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**DEPARTMENT OF ENERGY,
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BULLETIN 231

**YOHOIA WALCOTT AND
PLENOCARIS N. GEN., ARTHROPODS FROM THE BURGESS
SHALE, MIDDLE CAMBRIAN, BRITISH COLUMBIA**

H. B. Whittington

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ARTHROPODS FROM THE BURGESS SHALE,
MIDDLE CAMBRIAN, BRITISH COLUMBIA

Critical Readers
W. V. SLITER
C. J. HAVARD

Editor
DOROTHY J. WHYTE

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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 with the permission of the National and Historic Parks Branch, who have responsibility for the regulation of all activities related to the collection of natural history specimens in Canada's National Parks. 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 two more 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, February 26, 1973

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YOHIOIA WALCOTT AND PLENOCARIS N. GEN., ARTHROPODS FROM THE BURGESS SHALE, MIDDLE CAMBRIAN, BRITISH COLUMBIA

Abstract

Preparation and study of old and new collections, aided by photographs and camera lucida drawings, have revealed for the first time many morphological features of *Yohioia tenuis* and shown that the species *plena*, here made the type of the new genus *Plenocaris*, was a quite different phyllocarid-like animal. Specimens of either species are approximately 2 cm or less long, so that, despite the remarkable preservation, many features are either obscure or open to more than one interpretation.

The following reconstruction of *Yohioia tenuis* differs in many respects from that given by Simonetta (1970). The cephalic region included a frontal, median lobate area, immediately behind which was a pair of blunt, lobate areas; the nature of these areas is problematical. The rest of the cephalic region was covered by a semitubular cephalic shield, which was subrectangular in dorsal or lateral outline. The trunk consisted of fourteen somites, the first nine (or ten) with pleurae, the succeeding four (or three) cylindrical, the terminal telson being paddle-shaped. In the cephalic region, attached behind the lateral area, was a large anterior appendage of two segments, bearing four terminal spines. The cephalic region also bore three pairs of uniramous, presumably segmented appendages, possibly walking legs. The first trunk somite may have borne a biramous appendage consisting of a segmented walking leg with a lobate basal branch fringed with setae. The succeeding eight or nine somites bore only lobate appendages fringed with setae. The sagittal length ranged from 7 to 23 mm. There is no evidence that *Y. tenuis* was a developmental stage of a larger animal. It appears to have been benthonic in habitat, possibly swimming and feeding by metachronal movements of the setose, lobate appendages; the great anterior cephalic appendage may have aided in capturing food. The appendages are not trilobite-like, and resemblances to Anostraca or Malacostraca appear to be superficial.

The second species, placed in *Yohioia* by Walcott, is regarded as the type of a new genus, *Plenocaris plena*. It is phyllocarid-like, but the cephalic region bore only one pair of antennae; the trunk consisted of thirteen somites, the last being the telson, which bore a furca composed of two lobate rami. Appendages, apparently uniramous, were present only on somites 2 to 4 of the trunk. The carapace apparently included a rostral plate, and covered the cephalic region and the anterior part of the trunk. The sagittal length ranged from approximately 7 to 17 mm. *Plenocaris plena* is quite different from specimens of comparable size of *Waptia fieldensis* from the Burgess Shale; *Waptia fieldensis* had a similar carapace but had many more appendages on the trunk, including trilobite-like gill branches. The phyllocarid *Canadaspis perfecta* from the same shale is also different in that the trunk bore biramous appendages.

Résumé

La préparation et l'étude de collections anciennes et nouvelles, à l'aide de photographies et de dessins en chambre claire, ont révélé pour la première fois plusieurs caractéristiques morphologiques de *Yohoia tenuis* et ont montré que l'espèce *plena*, considérée ici comme le type du nouveau genre *Plenocaris*, est un animal très différent ressemblant aux phyllocarides. Les spécimens de l'une ou de l'autre espèce ont approximativement 2 cm ou moins de longueur de sorte qu'en dépit de leur préservation remarquable, plusieurs caractéristiques sont soit obscures, soit susceptibles de plus d'une interprétation.

