobite *Triarthrus* (*in* Moore, 1959, Figs. 14, 1; 55a, b), though the shaft is divided into many rings in *Marrella*. Thus the appendages of *Marrella* cannot be described as exactly like those of any known trilobite, and the resemblance may be superficial. *Marrella* appears to belong to a group separate from trilobites, and it is debatable whether or not the presence of first and second antennae is indicative of crustacean affinities. The view of Tiegs and Manton (1958, p. 314) may be slightly modified to suggest that *Marrella* is one of the fossils indicating the existence of an early arthropod fauna, characterized by serially uniform, generally trilobite-like limbs, by a labrum and by lack of jaws, features associated with particle and detritus feeding.

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ADDENDUM

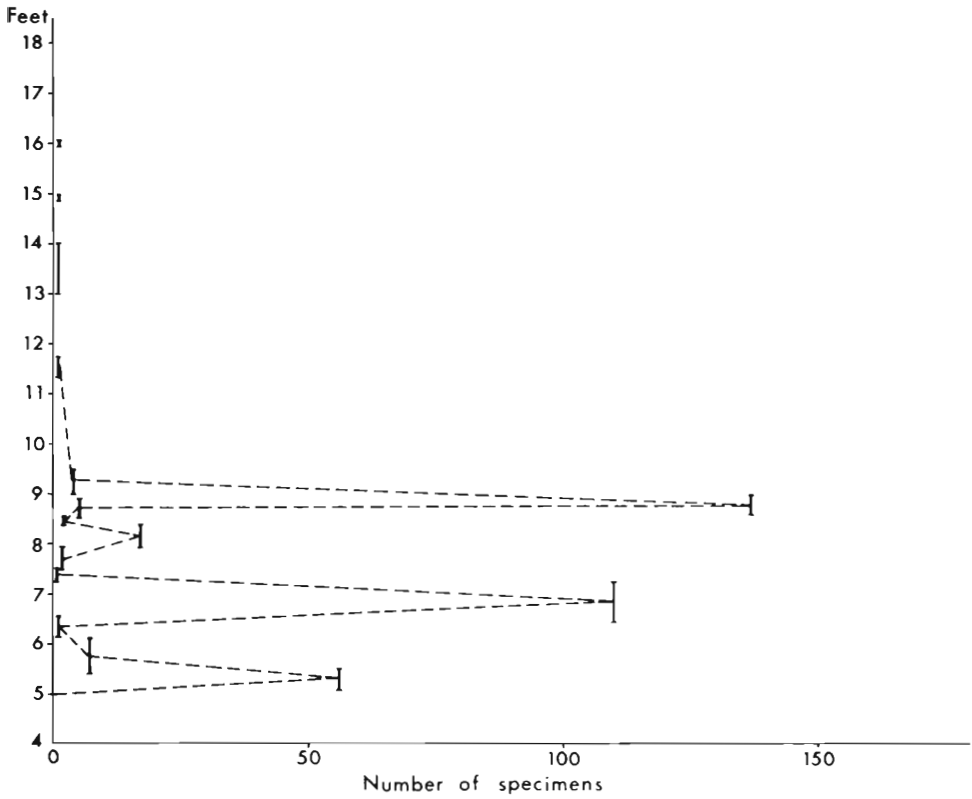
(September 8, 1971)

At the time the manuscript was completed, there was nothing to add to Rolfe's account (in Moore, 1969, p. R623-624, Text-fig. 397, 1) of *Mimetaster* and its similarities to *Marrella*. Birenheide (1971) has since described new material of *Mimetaster*, and shown that the appendages of the post-cephalic body were biramous. One branch was a walking leg of six segments (in addition to the basal segment), the terminal segment pointed; the other branch was many-segmented, each segment bearing a fine filament. These appendages decreased in size posteriorly, and were trilobite-like, as well as being like those of *Marrella*. They differed from the *Marrella* appendage in that there was one less segment in the walking leg, unless the terminal spike of *Mimetaster*, and terminal spines of *Marrella* are regarded as homologous. The walking legs of *Mimetaster* are not known to show the distal expansions of segments which characterized *Marrella*. The gill branch was similar in the two genera, though the outline may not have been identical. The number of appendage-bearing somites in the post-cephalic body of *Mimetaster* was about twenty-four, as in *Marrella*, there was a minute telson, and pleurae were lacking. The cephalic shield of *Mimetaster* is claimed to have had a labrum, but otherwise differed from that of *Marrella* in having borne six spines (each with lateral spines) in a star-shaped arrangement, and eyes, on the dorsal side. The appendages included one pair of antennae and two pairs of walking legs, much thicker and longer than those of the post-cephalic body. Thus, as Birenheide remarks, the cephalic shield and appendages of the two genera were quite different. He concludes that they belong in separate orders of the subclass Marrellomorpha, placing this group in the Trilobitoidea. He regards *Mimetaster* as having been a benthonic animal, and portrays it as having rested on the sea bottom, feeding on particles brought to the mouth by currents created by the gill branches. The resemblances between the two animals appear to indicate relationship and not homeomorphy. The notion (Rolfe, in Moore, 1969, p. R623) that either was the larval stage of some other animal appears unlikely.

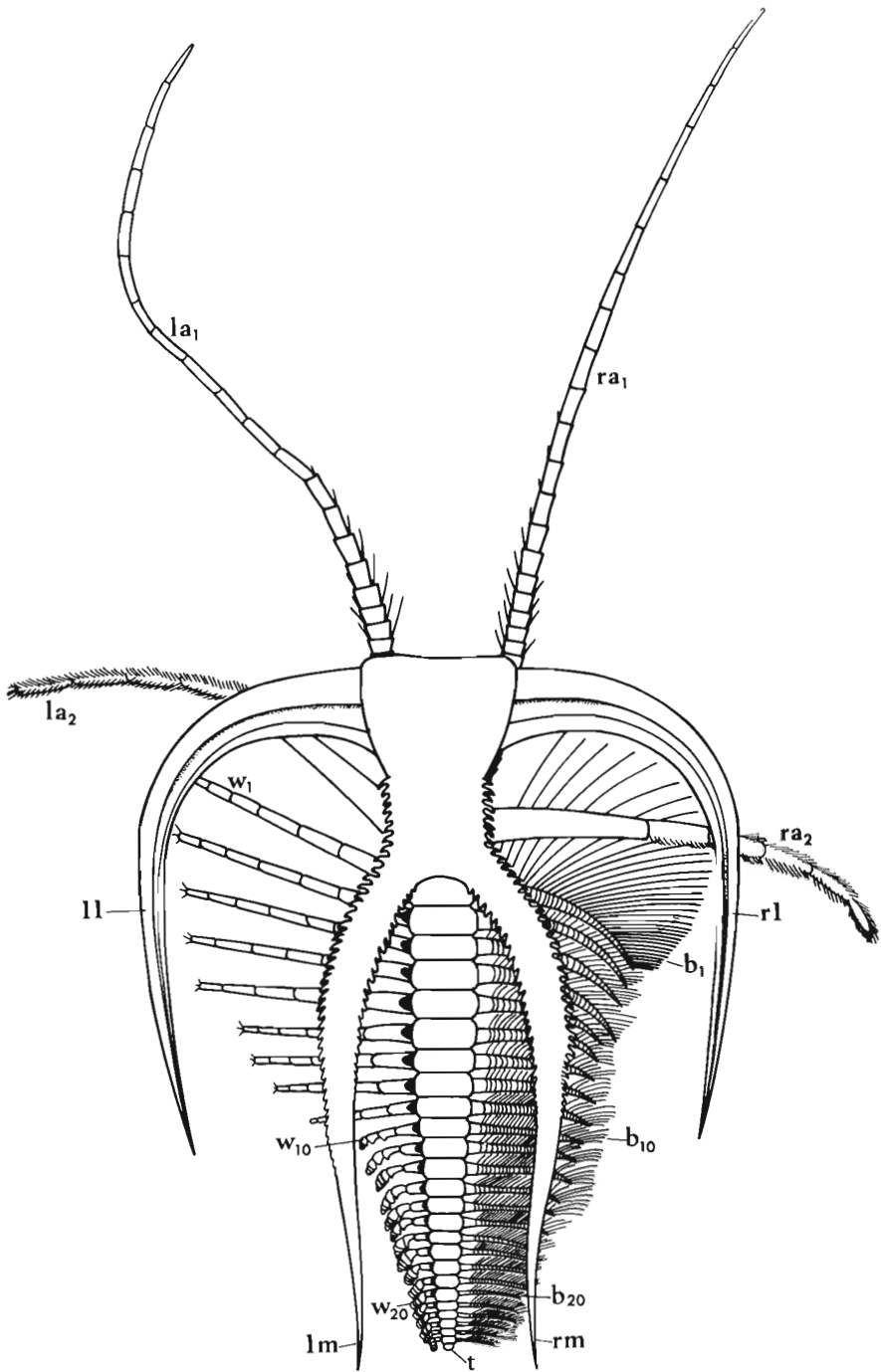
References

- Birenheide, R.
1971: Beobachtungen am "Scheinstern" *Mimetaster* aus dem Hunsrück-Schiefer; *Senckenbergiana lethaea*, vol. 52, p. 77-91.
- Moore, R. C. (ed.)
1969: Treatise on invertebrate paleontology, Pt. R, Arthropoda 4, p. xxxvi + 651; *Geol. Soc. Amer. and Univ. Kansas Press*.

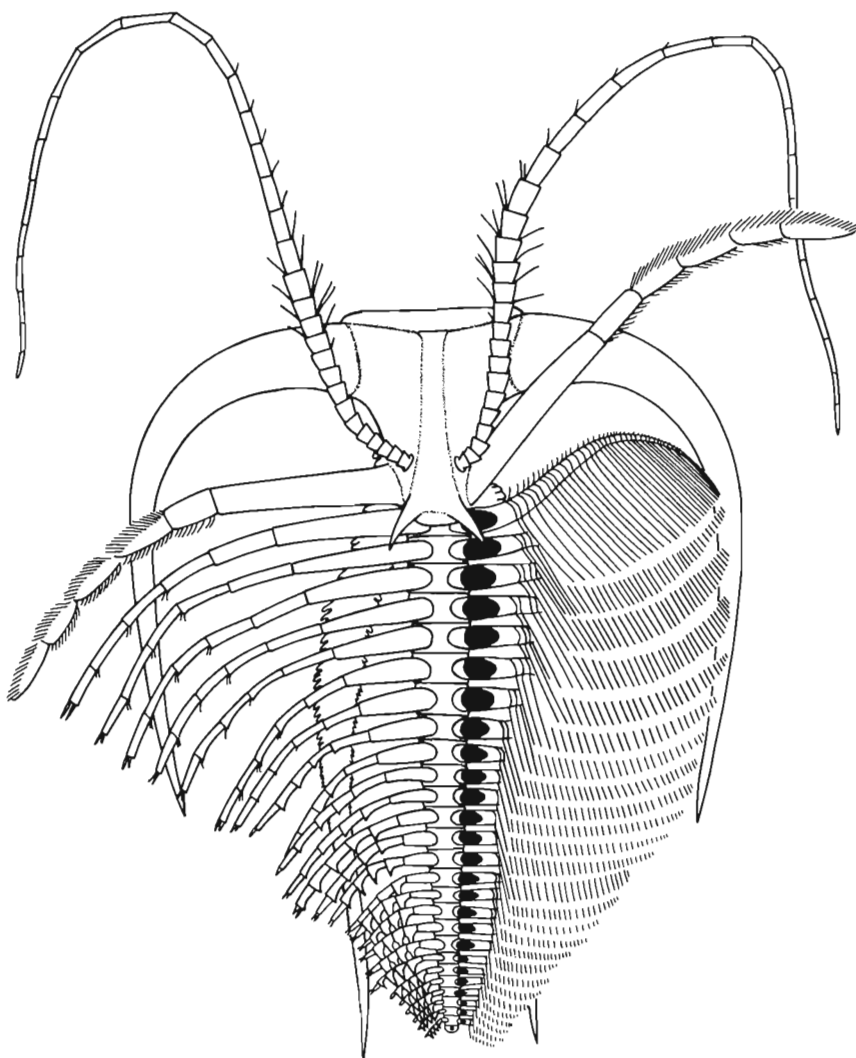
TEXT-FIGURES 1-9



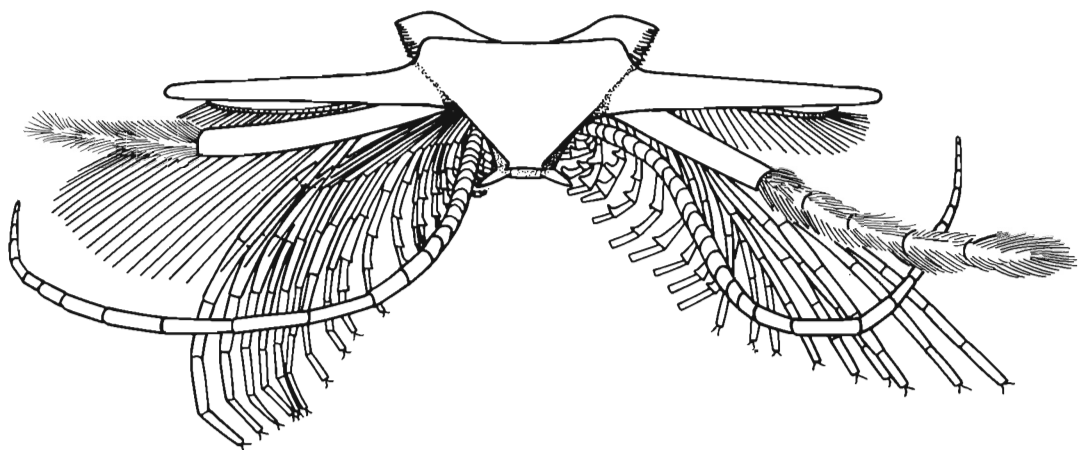
TEXT-FIGURE 1. Numbers of specimens of *Marrella splendens* collected by GSC party in 1966. Vertical bars indicate thickness of rock from which each sample came. Dashed line joins midpoint of bars. Level of 5 feet is at base of Phyllopod bed.



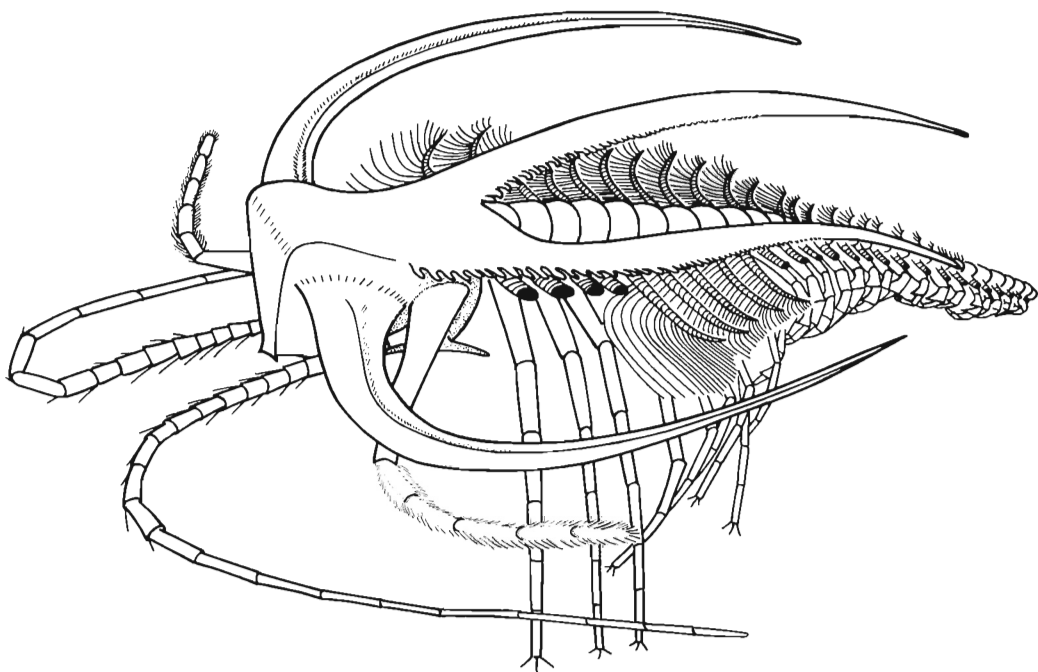
TEXT-FIGURE 2. *Marrella splendens*, restoration in dorsal aspect, gill branches (b) removed on left side, walking legs (w) on right side, c. $\times 6$. Drawn standing on w_6-8 , w_1-5 extending forward preparatory to being placed in succession 5 to 1 on sea floor; right gill branches inclined anteroventrally.



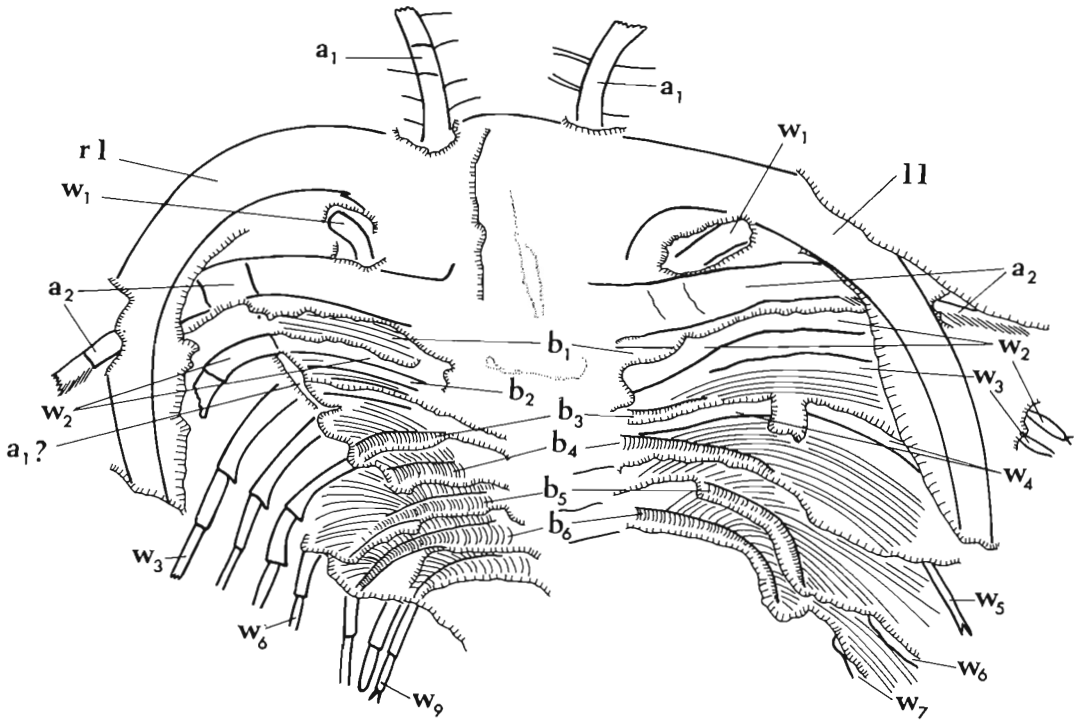
TEXT-FIGURE 3. *Marrella splendens*, restoration in ventral aspect, left walking legs and right gill branches removed, c. $\times 6$. Black oval area represents diagonal cut across basal segment of appendage on left side, immediately distad of insertion of gill branch.



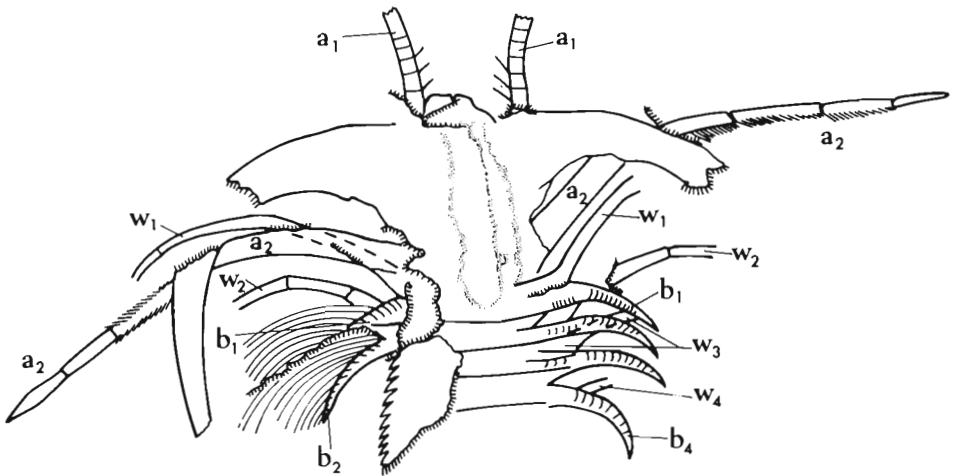
TEXT-FIGURE 4. *Marrella splendens*, restoration in anterior view, first gill branch only shown, c. $\times 6$. Based on original of Whittington, 1971, Fig. 18, walking legs probably less steeply inclined than when animal was walking on sea bottom.



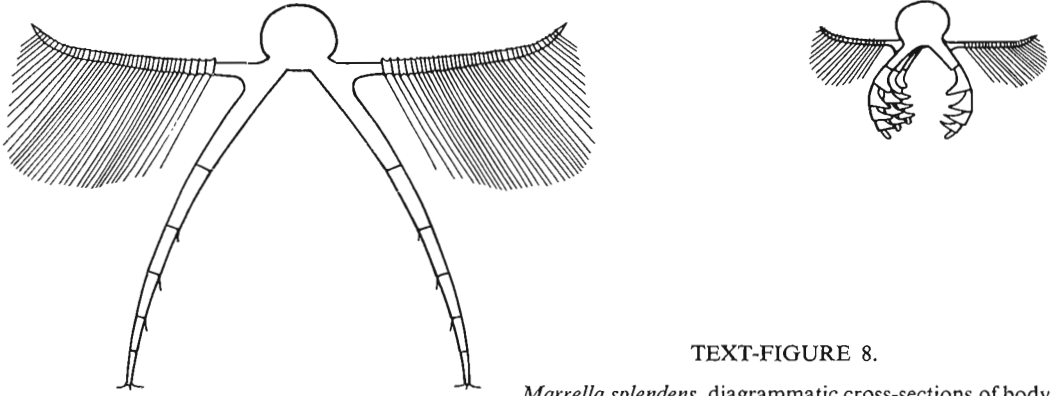
TEXT-FIGURE 5. *Marrella splendens*, restoration in oblique lateral view, represented standing on w_{1-3} ; while w_{4-9} are being brought forward in preparation for stepping on w_{9-1} , c. $\times 8$. Left gill branches 1-4 and 10-26 are cut off at the proximal part of the shaft and filaments are not shown; walking legs on right side omitted. Based on original of Pl. XXI, figs. 1, 2.



TEXT-FIGURE 6. *Marrella splendens*, drawing of part of USNM 83486e, original of Walcott, 1931, Pl. 22, fig. 6, and of Whittington, 1971, Fig. 8, c. $\times 6$. Exposed from ventral, gill branches inclined anteroventrally, walking legs preserved on a surface ventrad of them. Phyllopod bed, Walcott quarry.

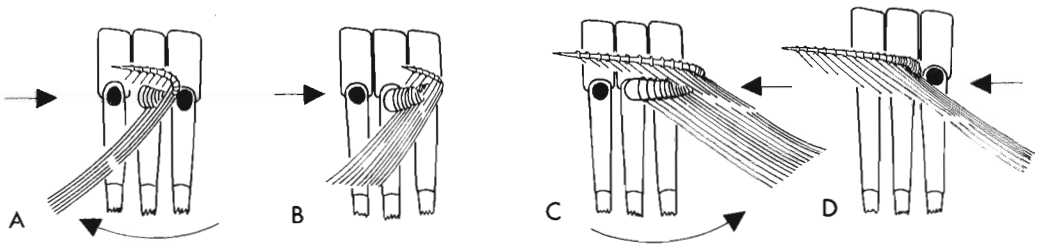


TEXT-FIGURE 7. *Marrella splendens*, drawing of part of GSC 25431, original of Whittington, 1971, Fig. 9, c. $\times 6$. Exposed from dorsal side, showing median triangular projection of cephalic shield and relationships between a_2 , w_1 , and b_1 . Walcott quarry, level 6 ft. $7\frac{1}{2}$ ins. to 7 ft. $3\frac{1}{2}$ ins.



TEXT-FIGURE 8.

Marrella splendens, diagrammatic cross-sections of body and appendages just behind cephalic shield (left) and at posterior portion (right). In latter, two succeeding walking legs are shown on right side (left in figure). Possible rings and filaments on most proximal part of gill branches are suggested.



TEXT-FIGURE 9. *Marrella splendens*, diagrammatic restorations of one anterior gill branch in different positions, arrows indicate possible movements of branch and rotation of filaments. Based on originals of Pl. IV, fig. 2; Pl. VI, figs. 1-3(A); Pl. V, figs. 1-3(B); Pl. VII, fig. 3; Pl. VIII, fig. 1(C); Text-fig. 6; Pl. XVII, fig. 1; Pl. XIX, figs. 1, 2(D).

Plates I–XXVI and Text-figures 10–33

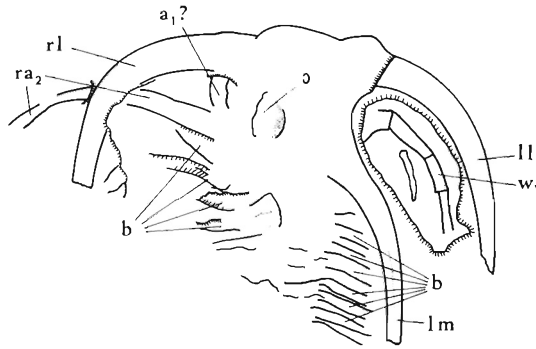
The photographs have been taken on panchromatic film in ultraviolet radiation, after focussing in ordinary light. The radiation has been directed at 30 degrees to the horizontal, and the direction from which it came is given as west, northwest, etc., relative to the margins of the plate. Photographs referred to as reflected (*see* Introduction) were taken in radiation coming from 65 degrees to the horizontal, and the specimen was tilted about 12 degrees so that the maximum reflective effect was directed into the camera. The orientation of the specimen relative to the bedding is given as parallel, oblique, etc., and the meaning of these terms explained in the Introduction. Text-figures 6, 7, 10–33, are camera-lucida drawings showing parts of the animal present in a specimen and their relative levels. All or part of a specimen is shown, and where counterparts are known the features preserved in part and counterpart are combined in a single drawing. Each is placed opposite the corresponding photograph and is intended to explain my interpretation of the specimen. Lettering on the text-figures and photographs is explained in the Introduction. Depositories of specimens are USNM, United States National Museum, Washington, D.C., and GSC, Geological Survey of Canada, Ottawa.

The items explaining individual figures on the plates are arranged in the following order: depository and specimen number; orientation of specimen and whether exposed from dorsal or ventral side; direction of radiation; magnification; reference to previous illustration; comment and/or reference to Text-figure; locality and horizon in terms discussed in the text.

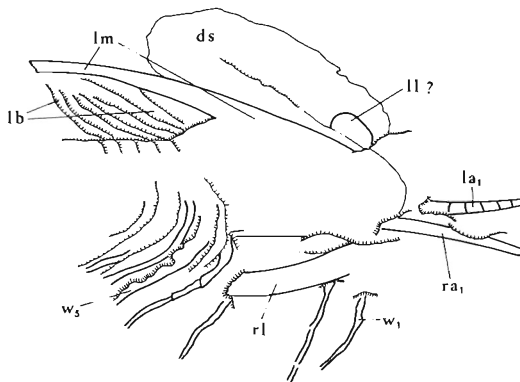
PLATE I

Marrella splendens Walcott, 1912
Phyllopod bed, Walcott quarry.

- Figure 1. USNM 57671, oblique, ventral, northwest, x5, original of Walcott, 1912, Pl. 26, fig. 2; see Text-fig. 10, in which 0 is area considered by Walcott to represent the hypostome.
- Figure 2. USNM 166589, parallel, ventral, north, x5, showing ostracode (?) shell on cephalic shield.
- Figure 3. USNM 166586, oblique, ventral, north, x5, showing ostracode (?) shell on cephalic shield.
- Figure 4. USNM 57667, lateral, north, x5, original of Walcott, 1912, Pl. 25, fig. 4; see Text-fig. 11, ll is area considered by Walcott to be the eye, but considered here to be proximal part of left lateral spine; see Pl. III, fig. 2.



TEXT-FIGURE 10



TEXT-FIGURE 11

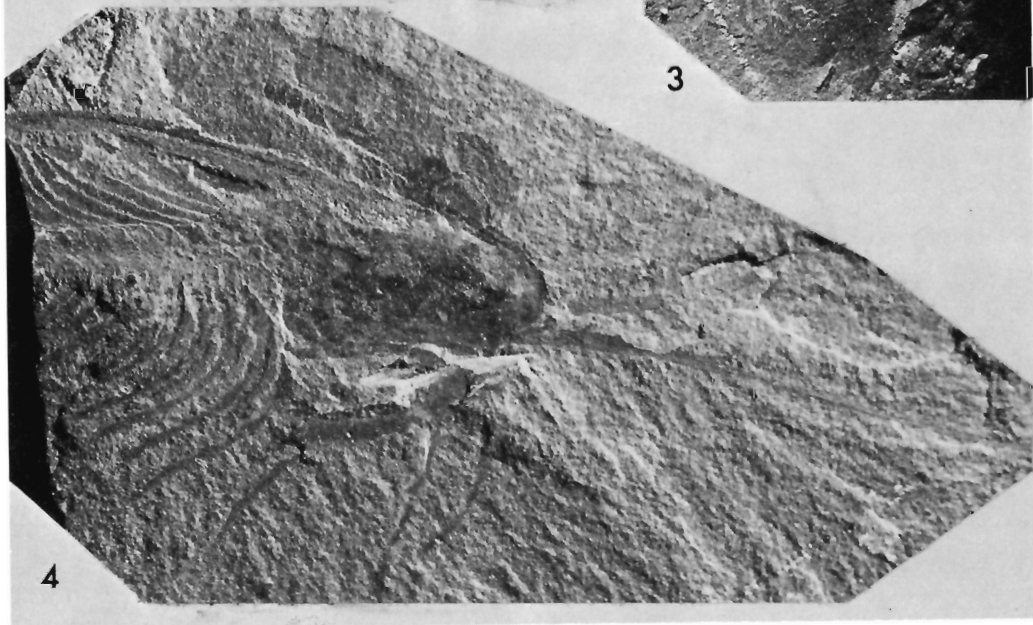
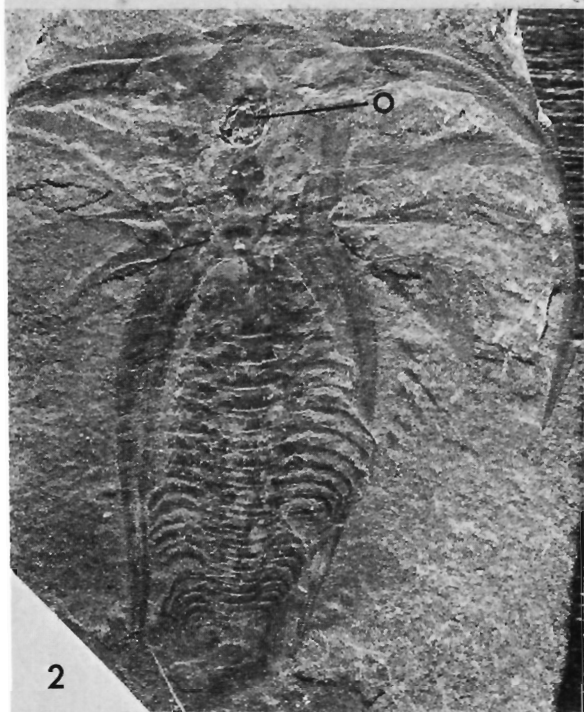
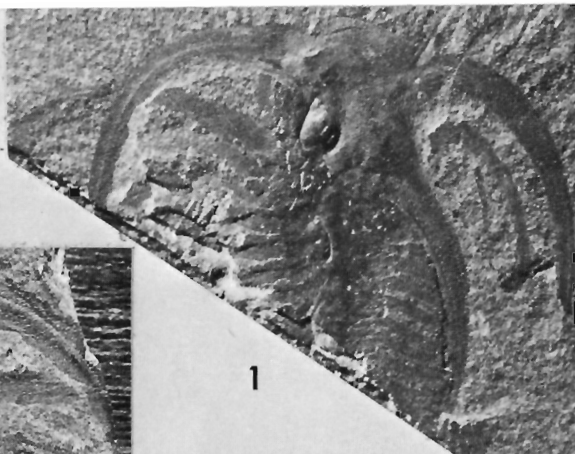
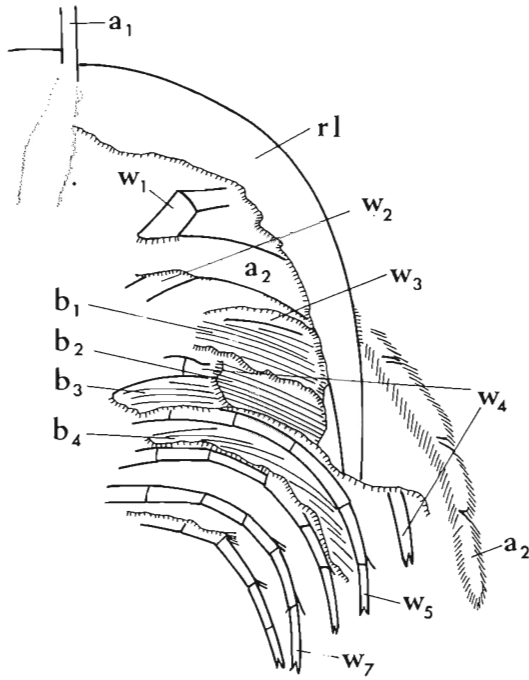


PLATE II

Marrella splendens Walcott, 1912
Phyllopod bed, Walcott quarry.

Figures 1, 2. USNM 57672, parallel forward, part and counterpart, fig. 1 from dorsal, north, x5, fig. 2 from ventral, northwest, x5; original of Walcott, 1912, Pl. 26, fig. 3, see Text-fig. 12 for interpretation of right side.



TEXT-FIGURE 12



1



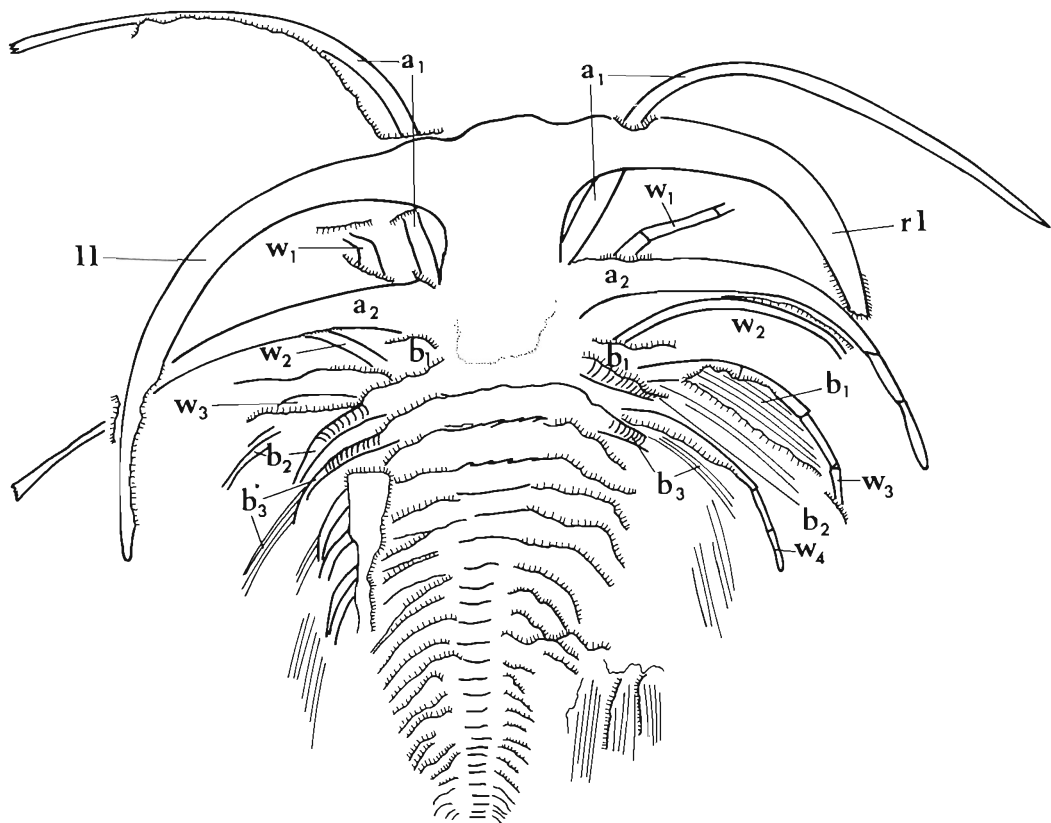
2

PLATE III

Marrella splendens Walcott, 1912
Phyllopod bed, Walcott quarry.

Figure 1. Lectotype, USNM 57674, parallel forward, dorsal, northwest, x7; original of Walcott, 1912, Pl. 26, fig. 5, *see* Text-fig. 13.

Figure 2. USNM 57667, lateral, reflected, x5; original of Walcott, 1912, Pl. 25, fig. 4; *see* Pl. I, fig. 4 and Text-fig. 11.