La reconstitution de *Yohoia tenuis* qui suit diffère à bien des égards de celle de Simonetta (1970). La région céphalique comprend une zone frontale médiane lobée, immédiatement précédée de deux zones lobées, aplaties; la nature de ces zones est problématique. Le reste de la région céphalique est couverte d'une carapace céphalique semitubulaire, laquelle est subrectangulaire dans les parties dorsales ou latérales. Le tronc est constitué de quatorze somites; les neuf (ou dix) premiers sont accompagnés de plèvres, les quatre (ou trois) qui suivent sont cylindriques et le telson terminal est en forme de nageoire. Dans la région céphalique, fixé derrière la partie latérale, se trouve un grand appendice antérieur en deux segments, portant quatre épines terminales. La région céphalique est aussi porteuse de trois paires de ce qui est probablement des appendices segmentés uniramés, peut-être des membres locomoteurs. Le premier somite du tronc peut avoir porté un appendice biramé constitué de membres locomoteurs en segments avec une ramification basale lobée bordée de poils raides. Les huit ou neuf somites qui suivent n'ont que des appendices lobés bordés de poils raides. La longueur sagittale varie de 7 à 23 millimètres. Il n'existe pas de preuve que *Y. tenuis* soit le représentant d'une étape du développement d'un animal plus gros. Il semble avoir eu un habitat benthique, nageant et se nourrissant peut-être par des mouvements métachronaux de ses appendices poilus et lobés; le grand appendice céphalique antérieur peut avoir aidé à la capture de nourriture. Les appendices ne sont pas comme ceux des trilobites, et les ressemblances avec ceux de l'Anostraca ou de Malacostraca semblent être superficielles.

La deuxième espèce, placée dans celle de *Yohoia* par Walcott, est considérée comme le type d'un nouveau genre, *Plenocaris plena*. Elle ressemble aux phyllocarides, mais la région céphalique n'est munie que d'une paire d'antennes, le tronc est constitué de treize somites, dont le dernier, le telson, est porteur d'une fourche composée de deux rameaux lobés. Il n'y a d'appendices, apparemment uniramés, que sur les somites 2 à 4 du tronc. La carapace comprend apparemment un plateau rostral et couvre la région céphalique et la partie antérieure du tronc. La longueur sagittale varie d'environ 7 à 17 mm. *Plenocaris plena* est très différent des spécimens de taille comparable de *Waptia fieldensis* du schiste Burgess; le *Waptia fieldensis* possède une carapace semblable mais compte beaucoup plus d'appendices fixés au tronc, y compris des branchies comme celles des trilobites. Le phyllocaride *Canadaspis perfecta* du même schiste est aussi différent en ce que le tronc porte des appendices biramés.

INTRODUCTION

Two species of arthropods, *Yohoia tenuis* and *Y. plena*, were originally described briefly by Walcott (1912) from six and one specimens respectively, *Y. tenuis* being designated the type of his new genus *Yohoia*. No further information was available on either species until Simonetta (1970) described additional specimens of *Y. tenuis* from Walcott's collection and gave a new reconstruction. Simonetta made no mention of the second species. The new investigation of the Burgess Shale (Whittington, 1971a) has yielded 26 specimens of *Y. tenuis*, and some 400 more are in Walcott's collection. The species *plena* is much rarer, no specimens having been obtained in the new collections, but there are 47 in the Walcott collection. All this material has been studied, and a suite from each species prepared, photographed, drawn and measured to give the basis for new descriptions. An understanding of the mode of preservation (see paragraphs below) is essential to interpretation of the specimens. Individual specimens are orientated at various angles to the bedding planes, and are not in a single plane, but parts of the exoskeleton lie in different planes, or may lie across these planes. The different levels are revealed in the splitting of the rock and by subsequent preparation. At a change in level there is a minute scarp, which is shown in the photographs as a shadow or light band, depending on the direction of the radiation. In the camera lucida drawings, hachures are used to show the scarps, directed down-slope from a solid line which runs along the upper edge of the break in slope. Recognition of these changes in level in individual specimens indicates whether one is seeing the left or right side of the exoskeleton, the inner or outer surface, the left or right of a pair of appendages, etc. Making the camera lucida drawings (Textfigs. 9-30) is thus a critical part of the investigation, since each requires decisions on what features a particular specimen reveals. The plates and textfigures give the evidence from which the reconstructions (Textfigs. 2, 6) have been prepared. They show the features for which the evidence is considered adequate; uncertain characters are shown tentatively. These techniques are those used previously (Whittington, 1971b, p. 1, 2); some additional details are given in the explanation of the plates.