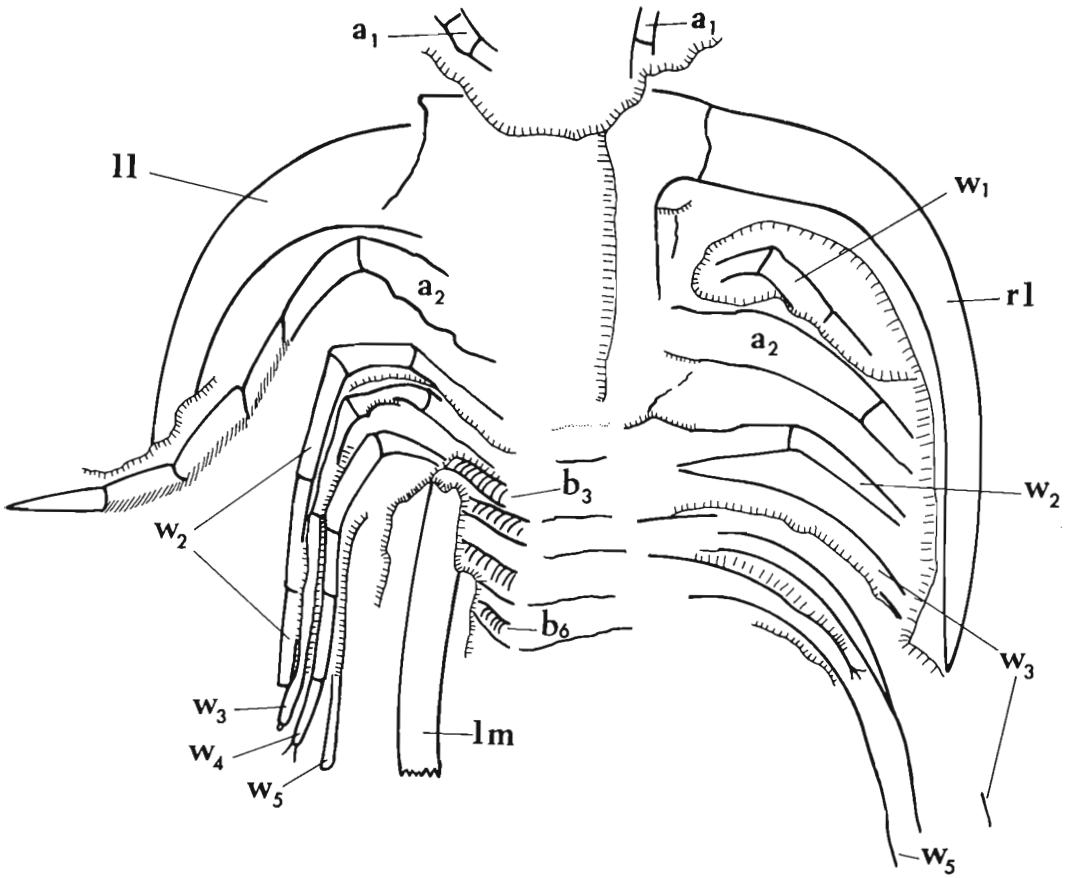
TEXT-FIGURE 13



PLATE IV

Marrella splendens Walcott, 1912
Phyllopod bed, Walcott quarry.

- Figures 1, 4. USNM 83486i, parallel forward, dorsal, fig. 1 northwest, fig. 4 reflected, x5; original of Walcott, 1931, Pl. 22, fig. 7; see Text-fig. 14.
- Figures 2, 3. USNM 139629, vertical backward, ventral, fig. 2 reflected, fig. 3 northwest, x5; original of Simonetta, 1962, Pl. 16, upper right.



TEXT-FIGURE 14

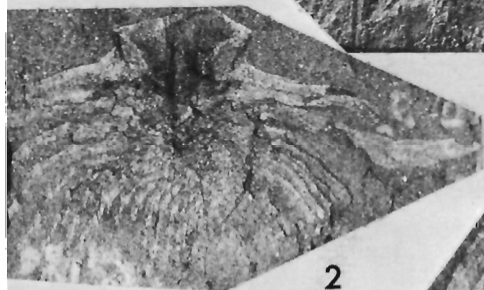
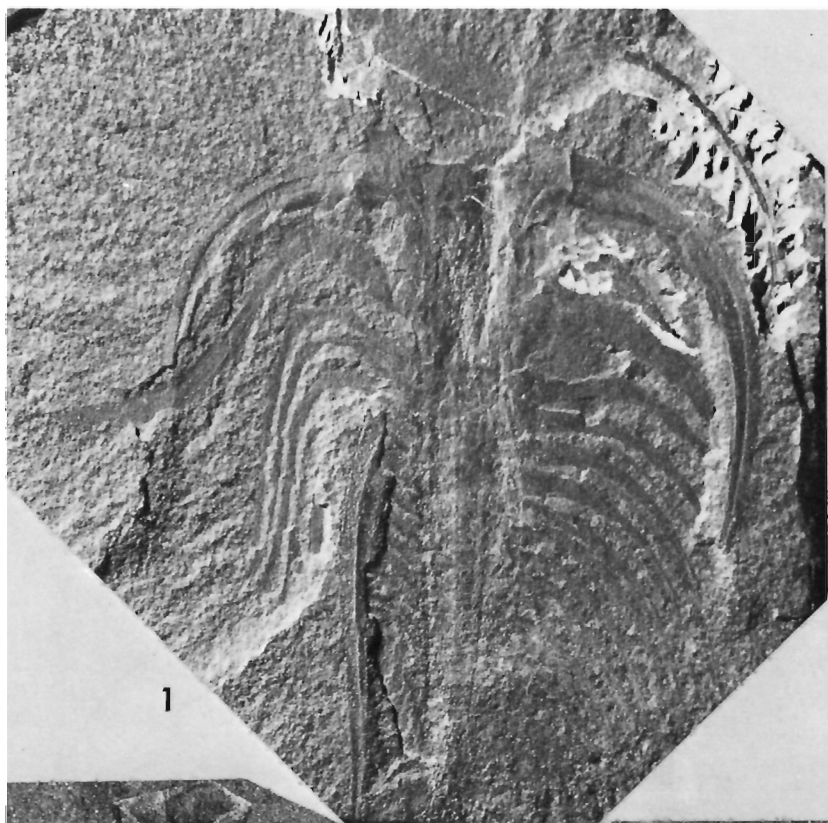
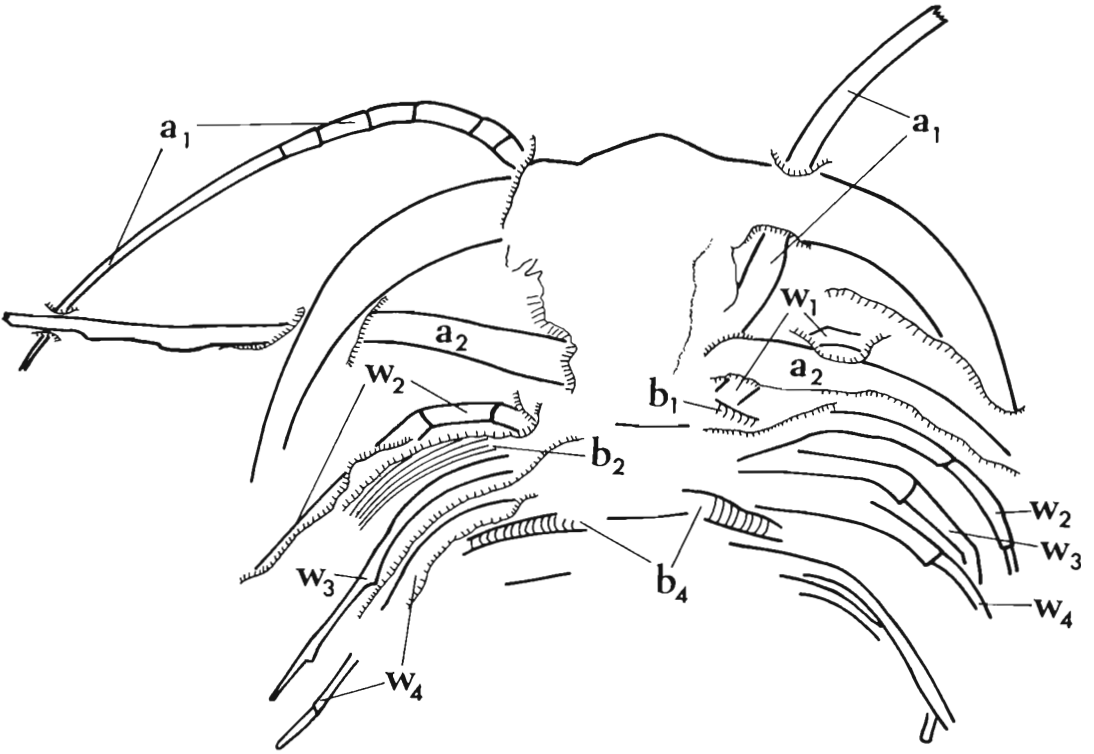


PLATE V

Marrella splendens Walcott, 1912
Phyllopod bed, Walcott quarry.

Figures 1, 2. USNM 83486c, parallel forward, dorsal, fig. 1 northwest, fig. 2 reflected, x5; original of Walcott, 1931, Pl. 22, fig. 4, see Text-fig. 15.

Figure 3. USNM 166601, oblique, ventral, reflected, x7, anterior portion only to show setae on a_1 and a_2 , and segmentation of a_2 .



TEXT-FIGURE 15

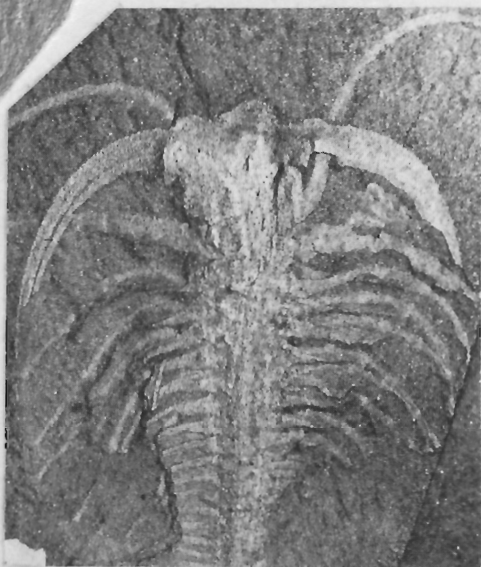
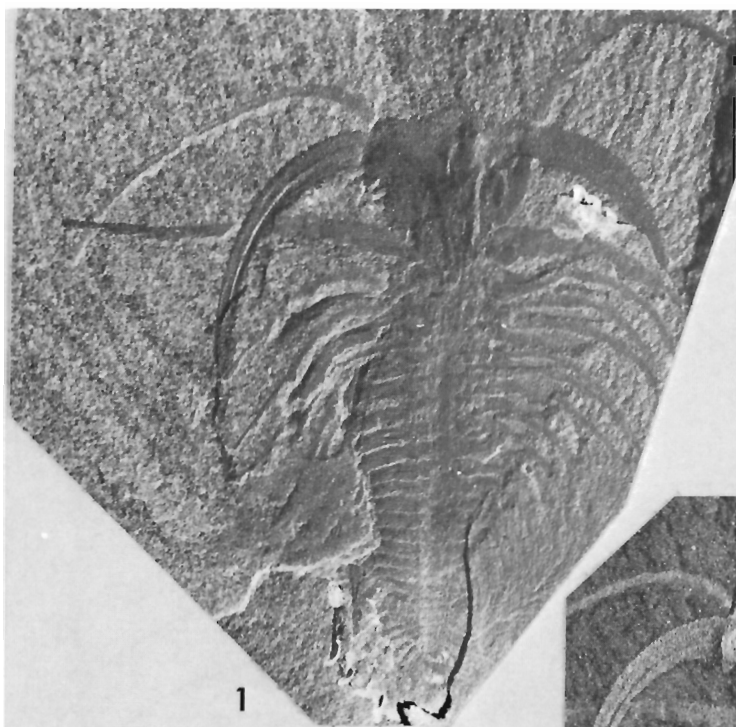
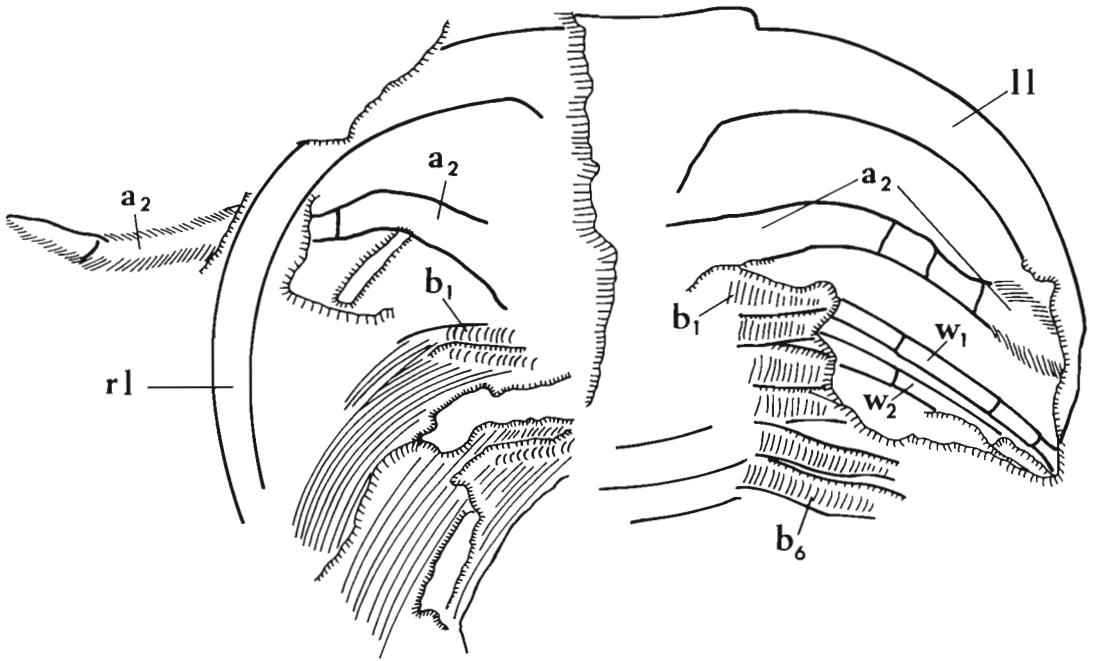


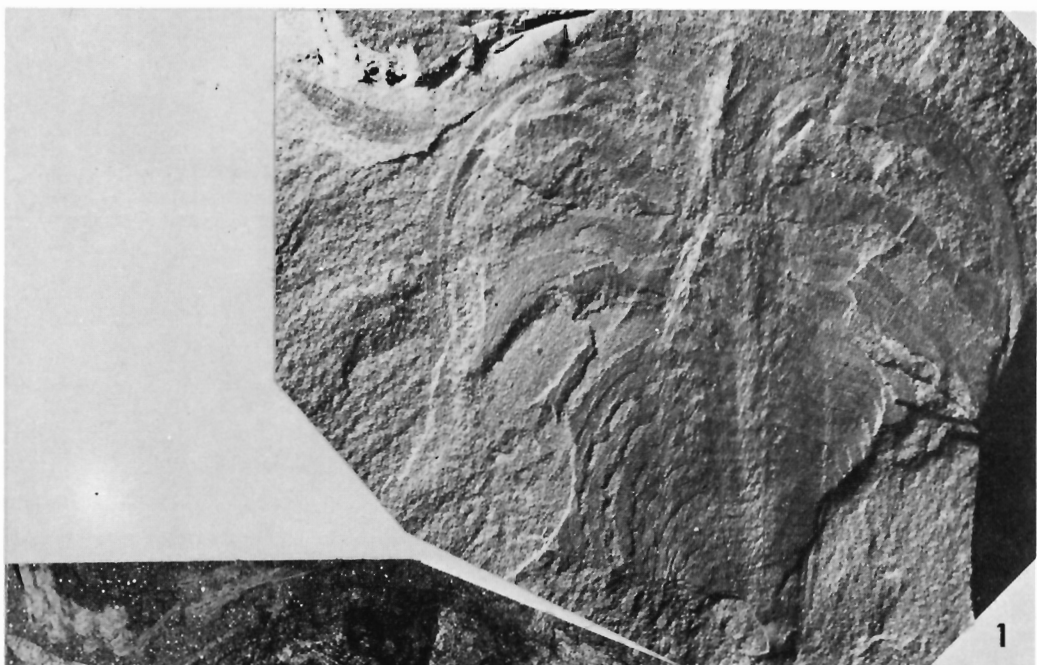
PLATE VI

Marrella splendens Walcott, 1912
Phyllopod bed, Walcott quarry.

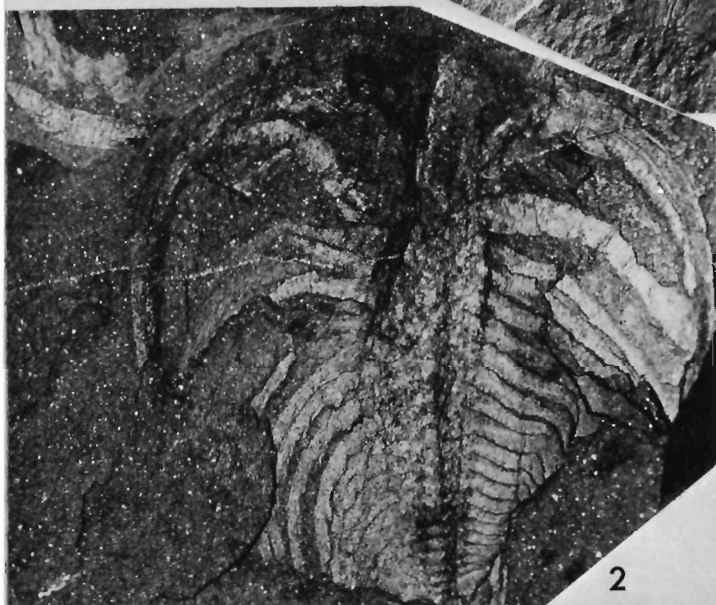
- Figures 1, 2. USNM 83486g, parallel forward, ventral fig. 1 northwest, fig. 2 reflected, x5; original of Walcott, 1931, Pl. 22, fig. 3, see Text-fig. 16.
- Figure 3. USNM 166574, oblique, dorsal, reflected, x5; original of Ruedemann, 1931, Pl. 6, fig. 2; see Pl. VIII, fig. 3.



TEXT-FIGURE 16



1



2

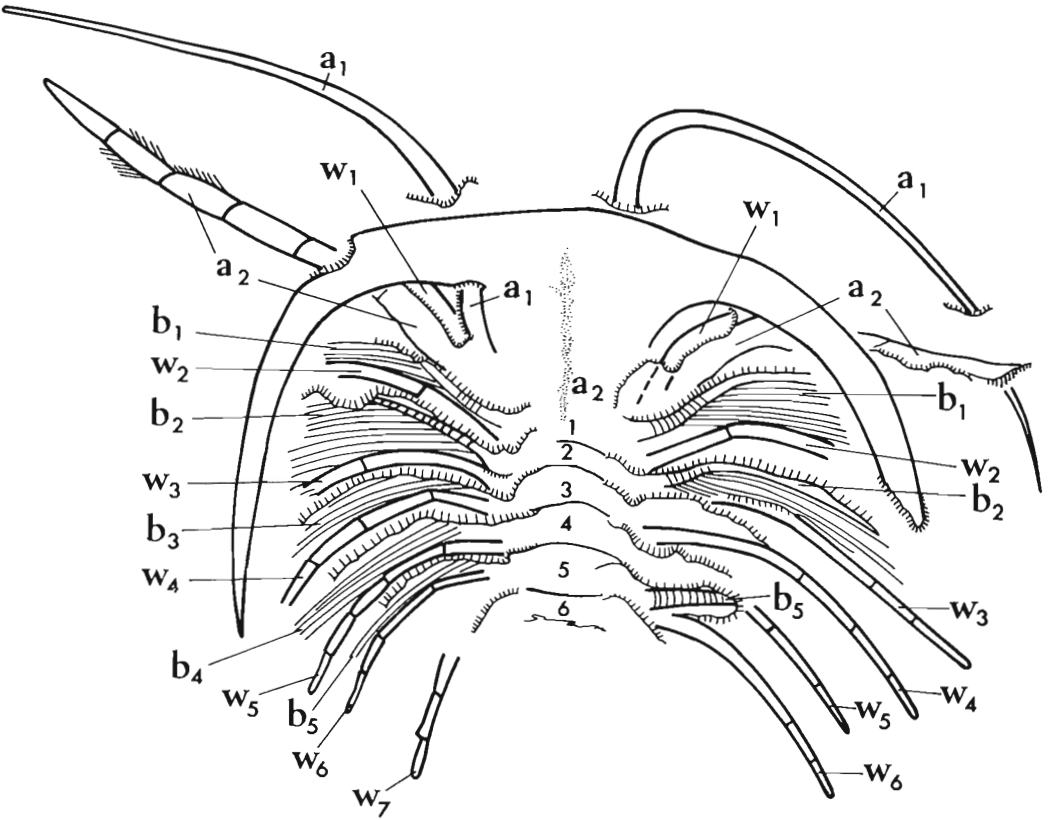


3

PLATE VII

Marrella splendens Walcott, 1912
Phyllopod bed, Walcott quarry

Figures 1-3. USNM 83486h (counterpart numbered 139652), parallel, fig. 1, counterpart, ventral, northwest, x7; fig. 2, counterpart, reflected, x5; fig. 3, dorsal, northwest, x5; original of Walcott, 1931, Pl. 22, fig. 1, see Text-fig. 17, in which somites of a_2 and appendages 1-6 are labelled.