The results of this study are summarized in the abstract, and a general description and summary are given of *Yohoia tenuis*, preceding the longer, detailed description. This animal (Textfig. 2) resembles Snodgrass' (1956, Fig. 1c) hypothetical primitive arthropod in that the alimentary canal extended the length of the body but, in the exoskeleton and appendages, *Y. tenuis* is clearly specialized. There were no multijointed antennae, and evidence for eyes is equivocal. My reconstruction is very different from Simonetta's (1970, Pl. IX, figs. 1, 2a-d) because his includes features that I regard as resulting from misinterpretations of specimens or for which I find no evidence. For example, I do not consider that the original of Plate II, figures 1 to 3, shows a large, triangular labrum in front of the cephalic shield, in which jointed antennules are lodged, but rather the folded-back great appendage. Simonetta portrays the trunk appendage as a jointed limb, from the base of which arises a lobate branch fringed with setae, and distally a second, short branch. I doubt whether jointed limbs are present on the trunk at all, except perhaps on the first somite; the lobate appendage, fringed with setae, is preserved in several specimens (e.g., Pl. III, figs. 1-3), but I can find no evidence for a

second branch. Thus the support for the case sketched by Simonetta (1970, p. 44) for considering *Yohioia* to be a crustacean is slight, and I am doubtful whether *Yohioia* should be placed in Trilobitoidea.

The species *plena*, as Henriksen (1928) and Størmer (1944) recognized, is quite different, and the reconstruction (Textfig. 6) shows it to have been phyllocarid-like and to have possessed antennae. Walcott (1912, p. 182–189) described five new genera and many new species of phyllocarids, in one of which, *Canadaspis perfecta*, appendages are well preserved. None of this material has yet been studied in detail, but it seems unlikely that *plena* belongs in any of these species or genera, nor does it seem to be like the trilobitoid *Waptia*. It is, therefore, made the type of a new genus, placed with question in Phyllocarida, since the trunk, with its few anterior pairs of appendages, is unlike that of *Canadaspis* and younger members of the subclass.

The specimens of both the species are small, most being 1 to 2 cm long. Details are thus difficult to see, and only the most anterior (most heavily sclerotized?) appendages are well preserved, the rest appearing as ill-defined, carbonaceous areas. Hence the uncertainty as to the number, nature, and manner of attachment to the body of the appendages. To show particular details, the direction of radiation has been varied from photograph to photograph, which may mean that other features are obscured. In making a drawing, the specimen was studied in light directed at a variety of angles, so that certain features shown may be obscure in the photographs selected. Such difficulties are unavoidable, but it should be evident that whereas the exoskeleton is sharply outlined, appendages are not clearly bounded and structures such as joints and fringes of setae are rarely visible.

In the descriptions I have used such terms as carapace, cephalic shield, exoskeleton, joint, segment, somite, telson, trunk, as defined by Moore and McCormick (*in* Moore, 1969). Sagittal (sag.) refers to the median line, exsagittal (exs.) to a line parallel to the median, and transverse (tr.) to the direction at right angles. Symbols used in the textfigures are explained below. I am indebted to Drs. C. P. Hughes and W. D. I. Rolfe for discussion and help on many points, particularly to Dr. Hughes for devising Textfigures 3, 4, 7, and 8, and calculating statistics. Dr. Porter M. Kier of the U.S. National Museum (abbreviated USNM), gave every facility for studying the Walcott collection. Officers of the Geological Survey of Canada (GSC) kindly invited me to undertake this study, and I am grateful for the support of the Natural Environmental Research Council, London, Grant GR3/285. My photographs have been enlarged by Mr. David Bursill, and my pencil drawings redrawn by Mr. John Lewis.