TEXT-FIGURE 17

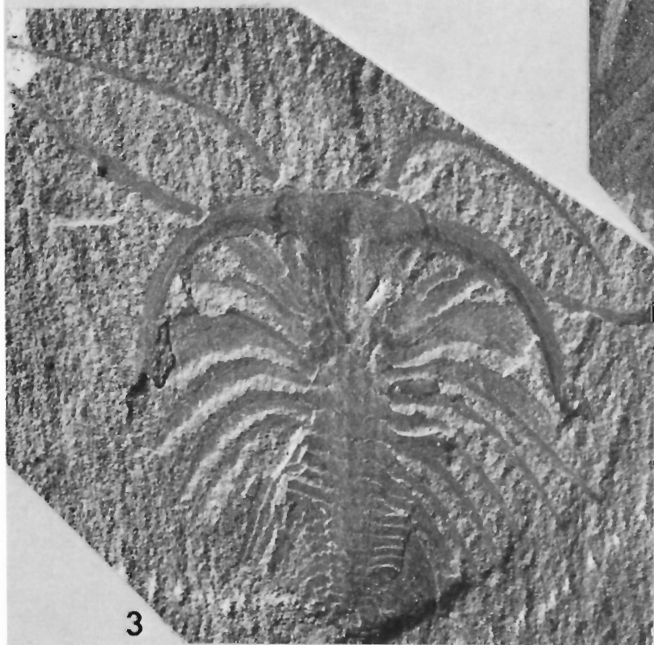
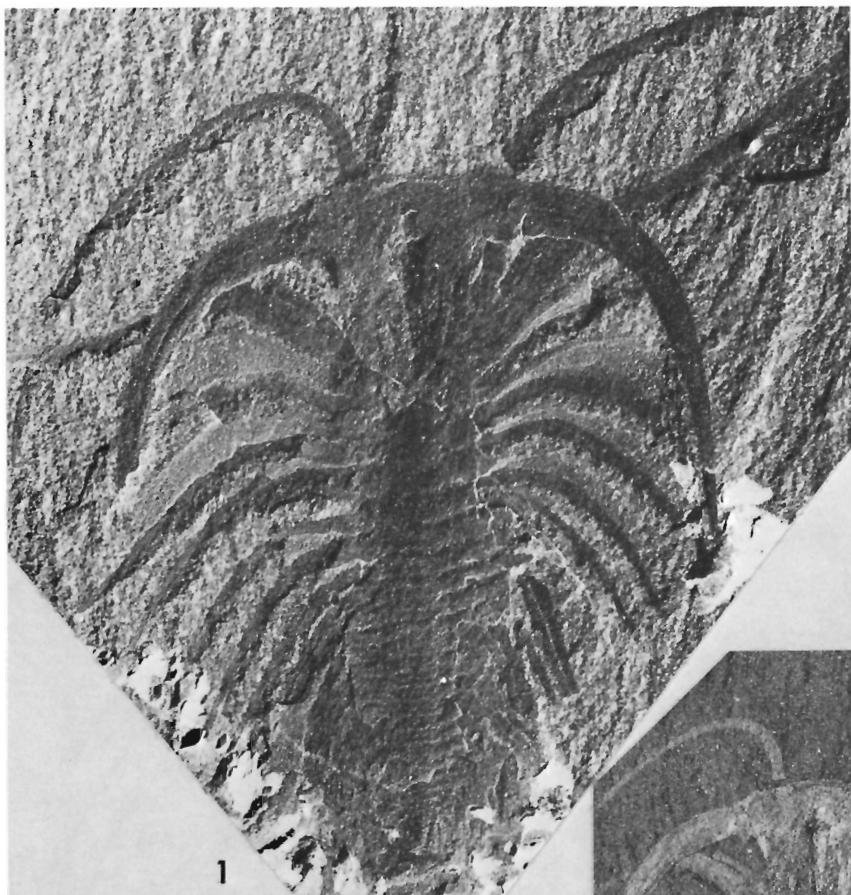
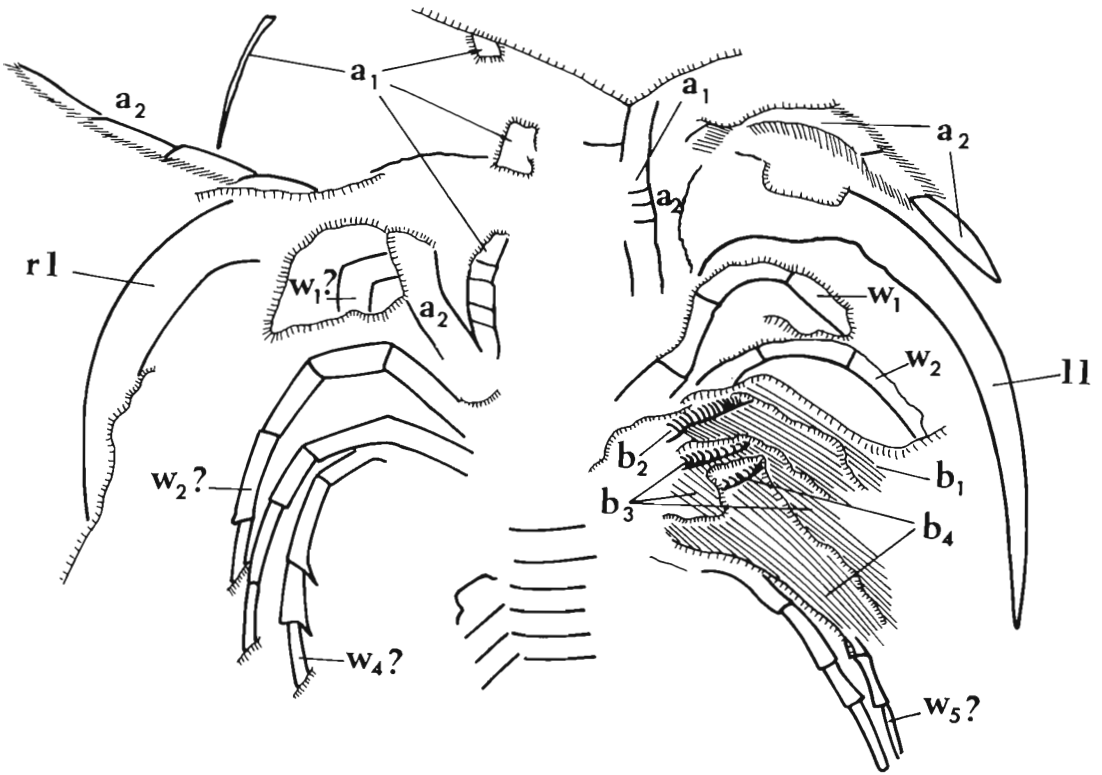


PLATE VIII

Marrella splendens Walcott, 1912
Phyllopod bed, Walcott quarry

Figures 1, 2. USNM 83486a, parallel forward, ventral, fig. 1 northwest, fig. 2 reflected, x5, original of Walcott, 1931, Pl. 22, fig. 2, see Text-fig. 18.

Figure 3. USNM 166574, oblique, dorsal, southwest, x5; original of Ruedemann, 1931, Pl. 6, fig. 2; see Pl. VI, fig. 3.



TEXT-FIGURE 18

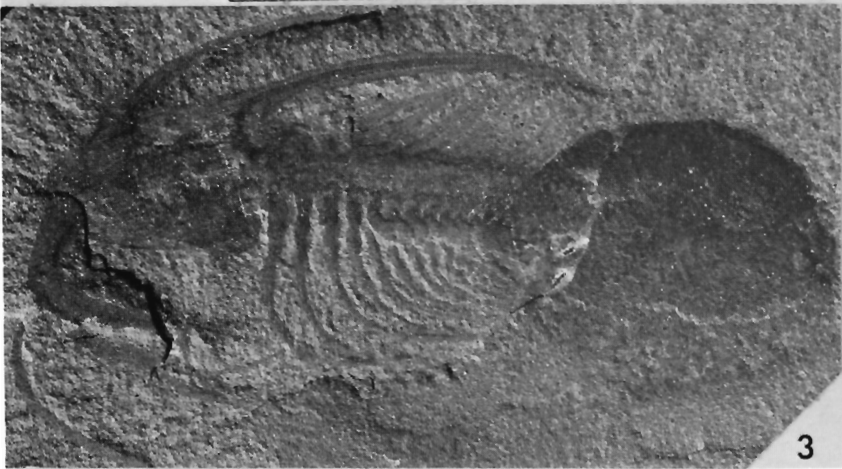
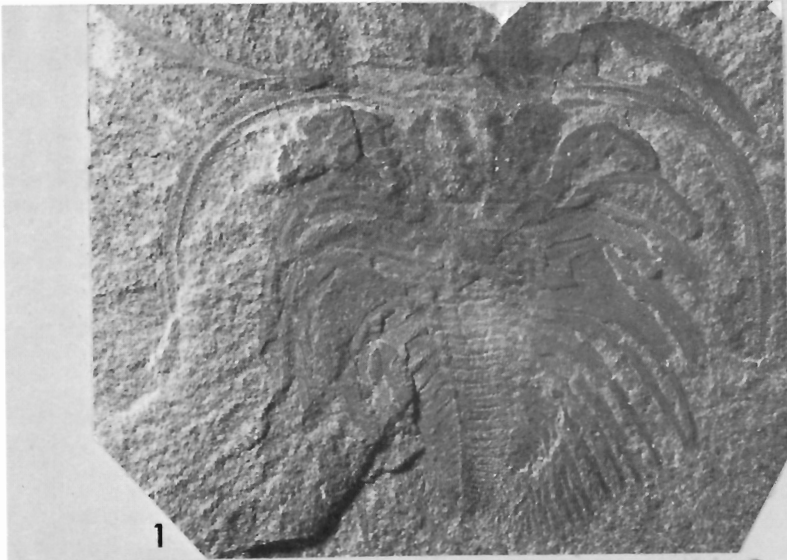
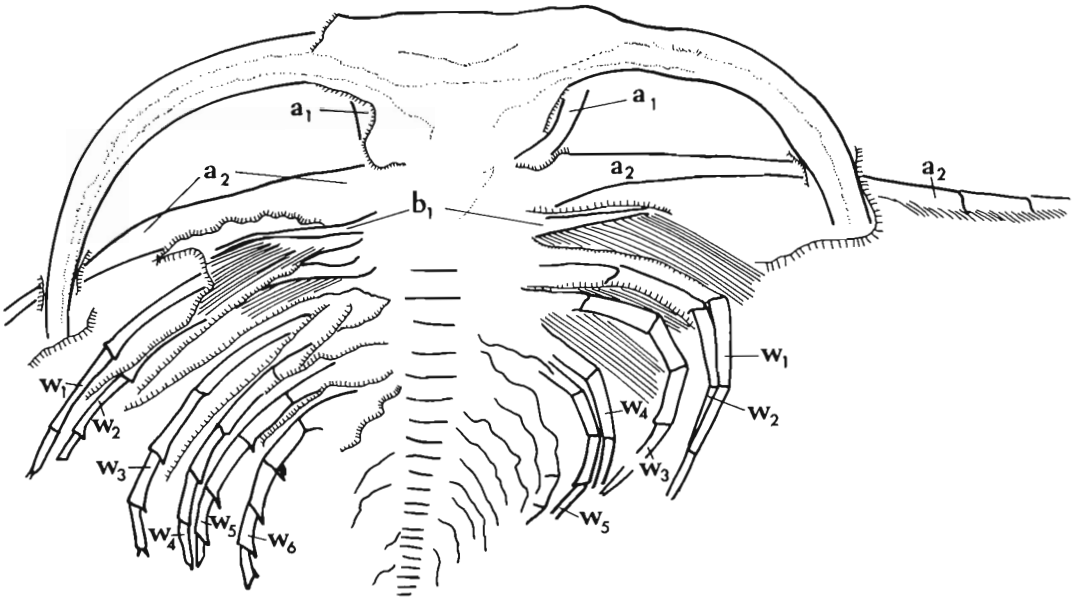


PLATE IX

Marrella splendens Walcott, 1912
Phyllopod bed, Walcott quarry.

Figures 1-3. USNM 83486, parallel forward, fig. 1, dorsal, northwest, fig. 2, reflected, original of Ruedemann, 1931, Pl. 7, fig. 1; fig. 3, counterpart, reflected; x5; see Text-fig. 19.



TEXT-FIGURE 19

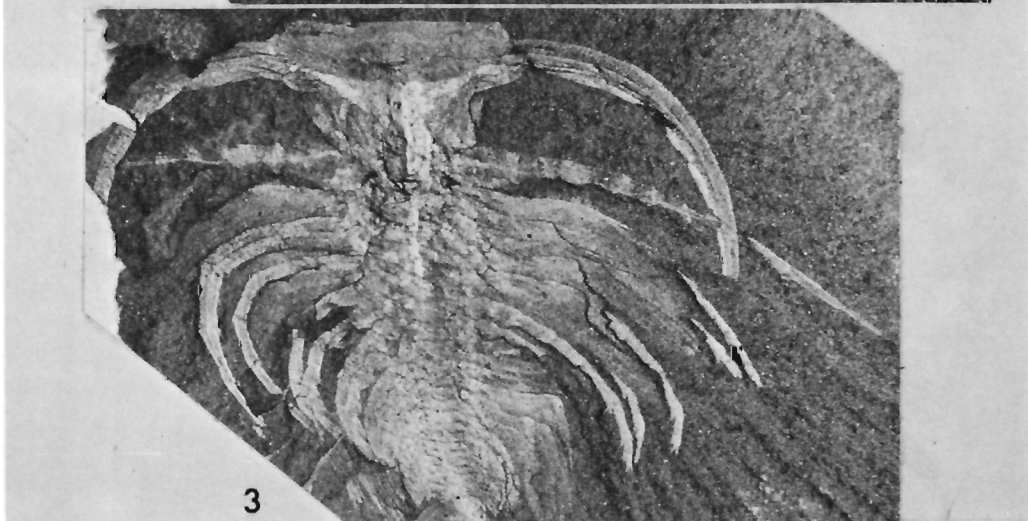
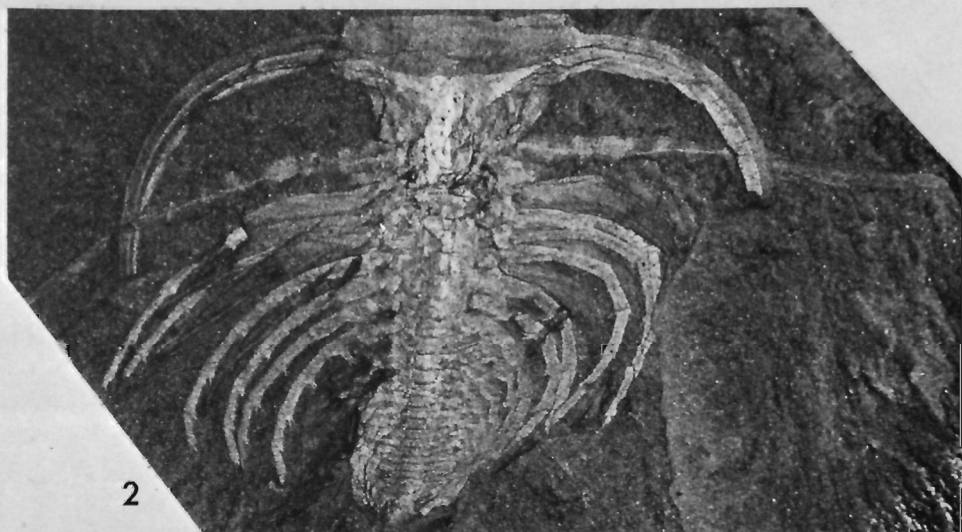
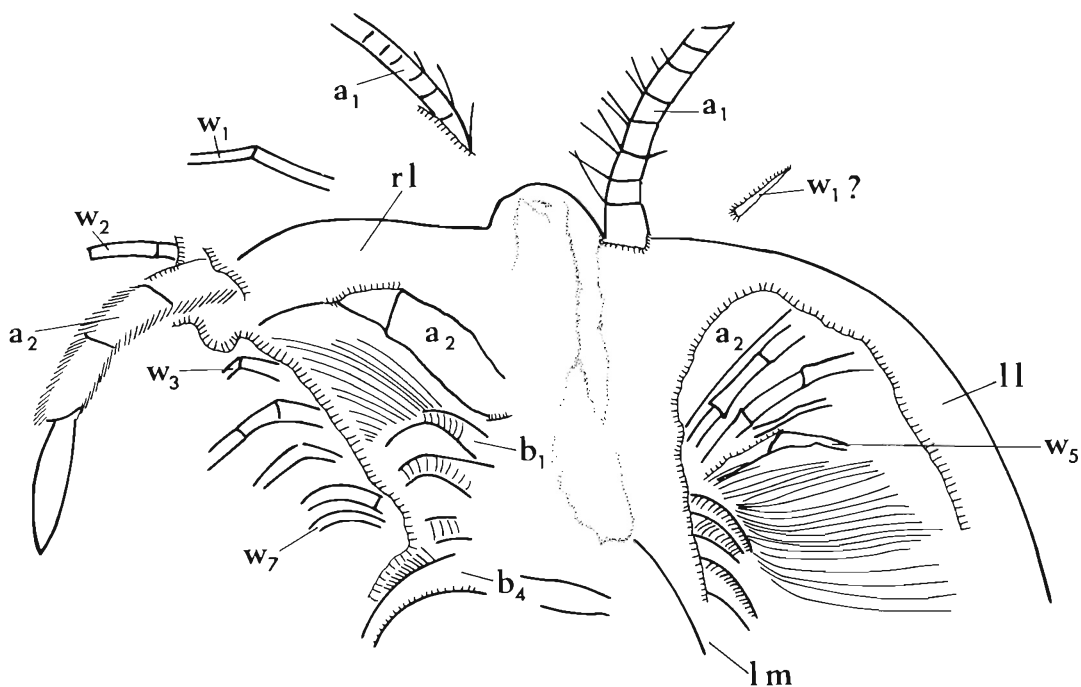


PLATE X

Marrella splendens Walcott, 1912
Phyllopod bed, Walcott quarry.