Explanation of Symbols on Textfigures and Plates

- a = anus
 an = antenna
 al = alimentary canal, shown as stippled area with solid line boundary
 ap = appendage of trunk, when ill-defined shown as finely stippled area with or without solid line boundary
 cap = cephalic appendage following great appendage; in *Yohoia tenuis*, may be shown as stippled area, as ap.
 car = carapace
 cr = cephalic region
 cs = cephalic shield
 d = doublure of carapace
 ds = dark stain in surrounding rock
 f = furca of telson
 ga = great appendage of *Yohoia tenuis*
 l = lateral area of cephalon in *Yohoia tenuis*; also prefix indicating left side
 m = median frontal lobe, most anterior portion of cephalon in *Yohoia tenuis*
 pl = pleura
 r = prefix indicating right side
 ros = rostral plate
 t = telson
 te = tergite
 vm = ventral margin of exoskeleton
 wl4 ? = possible fourth walking leg in *Yohoia tenuis*
 1—n = number of trunk somite

Hachures show breaks in slope, the solid line at the upper edge of the break, the hachures directed down-slope from this line. Carbonaceous areas are shown in fine stipple, presence of pyrite (Textfig. 26) in short diagonal lines.

SYSTEMATIC DESCRIPTIONS

Class TRILOBITOIDEA Størmer, 1959?

Family YOHOIIDAE Henriksen, 1928

Genus *Yohoa* Walcott, 1912

Type species. *Yohoa tenuis* Walcott, 1912, by original designation.

Diagnosis. Body elongate, not trilobed; cephalic shield subrectangular in outline, extending over dorsal surface and including pleural regions; trunk of fourteen somites, subcircular in cross-section, first ten tergites with pleurae, next three somites with cylindrical exoskeleton, telson a flattened plate, lobate in outline. Cephalic region with median, and pair of short (exs.), lobate areas at anterior margin; mouth on ventral surface of median frontal lobe, nature of lateral lobate area uncertain. Anterior great appendage of two segments, and bearing four terminal spines; three additional appendages on cephalon, each ?uniramous, segmented. First trunk somite may have borne biramous appendage, consisting of segmented walking leg and lobate branch with fringe of setae from base; succeeding nine (or ten) somites with lobate appendage bearing fringe of setae only; posterior four (or three) somites lacked appendages.

Geological horizon. Middle Cambrian, Stephen Formation, Burgess Shale Member, *Bathyriscus-Elrathina* Zone, British Columbia.

Yohoa tenuis Walcott, 1912 Plates I–XI; Textfigures 1–5, 9–23

- 1912 Walcott, p. 172–173, Pl. 29, figs. 7–13.
- 1920 Raymond, p. 109–110.
- 1925 Fedotov, p. 385, 389.
- 1928 Henriksen, p. 9–10.
- 1930 Hutchinson, p. 2, 11, 13.
- 1932 Richter, p. 856.
- 1935 Raymond, p. 227.
- 1944 Størmer, p. 93–95, 135, Textfig. 18a, c, d (not Textfig. 18b).
- 1953 Dechaseaux, in Piveteau, p. 39, Fig. 13.
- 1958 Tiegs and Manton, p. 291, Fig. 14e (not upper left figure of this group).
- 1959 Størmer, in Moore, 1959, p. O35–O36, Fig. 24, 1–4.
- 1970 Simonetta, p. 42–43, 44, Pl. IX, figs. 1, 2a–d; Pl. X, figs. 5–19.

Lectotype (here designated). USNM 57699, Plate I, figures 3, 4, original of Walcott, 1912, Plate 29, figures 12, 13.

Other material. USNM 57694–8, originals of Walcott, 1912, Plate 29, figures 7–11, USNM 155601–622, studied by Simonetta, 1970. USNM 155609 is the counterpart of 57696. Some of these specimens were figured by Simonetta, but there are the following errors in the explanation of his Plate X: for N.4, read N.5, which is a figure of USNM 57694, not 57697; N.6 is a figure of USNM 57698, not 57697; for his second N.6, read N.7; N.9 is a figure of USNM 57697, not 155602; N.11 is a figure of USNM 155608, not 155602. USNM 179008 to 179128,

originals figured and measured herein; some 250 additional specimens in USNM. GSC 31131 to 31141, figured and measured herein, and 15 additional specimens in GSC collection (including one on GSC 26594 with *Marrella splendens*).