- Figure 1. USNM 139624, parallel, ventral, north, x7; original of Simonetta, 1962, Pl. 16. Numbers 2 to 5 indicate joints of a_2 .
- Figure 2. USNM 139625, oblique, ventral, reflected, x10; original of Simonetta, 1962, Pl. 15, showing short filaments (s) on upper side of gill branch.
- Figure 3. USNM 139626, parallel backward, ventral, north, x5; original of Simonetta, 1962, Pl. 14, prepared on right side (left in figure), see Text-fig. 20 and Pl. XVIII, fig. 6.



TEXT-FIGURE 20

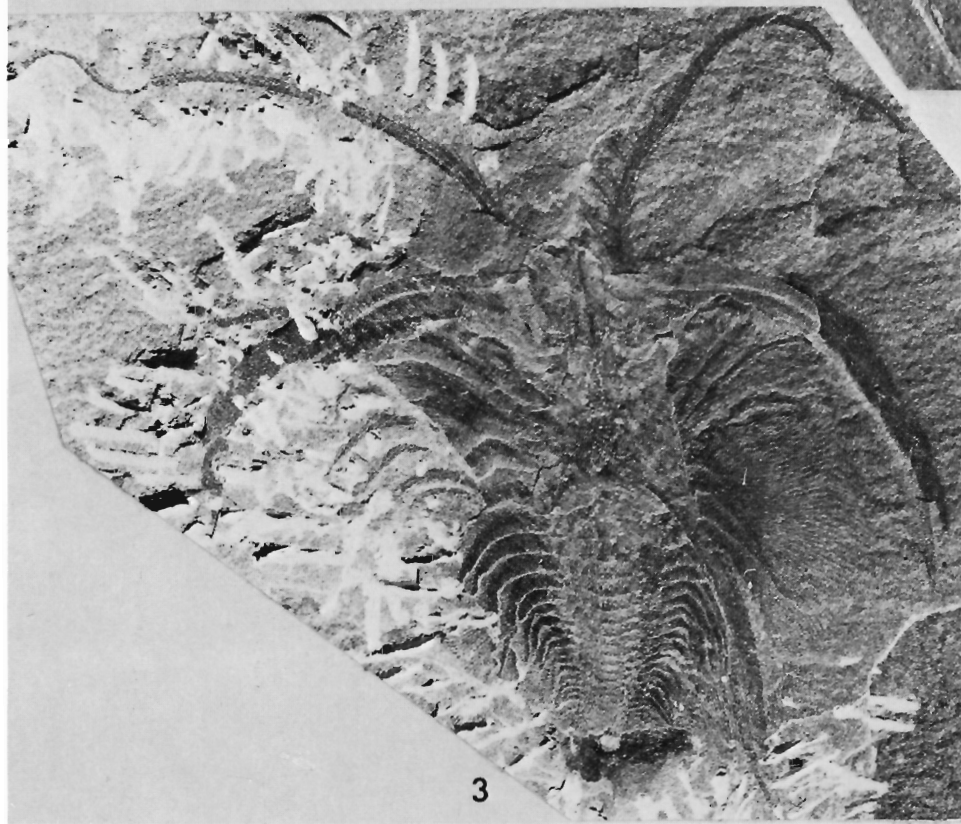
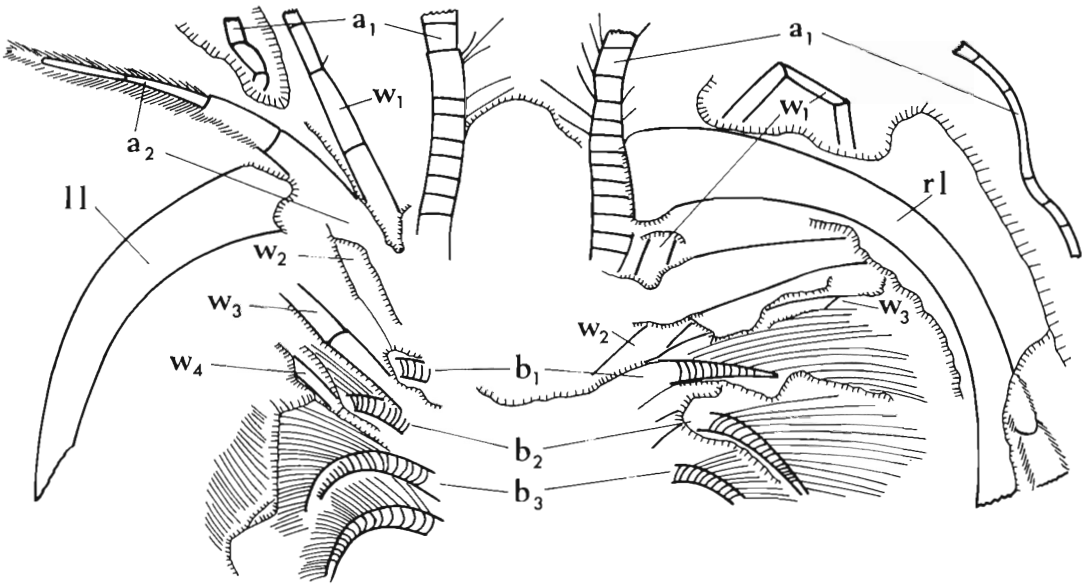


PLATE XI

Marrella splendens Walcott, 1912
Phyllopod bed, Walcott quarry.

- Figure 1. USNM 139631, parallel backward, dorsal, south, x5, original of Simonetta, 1962, Pl. 17, after preparation; see Text-fig. 21.
- Figure 2. USNM 166585, oblique, ventral, west, x5, showing bifid tip of right median cephalic spine (lower left of figure).
- Figure 3. USNM 166587, parallel, dorsal, reflected, x5, showing spines at tips of walking legs.



TEXT-FIGURE 21

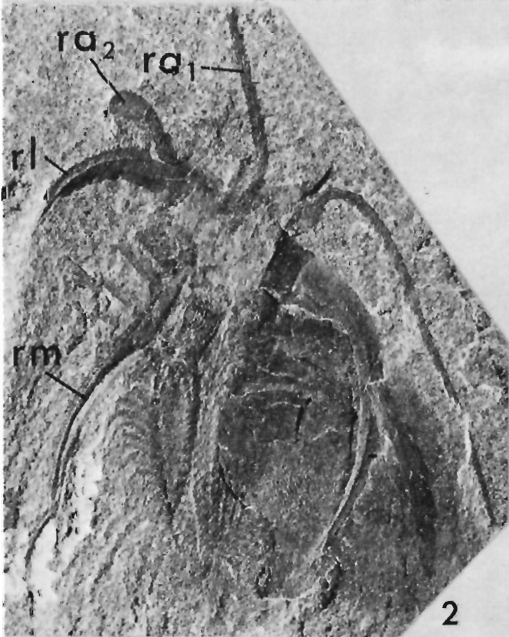
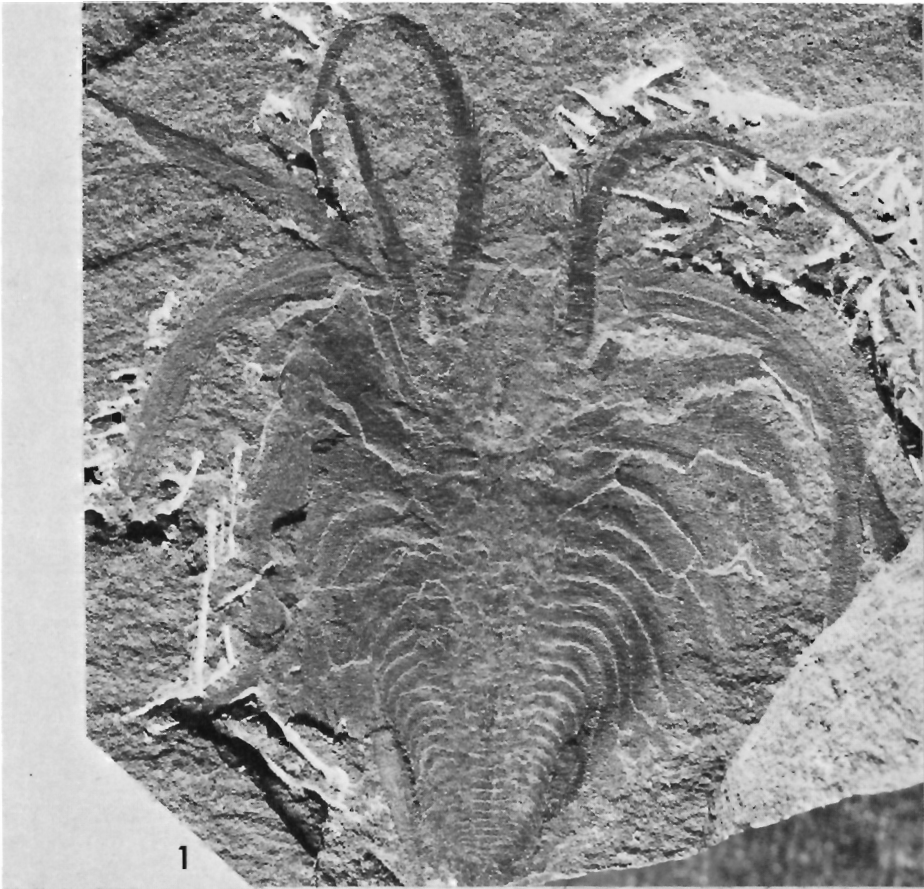
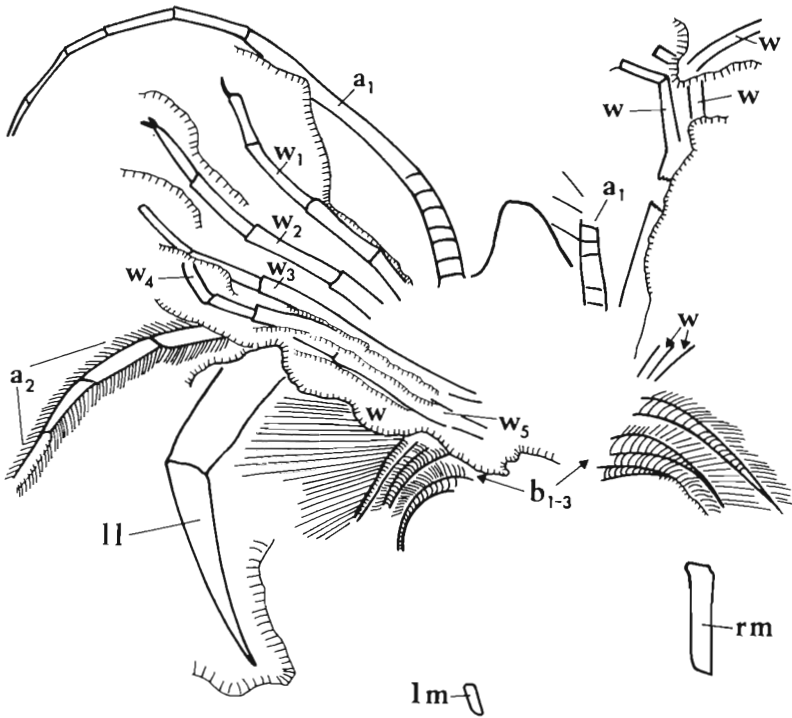


PLATE XII

Marrella splendens, Walcott, 1912
Phyllopod bed, Walcott quarry

- Figure 1. USNM 139633, parallel backward, ventral, northwest, x7; original of Simonetta, 1962, Pl. 17, after preparation; see Text-fig. 22.
- Figure 2. USNM 57670, parallel, ventral, northwest, original of Walcott, 1912, Pl. 26, fig. 1, and Ruedemann, 1931, fig. 4.



TEXT-FIGURE 22

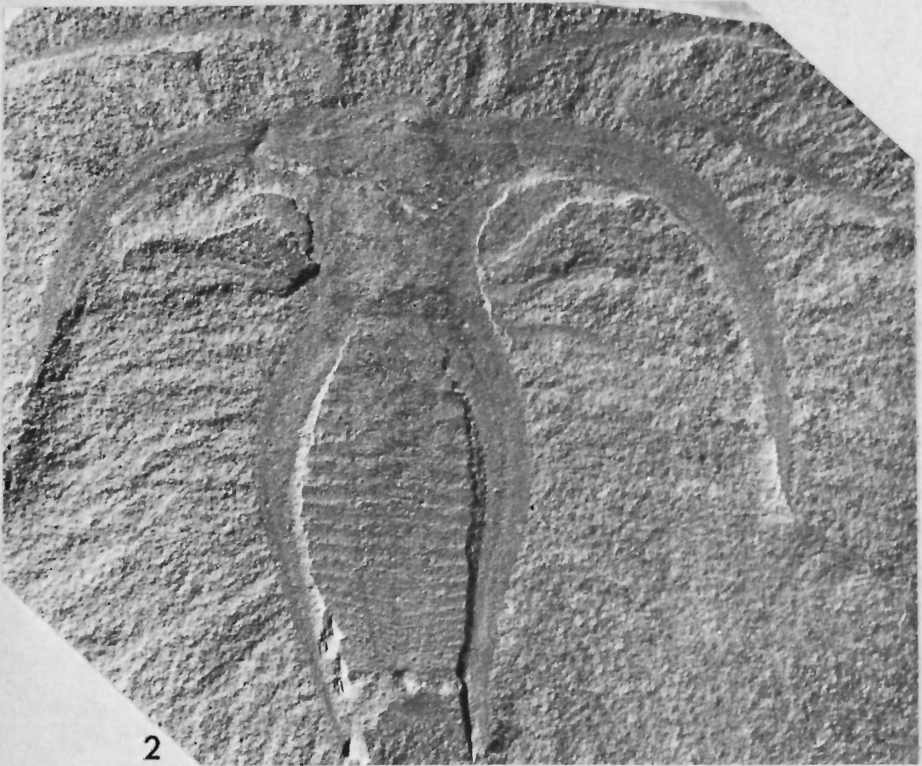


PLATE XIII

Marrella splendens Walcott, 1912.

- Figure 1. GSC 26591, parallel forward, dorsal, north, x7, showing gill branches sloping postero-ventrally and their presence on most posterior somites. Walcott quarry, level 6 ft. 7½ ins. to 7 ft. 3½ ins.
- Figures 2, 3. USNM 166588, vertical backward, ventral, fig. 2, north, fig. 3, reflected, x5, showing triangular cross-section of cephalic shield. Phyllopod bed, Walcott quarry.

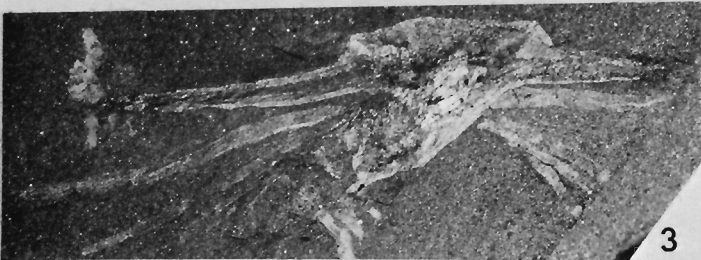
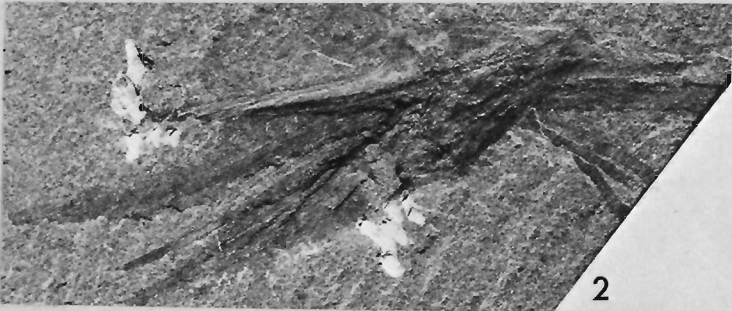
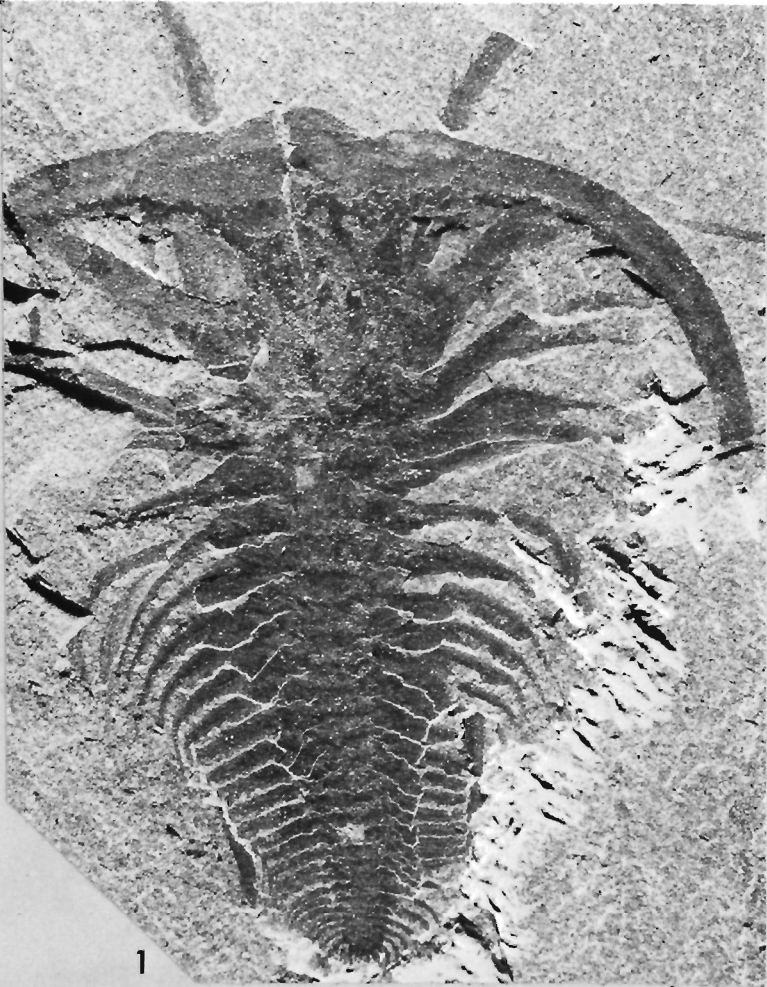
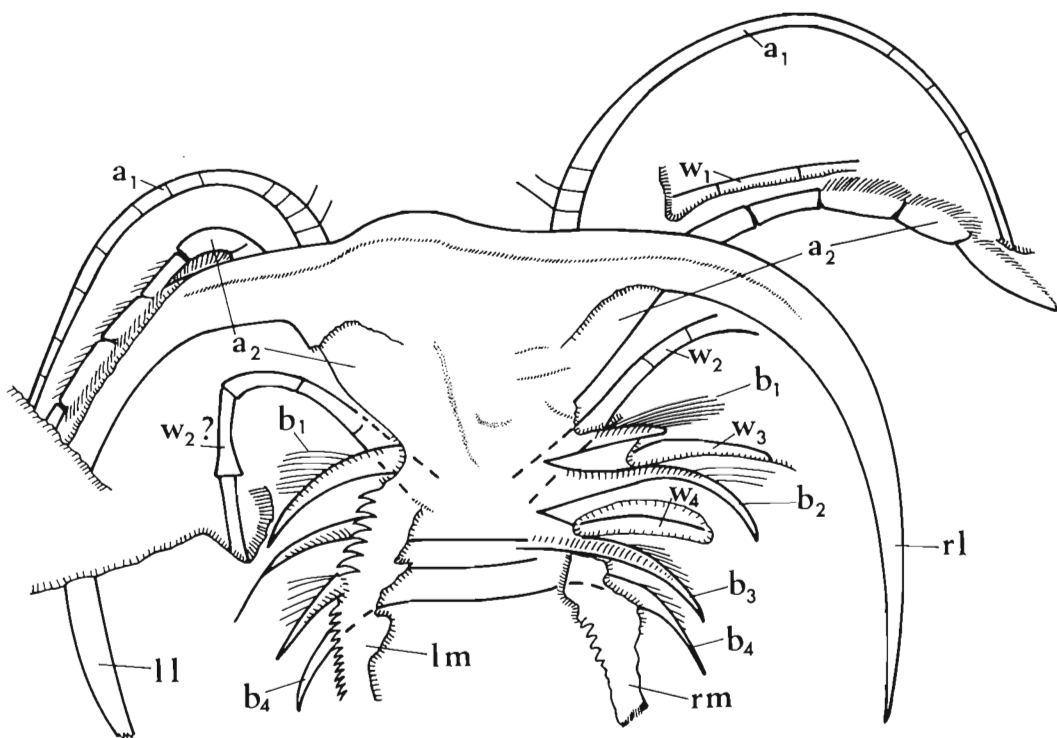