Locality, stratigraphical horizon, numbers of specimens. Middle Cambrian, Stephen Formation, Burgess Shale Member, *Pagetia bootes* faunule of *Bathyriscus-Elrathina* Zone, situated on ridge between Wapta Mountain and Mount Field, at an elevation of about 7,500 feet, 3 miles north of Field, southern British Columbia (see Fritz, 1971, for an account of the stratigraphy of the shale).

Yohioia tenuis has been found at two levels in the Phyllopod bed, 7 feet 7 inches thick, exposed in the Walcott quarry (Textfig. 1). The position of the quarry, and of levels at which GSC collections were made, have been explained previously (Whittington, 1971a, p. 1175-8, Figs. 1-3). *Marrella splendens* was found abundantly at the same two levels, far more specimens coming from the upper level at about 6 feet 11 inches to 7 feet 2 inches (Whittington, 1971a, Fig. 5). The exact levels in the Walcott quarry from which the approximately 400 specimens in the U.S. National Museum came is not known, but *M. splendens* is on the same slab as 13 of them. Single examples also occur of *Y. tenuis* with *Waptia fieldensis*, *Burgessia bella*, and with the worms *Wiwaxia corrugata* and *Canadia setigera*. One specimen in the Walcott collection is labelled 35k/10, and so presumably came from the Raymond quarry, 65 to 75 feet higher than the base of the Walcott quarry (Whittington, 1971a, p. 1172-3, Fig. 1).

General Description and Summary

Walcott (1912) gave a brief description and figured six specimens, preserved in different attitudes in the rock, which showed little of the appendages. The large number of specimens he subsequently collected had not been studied previous to Simonetta's work. Therefore, it is not surprising that, prior to 1970, little reference to *Yohioia* had been made, and that Størmer's (in Moore, 1959) summary expresses doubts both on the morphology and systematic position. I have examined Walcott's entire collection and the specimens obtained in 1966 and 1967 by the GSC party, and prepared more than 150 of them. This has enabled a new reconstruction to be made (Textfigs. 2A, 2B, 5), but the poor preservation of the appendages means that an unequivocal interpretation is impossible. My reconstruction differs in many respects from Simonetta's; these differences are summarized in this section and the evidence considered in the detailed description that follows.

A cephalic shield, sub-square in outline in dorsal or lateral aspect, curved over the dorsal side and was extended downward by the pleural region. This region of the shield bore three transverse ridges that merged into the lateral marginal ridge. At the anterior margin of the shield a median and a pair of lateral lobate areas are preserved. The median is presumably the most anterior part of the cephalon, and bore the mouth on the ventral side; no further details are shown. The lateral lobate area was interpreted by Walcott (1912) and Simonetta (1970) as a pedunculate eye, but again no detail is shown and it may be a short, blunt, anterior appendage. The best preserved and most conspicuous appendage is the great appendage, which consisted of two segments and bore four spines articulated at the tip; it was attached to the body beneath the cephalic shield immediately behind the lateral lobate area. Seemingly three pairs of poorly preserved but probably segmented appendages also projected from beneath the cephalic shield; they were attached successively behind the great appendage, and may have been walking legs. The large, triangular "labrum" shown by Simonetta (1970) as articulated at the median, anterior margin of the cephalic shield is based on a misinterpretation, and I have found no evidence of a pair of antennules composed of three segments. The trunk consisted of 14 somites, the tergite of the first short (sag.), the pleura short (tr.); it