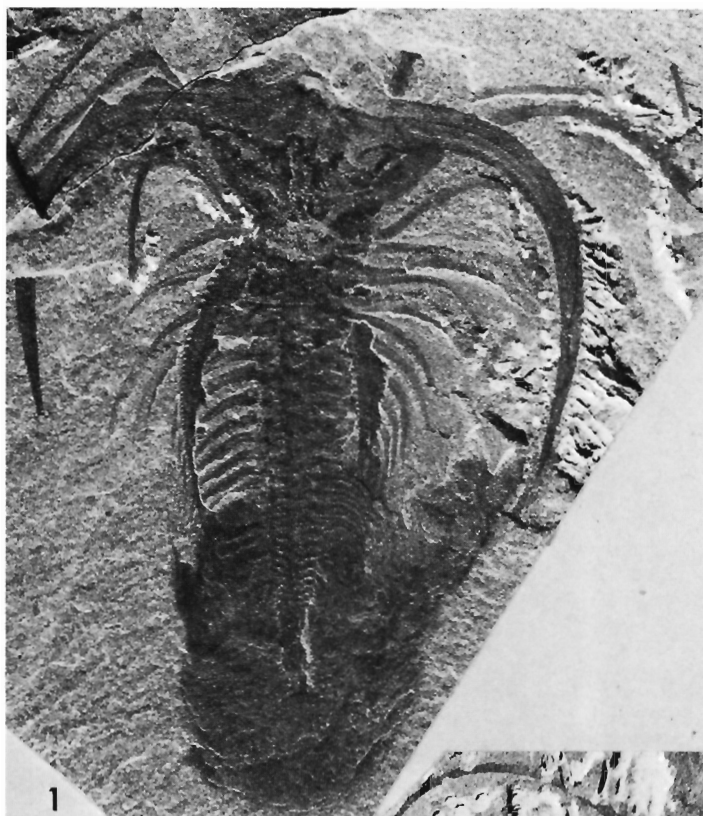
PLATE XIV

Marrella splendens Walcott, 1912
Walcott quarry, level 6 ft. 7½ ins. to 7 ft. 3½ ins.

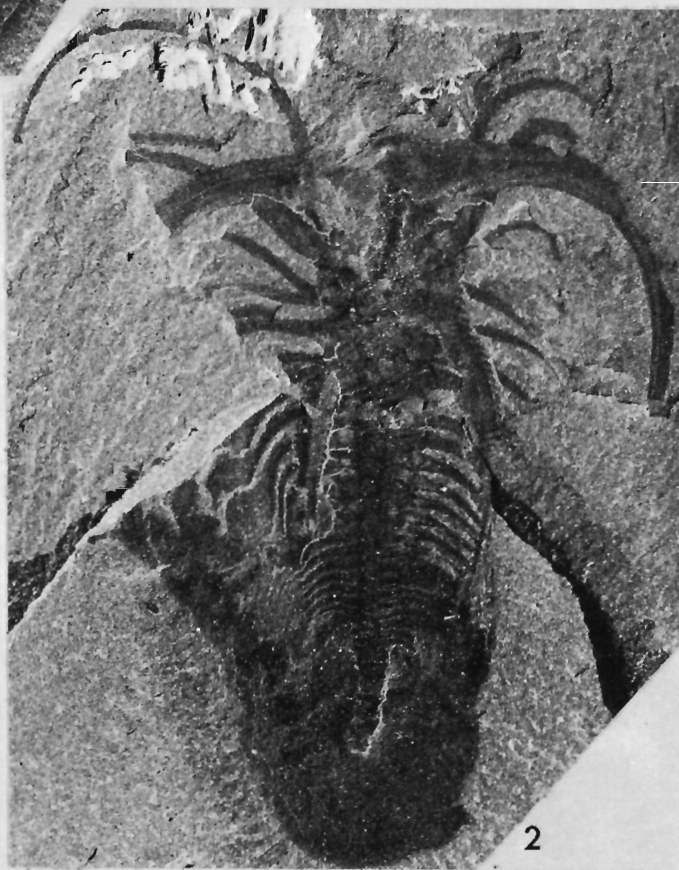
Figures 1, 2. GSC 26592, parallel forward, fig. 1, part, dorsal, north; fig. 2, counterpart, ventral, west; x5; see Text-fig. 23.



TEXT-FIGURE 23



1



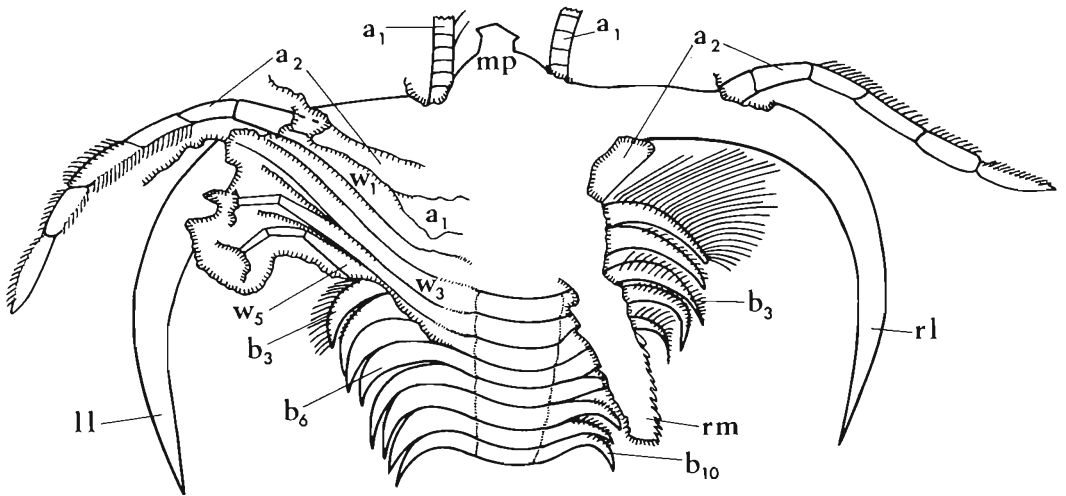
2

PLATE XV

Marrella splendens Walcott, 1912

Figure 1. GSC 26593, parallel backward, dorsal, west, $\times 10$, showing triangular median anterior projection formed by compression of frontal slope and anteroventral angle of cephalic shield. Walcott quarry, level 6 ft. $7\frac{1}{2}$ ins. to 7 ft. $3\frac{1}{2}$ ins.

Figure 2. GSC 26594, parallel-backward, dorsal, west, $\times 10$; see Text-fig. 24 and Pl. XVI, fig. 2. Walcott quarry, level 6 ft. 11 ins. to 7 ft. 2 ins.



TEXT-FIGURE 24

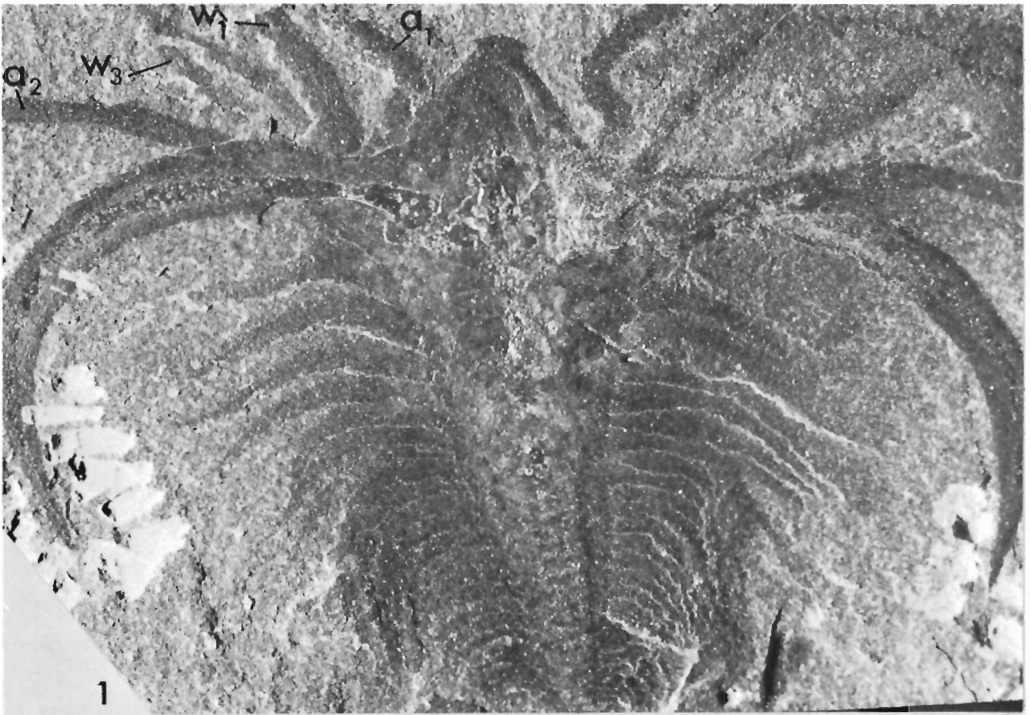
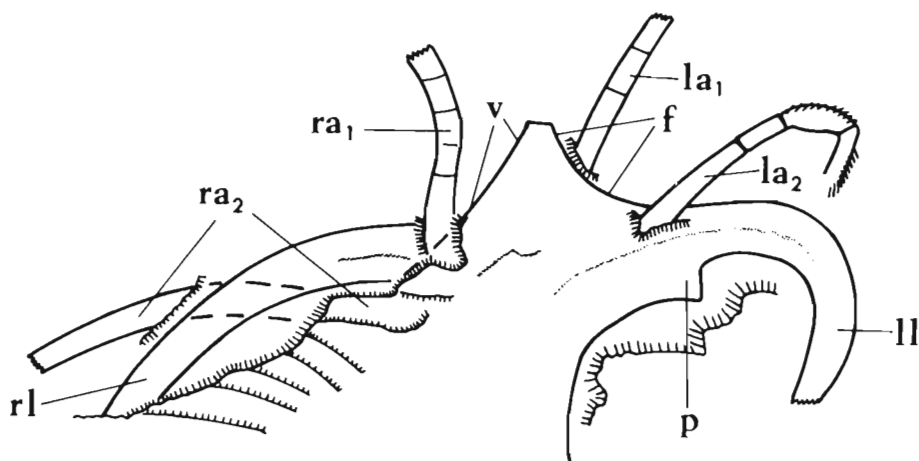


PLATE XVI

Marrella splendens Walcott, 1912

Figure 1. GSC 26595, oblique, ventral, northeast, x5, see Text-fig. 25 (drawn using counterpart to show additional portions of a₂). Walcott quarry, level 6 ft. 7½ ins. to 7 ft. 3½ ins.

Figure 2. GSC 26594, parallel backward, ventral (counterpart of original of Pl. XV, fig. 2), north, x5; specimen washed for a few seconds in dilute hydrofluoric acid to bleach rock and heighten contrast. Walcott quarry, level 6 ft. 11 ins. to 7 ft. 2 ins.



TEXT-FIGURE 25

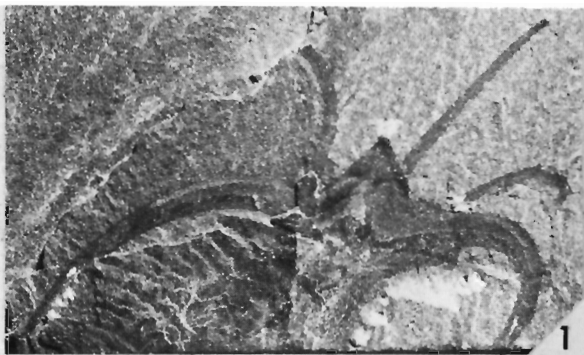
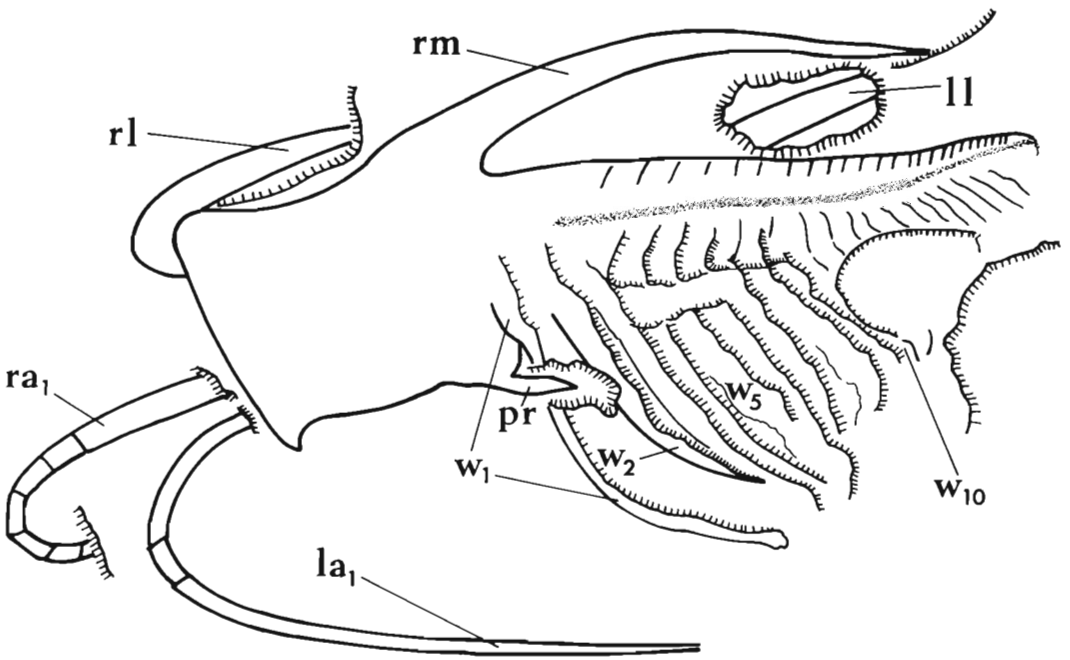


PLATE XVII

Marrella splendens Walcott, 1912

Figures 1, 2. GSC 26596, counterparts, lateral, northwest, x5; see Text-fig. 26. Walcott quarry, level 6 ft. 7½ ins. to 7 ft. 3½ ins.

Figure 3. GSC 26597, oblique, dorsal, west, x5, body lying outside median spines. Walcott quarry, level 5 ft. 1 ins. to 5 ft. 5 ins.



TEXT-FIGURE 26

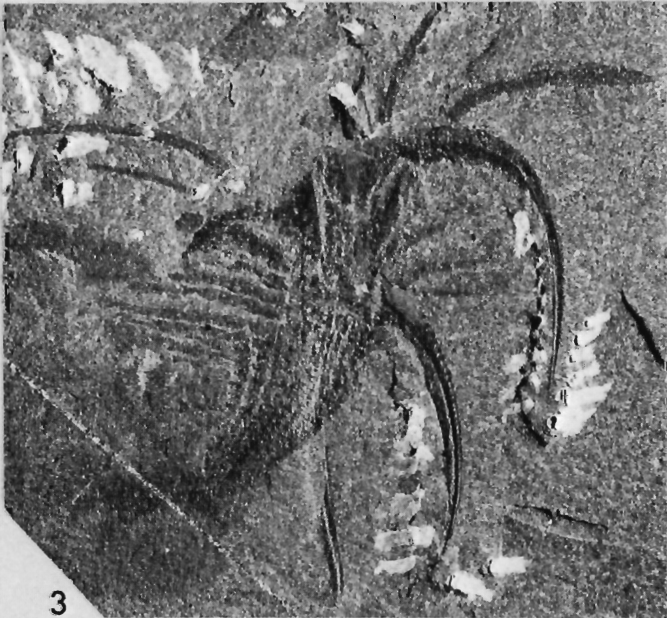
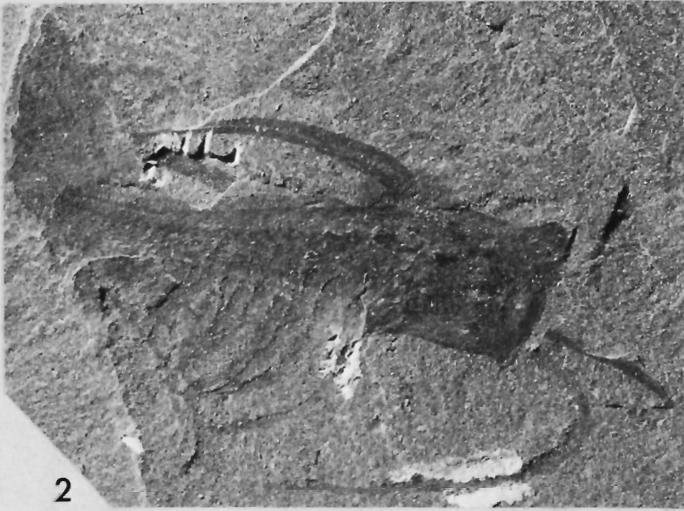


PLATE XVIII

Marrella splendens Walcott, 1912

- Figure 1. GSC 26598, parallel, dorsal, north, x5; showing expansions of segments of walking legs at left posterior. Walcott quarry, level 6 ft. 11 ins. to 7 ft. 4 ins.
- Figure 2. GSC 26599, parallel, ventral, north, x10; small individual. Walcott quarry, level 5 ft. 1 ins. to 5 ft. 5 ins.
- Figure 3. GSC 26600, parallel, reflected, x5; poorly preserved individual showing branching of lateral spines. Walcott quarry, level 6 ft. 8 ins. to 6 ft. 11 ins.
- Figure 4. GSC 26601, parallel, ventral, north, x5; a₂ on right side of figure shows long, undivided basal segment. Walcott quarry, level 5 ft. 1 ins. to 5 ft. 5 ins.
- Figure 5. GSC 26602, parallel, dorsal, north, x5; rare example of isolated cephalic shield. Walcott quarry, level 8 ft. 0 ins. to 8 ft. 7 ins.
- Figure 6. USNM 139626, part of original of Pl. X, fig. 3, reflected, x5, showing setae on first antenna and structure of gill branches. Phyllopod bed, Walcott quarry.