was not observed by Walcott. The succeeding nine somites had the tergite continuous with a pleura which curved to a backwardly directed point; the pleura of the last of these somites (the tenth) reduced. The succeeding three somites appear to have been cylindrical. The 14th somite was a paddle-shaped plate, spinose distally, and is called the telson since the alimentary canal ended in the anterior part of this somite. Appendages of the trunk are preserved as carbonaceous films, the boundaries ill-defined in most specimens. On the anterior nine, and possibly the tenth, somites, a lobate appendage was present, fringed with setae which were progressively longer distally. A walking leg, similar to those of the cephalon, may have been present on the first trunk somite, so that this appendage was biramous. I have found no clear evidence that such walking legs were present on any succeeding segment, nor any suggesting that the lobate, fringed branches were present beneath the cephalic shield. I have observed no evidence for the rod-like branch ("exopodite") claimed to be present on the walking leg of the trunk by Simonetta (1970). The alimentary canal is preserved as a dark or reflective band, running from the median frontal lobe of the cephalon along the ventral side of the trunk to the telson. The band is widest in the cephalic shield, presumably indicating the size and position of the stomach. Diverticulae may have been present in the cephalic region, and in each succeeding somite. A dark stain may be visible in the rock adjacent to the ventral side of the posterior three or four somites. By analogy with *Marrella*, this stain may represent the squeezed-out contents of the body.

Most specimens are complete and preserved in a variety of orientations: parallel, oblique, or lateral to the bedding. The body may be extended almost straight, or flexed in an arc of up to 180 degrees, the telson above or below the rest of the body. The lobate, fringed appendages overlap one another slightly. Preservation appears to be like that described for *Marrella* (Whittington, 1971a, p. 1180-1196), though the known size range, from 6.8 to 23 mm, is unimodal in distribution (Textfig. 3).

Yohioia tenuis does not appear to have possessed long, multijointed antennae. The presumed walking legs of the cephalic region may have enabled *Y. tenuis* to stand on the sea bottom, movements of the lobate fringed appendages having enabled it to swim and also having created currents carrying food particles forward ventrally along the midline of the body to the mouth (Textfig. 5). These appendages also may have functioned as gills, the marginal setae forming valves during the metachronal movements. The great anterior appendage could be extended forward horizontally and, when retracted, the spinose tips could be brought adjacent to the mouth, beneath the median frontal lobe of the cephalon. It is tempting to assume that this appendage was used to gather food particles and bring them to the mouth. The mode of preservation inferred for *Marrella* seems to apply for *Yohioia*, suggesting that it lived near the sea bottom, swimming and gathering food particles, and resting or feeding on the bottom by stirring up mud and food particles. The evident flexibility of the body suggests that a downward and forward movement of the paddle-shaped telson could have enabled the animal to dart backward.

No evidence is adduced that *Y. tenuis* was the developmental stage of a larger animal. The body does not appear to have been trilobate in form; that is, there was no longitudinal groove or sharp change in slope between axis and pleurae. The cephalic region appears to include at least five somites. The appendages are not trilobite-like, that is they do not include a long, multijointed first antenna, and there appears to be no series of similar, biramous appendages. The presence of a compound eye is not conclusively demonstrated, and the great anterior appendage does not appear to be the male clasper, since it is present in the majority of specimens. Resemblances to Anostraca or Malacostraca appear to be superficial, and only when the Burgess Shale arthropods are better known will it be possible to re-assess the relationships of *Yohioia*.