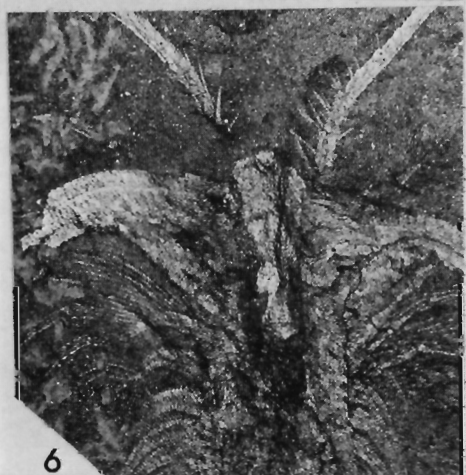
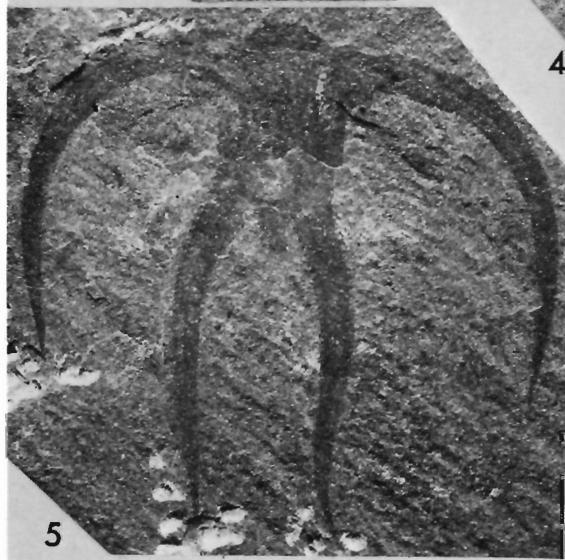
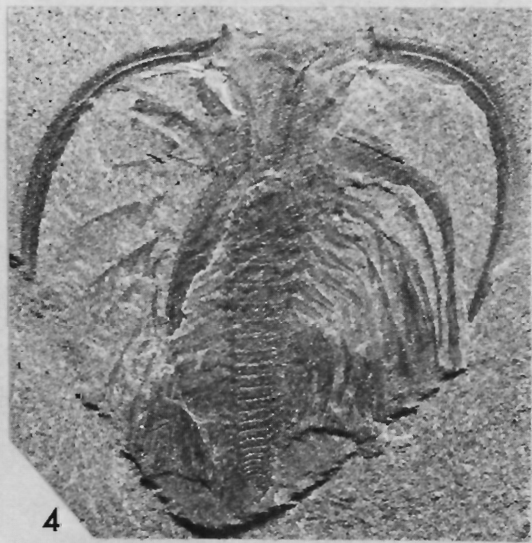
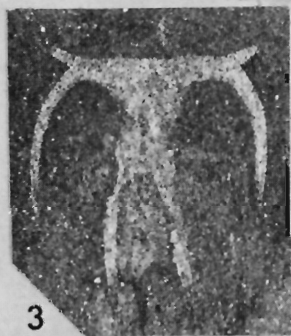
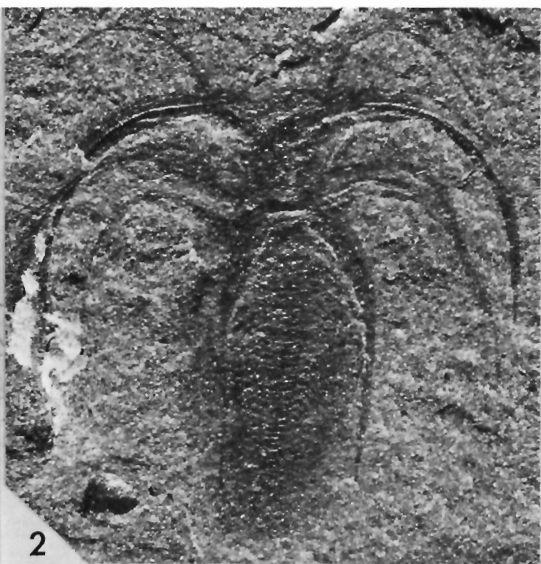
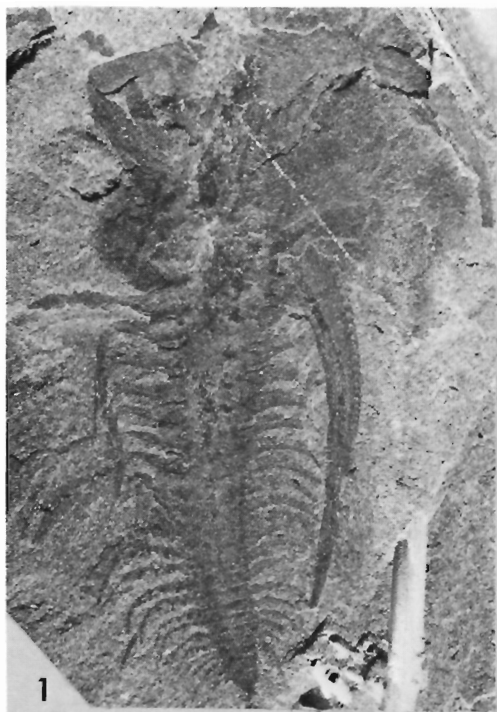


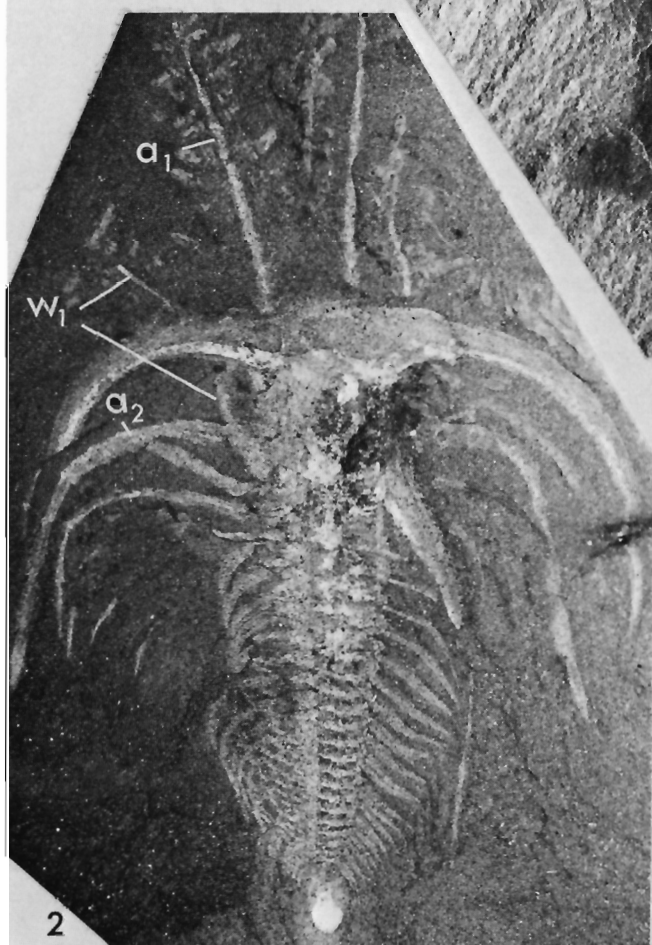
PLATE XIX

Marrella splendens Walcott, 1912
Walcott quarry, level 7 ft. 0 ins.

Figures 1, 2. GSC 26603, part, dorsal, fig. 1 northwest, fig. 2 reflected, x5; showing on left position of w_1 and expansion of joints of walking legs posteriorly, highly reflective area at posterior tip of body. Compare Pl. XX, figs. 2, 3.



1

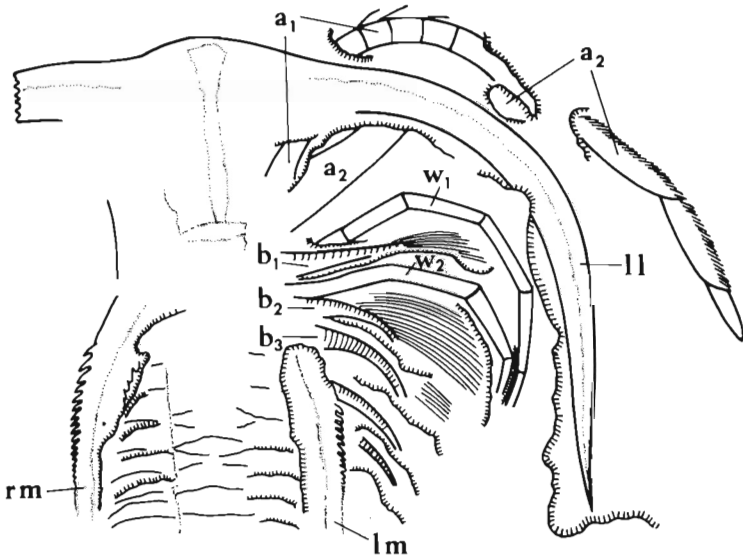


2

PLATE XX

Marrella splendens Walcott, 1912

- Figure 1. GSC 26604, parallel forward, ventral, north, x5; see Text-fig. 27. Walcott quarry, level 6 ft. 7½ ins. to 7 ft. 3¼ ins.
- Figures 2, 3. GSC 26603, counterpart of original of Pl. XIX, figs. 1, 2; ventral, fig. 2 west, fig. 3 reflected, x5. Walcott quarry, level 7 ft. 0 ins.



TEXT-FIGURE 27

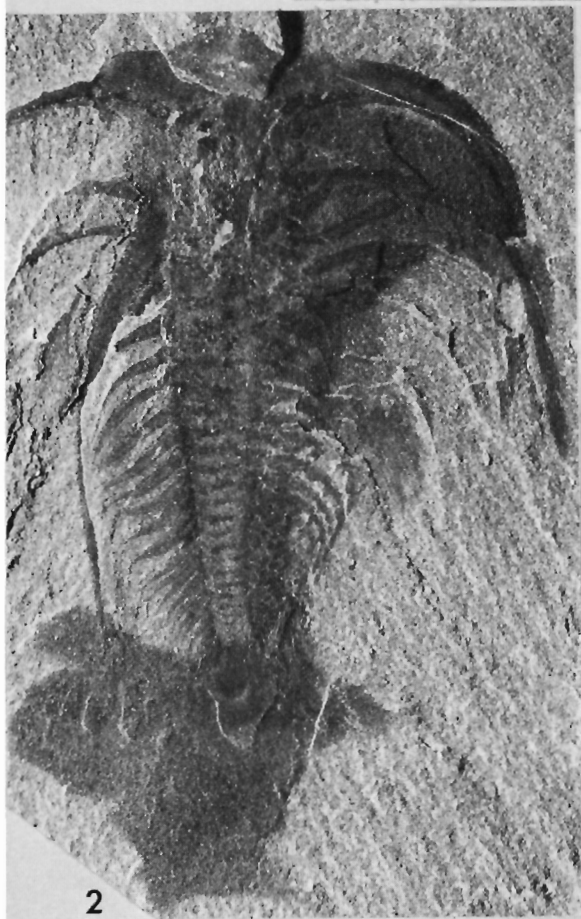
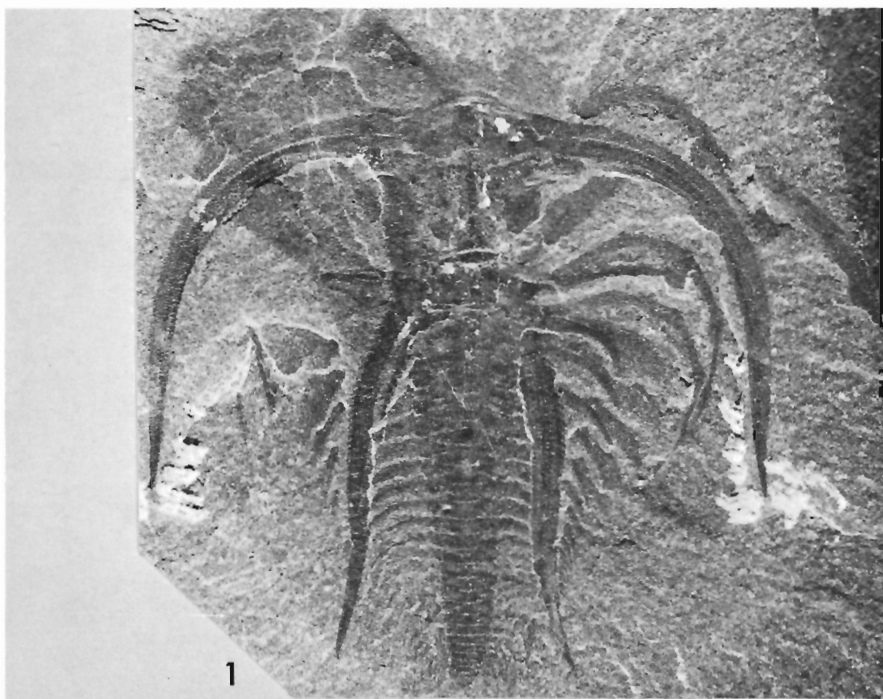
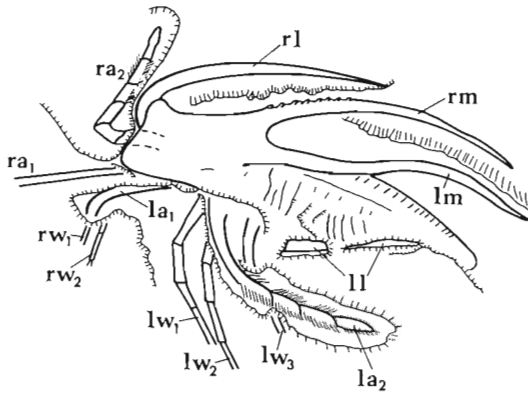


PLATE XXI

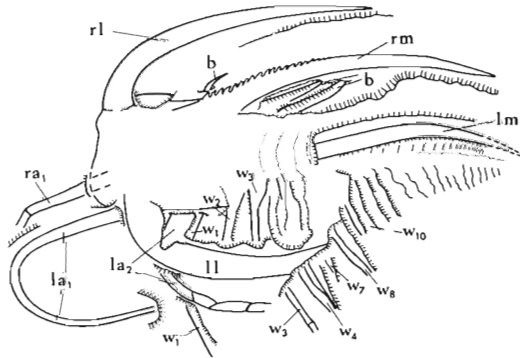
Marrella splendens Walcott, 1912
 Walcott quarry, level 6 ft. 7½ ins. to 7 ft. 3½ ins.

Figures 1, 2. GSC 26605, counterparts, oblique, west, x7; showing four cephalic spines (ll on fig. 2), see Text-fig. 28.

Figures 3, 4. GSC 26606, counterparts, oblique, fig. 3 west, fig. 4 east, x7; showing four cephalic spines, see Text-fig. 29.



TEXT-FIGURE 28



TEXT-FIGURE 29

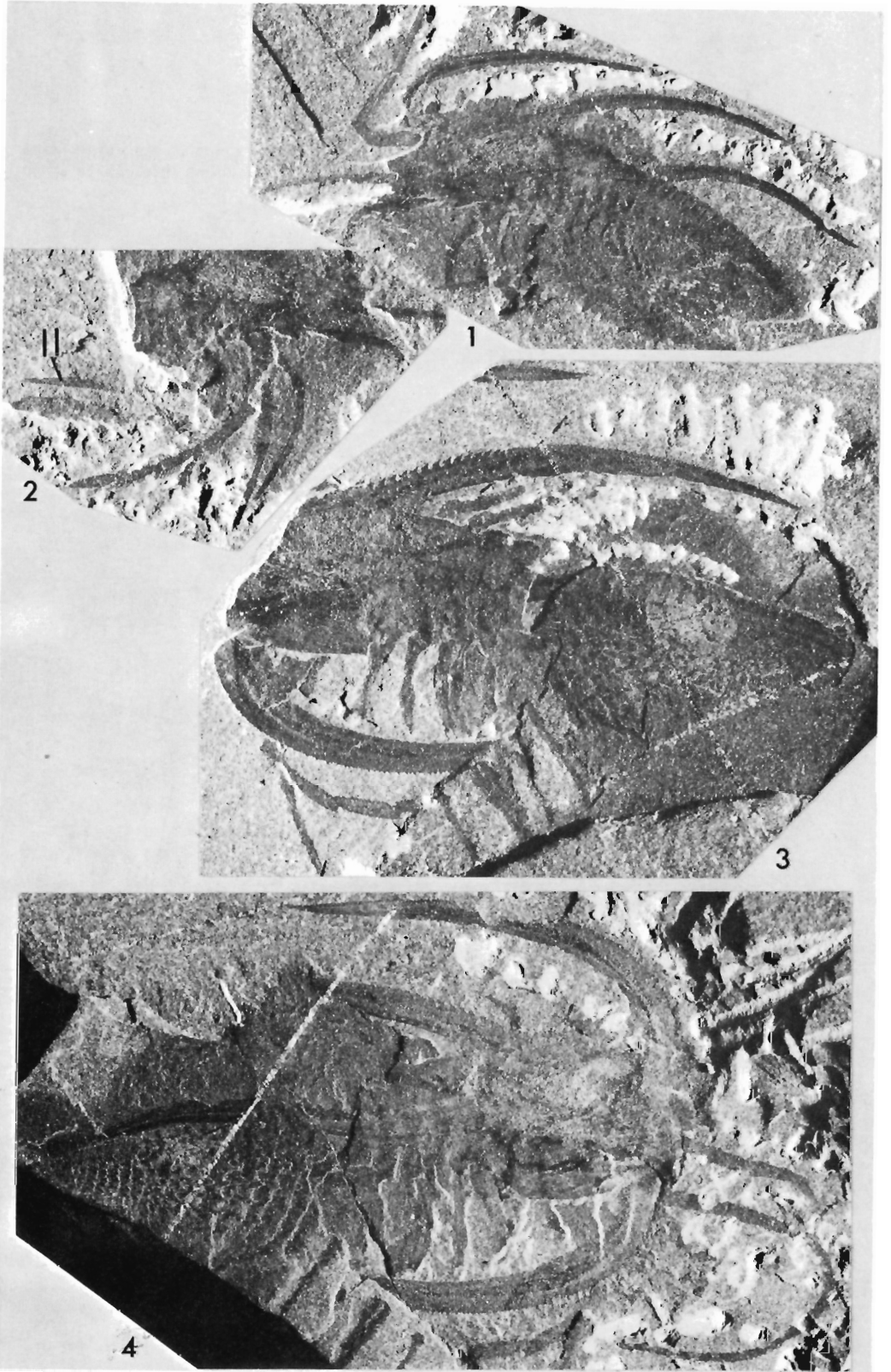
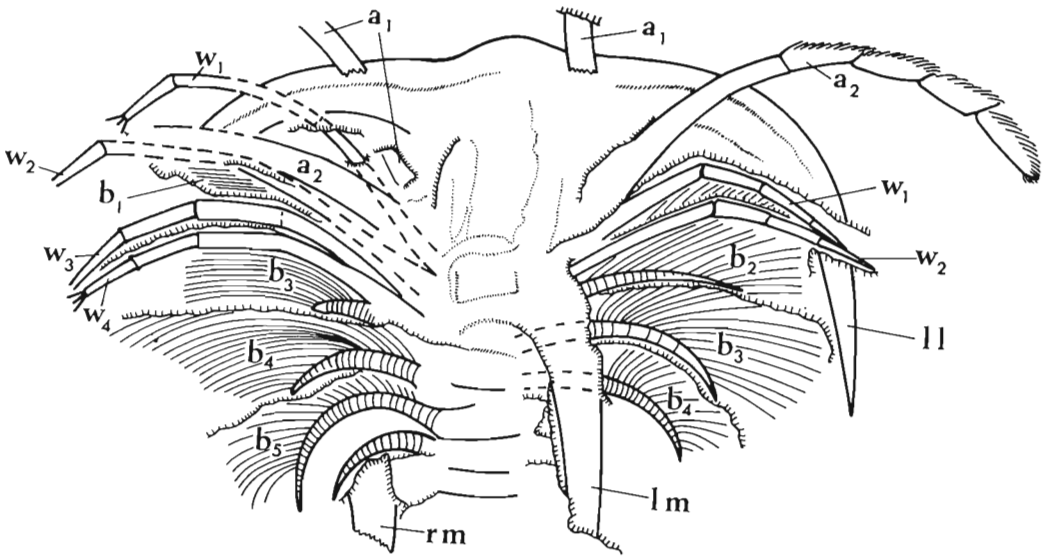


PLATE XXII

Marrella splendens Walcott, 1912

Walcott quarry, level 6 ft. 6 ins. to 7 ft. 0 ins.

Figures 1, 2. GSC 25430, fig. 1, counterpart, ventral, west x10; fig. 2, part, dorsal, west, x5; original of Whittington, 1970, figs. 7a, b; see Text-fig. 30. Fig. 1 shows three spines at tip of w₄.



TEXT-FIGURE 30

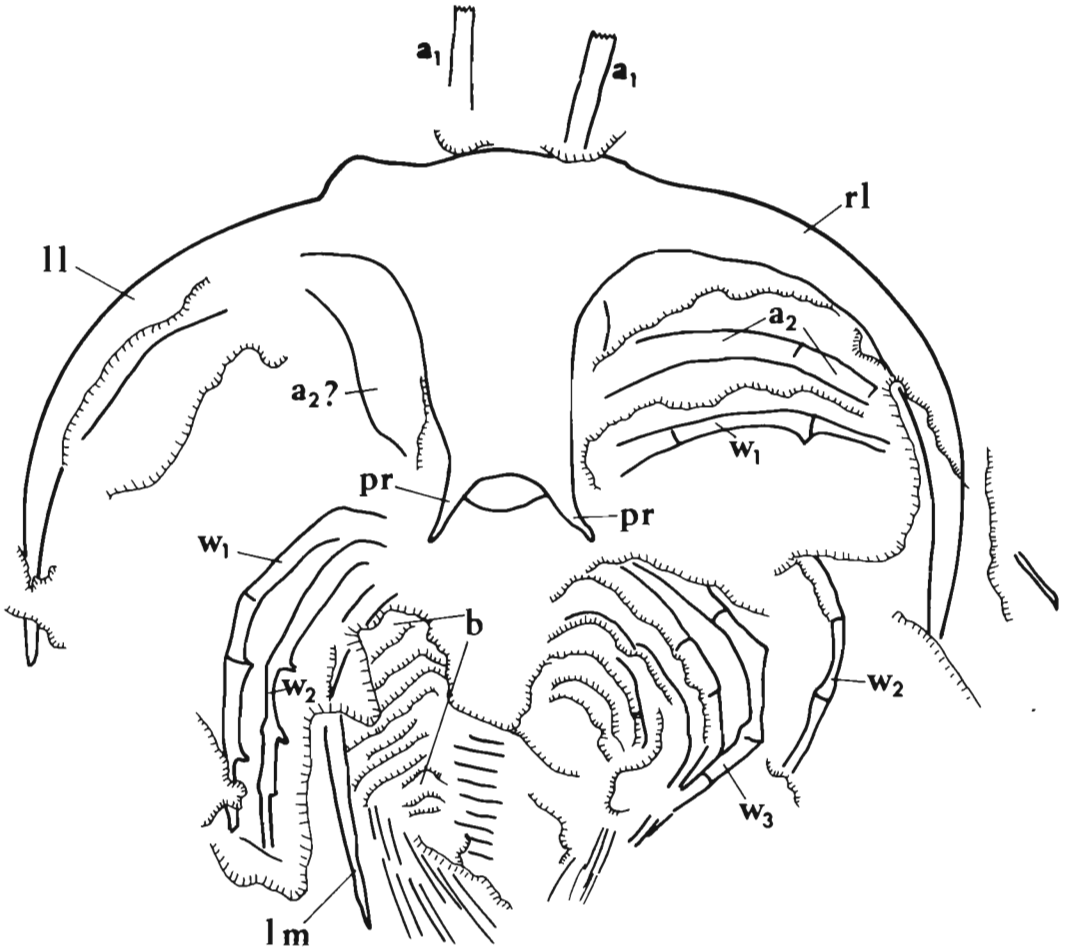


PLATE XXIII

Marrella splendens Walcott, 1912

Walcott quarry, level 6 ft. 11 ins. to 7 ft. 0 ins.

Figures 1, 2. GSC 26607, parallel forward, dorsal, north and reflected respectively, x5; showing projection from posterolateral angle of ventral surface of cephalic shield, see Text-fig. 31.



TEXT-FIGURE 31

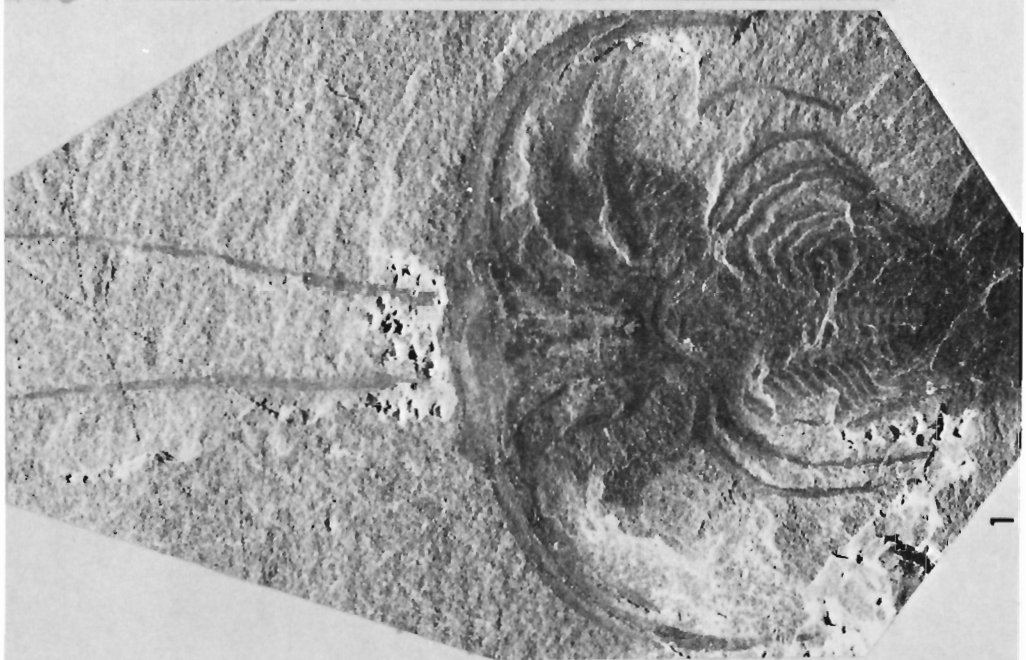
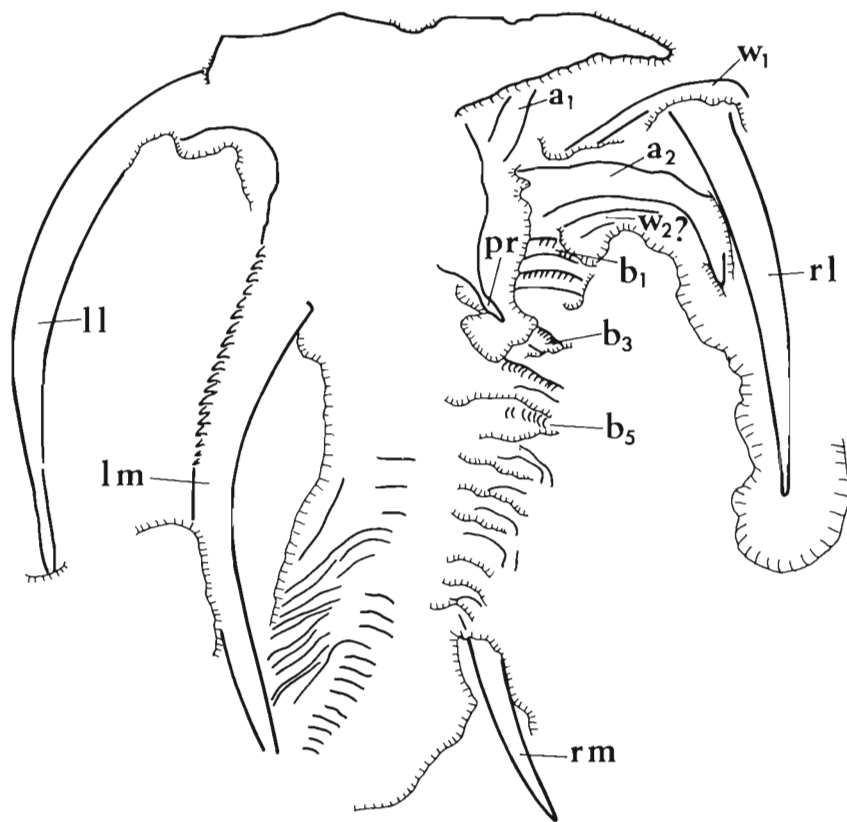


PLATE XXIV

Marrella splendens Walcott, 1912

- Figures 1, 2. GSC 26608, oblique, dorsal, fig. 1 northwest, fig. 2 reflected, x5; see Text-fig. 32, specimen has been excavated to show projection from right posterolateral angle of ventral surface of cephalic shield, lying ventral to proximal parts of appendages. Walcott quarry, level 6 ft. 11 ins.
- Figures 3, 4. GSC 26609, oblique, fig. 3 reflected, fig. 4 northwest, x5; showing frontal and ventral profile of cephalic shield with posterolateral projection. Reflected photograph shows area interpreted as U-shaped stomach (st) in cephalic shield and probable position of mouth on posterior wall. Walcott quarry, level 8 ft. 7 ins. to 8 ft. 9 ins.



TEXT-FIGURE 32

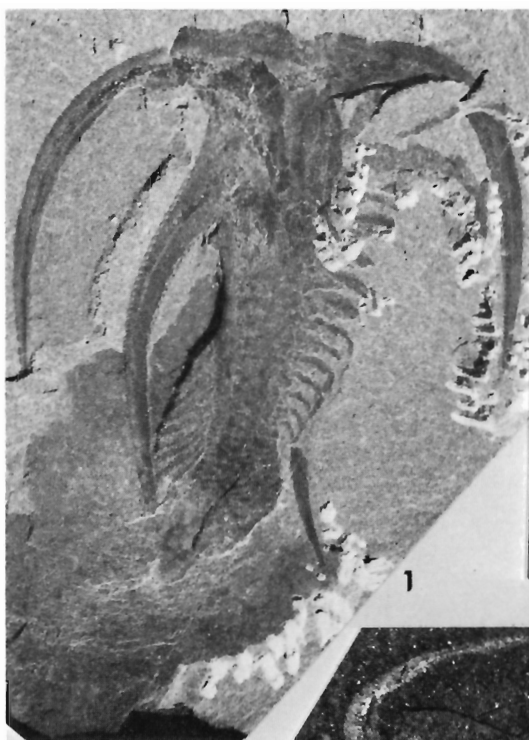


PLATE XXV

Marrella splendens Walcott, 1912

Figure 1. GSC 26610, lateral, west, x5; showing lateral profile of cephalic shield and posterolateral projection. Walcott quarry, level 6 ft. 11 ins. to 7 ft. 0 ins.

Figures 2, 3. GSC 26611, dorsal, fig. 2 north, fig. 3 reflected, x5; showing on left side sharp flexure of gill branches, filaments on distal parts directed posterolaterally. Walcott quarry, level 7 ft. 11 ins. to 8 ft. 4 ins.

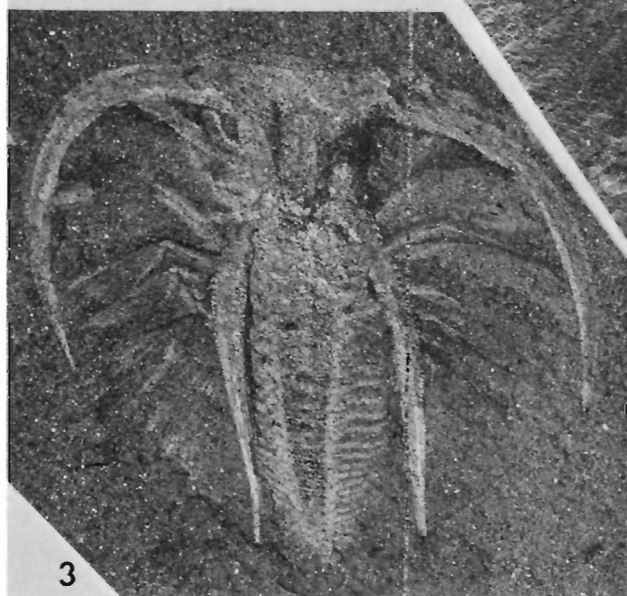
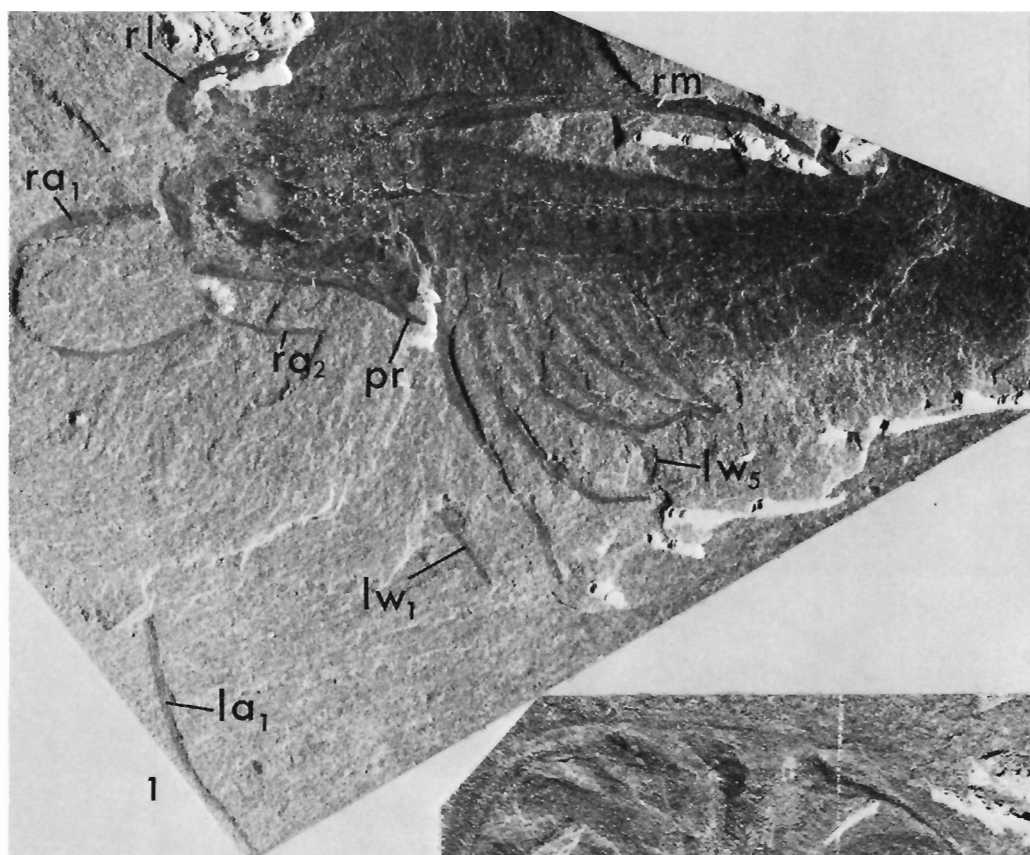
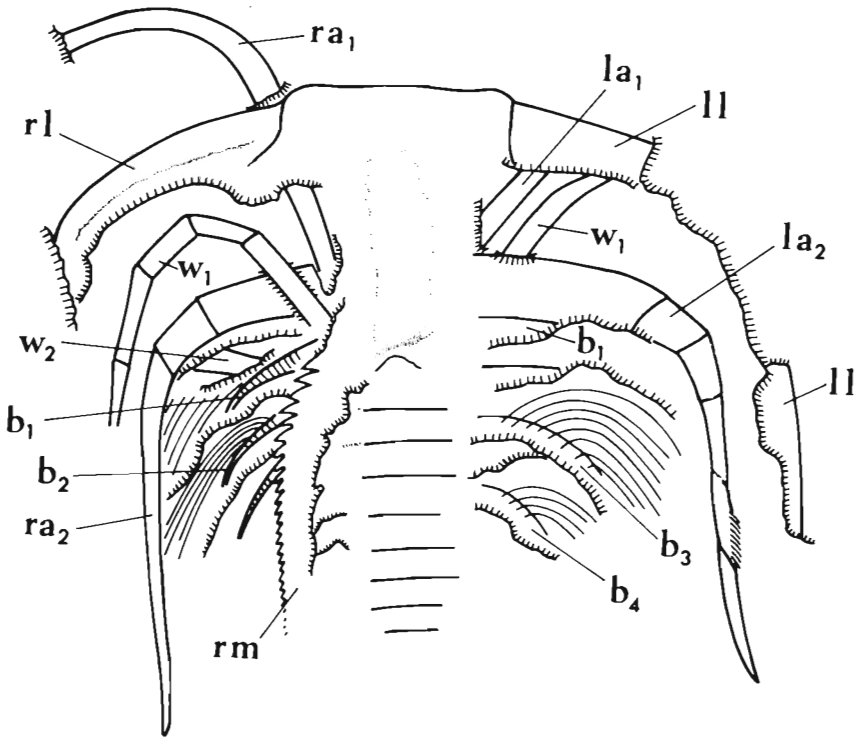


PLATE XXVI

Marrella splendens Walcott, 1912
Walcott quarry, level 6 ft. 7½ ins. to 7 ft. 3½ ins.

- Figures 1, 2. GSC 26612, counterparts, parallel forward, fig. 1 ventral, northwest, fig. 2 dorsal, northwest, x5; showing proximal segment of w_1 passing beneath proximal part of a_2 , see Text-fig. 33.
- Figure 3. GSC 26613, parallel forward, dorsal, west, x10; gill branches on left side, and first three on right side, inclined posteroventrally, remainder on right side inclined anteroventrally.



TEXT-FIGURE 33



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