Preservation

Individual specimens may be oriented *parallel* to the bedding planes, i.e., with the sagittal plane at right angles to those planes; or *lateral*, the sagittal plane parallel to the bedding planes; or *oblique*, the dorsoventral axis of the animal at an angle to the bedding plane. Oblique specimens approximate to the parallel or lateral position, and have not been observed approaching the vertical position, the position in which the anterior-posterior axis of the animal was at right angles to the bedding planes. The body may be extended in an approximately straight line, or flexed in a variety of ways: curved up to 180 degrees (Pl. XI, fig. 1), with the telson lying dorsal (Pl. IX, fig. 3) or ventral of the head; or the body may be flexed in a double curve (Pl. II, fig. 6). The exoskeleton is preserved as an exceedingly thin, dark, apparently carbonaceous film with which pyrite may be associated. The pyrite may be fine grained, or in scattered spherical bodies (Pl. X, figs. 1-4). The entire exoskeleton may be reflective (Pl. VII, fig. 3), or certain areas, which appear to be the sites of fluid-filled canals in the animal, are more intensely reflective (Pl. IV, fig. 1; Pl. IX, figs. 1, 2; Pl. XI, figs. 3, 6). When the rock was split to reveal the specimen, in certain cases the split appears to have followed the external or internal surface of the exoskeleton, in others to have passed between these surfaces. Thus, in the counterparts of Plate II, figures 1, 3, in the original of figure 1 the tergites are concave, the external ridges of the cephalic shield and pleurae appearing as grooves; this specimen is thus referred to as showing the inner surface of the exoskeleton. The counterpart (Pl. II, fig. 3) has the tergites preserved convexly, the external ridges of cephalic shield and pleurae preserved as ridges; this specimen is referred to as showing the outer surface of the exoskeleton. True inner and outer surfaces cannot be shown by counterparts, each of which shows the dark carbonaceous film. They are not external and internal moulds, but the split has passed through the exoskeleton. In lateral counterparts; for example, Plate IX, figures 4-6, the split has passed through one side of the exoskeleton, in this case the right side. In the original of Plate IX, figure 5, the inner surface of the right side of the exoskeleton is shown, the appendages lying above (inside); the counterpart (Pl. IX, fig. 6) appears to show the external surface of the right side, the appendages preserved below it. Textfigures and plate explanations give such details. In examples of oblique specimens (Pl. VI, figs. 1, 2; Pl. VII, fig. 5) the external surface of the exoskeleton, with ridges on cephalic shield and pleurae, is clearly revealed.

One hundred specimens of the measured sample (Textfig. 3) were examined, of which 98 appear to have been complete when buried, that is, they show the exoskeleton of the cephalic shield and succeeding somites, including the telson. Of these same 100 specimens, 89 show the median frontal lobe anterior to the cephalic shield, 76 the great anterior appendage, and 54 traces of additional appendages.

In orientation of the specimens and completeness, it is evident that *Y. tenuis* is preserved in a similar manner to *Marrella splendens* (Whittington, 1971a, b). A dark stain is also associated with *Y. tenuis* (Pl. IV, figs. 3, 4; Pl. VIII, fig. 5), but the size distribution (Textfig. 3) is not bimodal.

Detailed Description and Discussion

Cephalic Region

The cephalic shield (Pl. II, figs. 1-3; Pl. VII, figs. 3-5; Pl. VIII, figs. 2, 3) was of length (sag.) approximately equal to the height, subsquare in dorsal or lateral view, the anterolateral and posterolateral angles drawn out into oblique points, the former the most prominent. There appears to have been a median part of semitubular shape, the lateral, pleural part sloping steeply downward and outward. This pleural part bore three outwardly and slightly forwardly directed ridges, which merged distally with the lateral marginal ridge. The anterior

ridge ran along the anterior margin distally, proximally running a short distance in from the margin before dying out. The three ridges divided the pleural region into three approximately equal areas, but the posterior margin does not appear to have borne a ridge. The pleural parts of the cephalic shield, separated by matrix, are shown in the original of Plate VIII, figure 1, the ridges present on the outer surface of the left pleural region, the inner surface of the right pleural region showing grooves. Other oblique specimens (Pl. II, fig. 5; Pl. VII, fig. 5) also show the ridges on the external surface. These oblique as well as certain parallel specimens (Pl. II, figs. 1-3) may show a "trilobation" of the cephalic shield, a ridge or flexure running longitudinally at the inner margin of the pleural region. I regard this ridge or flexure as not original, but probably a postburial feature resulting from differential compaction between the thin pleural region and the median cephalic region with its soft parts, including the possibly sediment-filled stomach.

Walcott (1912, p. 172) made contradictory statements as to whether there was or was not a "carapace," but the cephalic shield is clearly visible in lateral view in certain of his originals (Pl. I, figs. 1, 3, 4). In each example the inner surface of the pleural region shows grooves. In another of his originals (Pl. II, figs. 1-3) the shield is preserved in dorsal aspect, the pleural ridges preserved. Størmer (1944, p. 93) accepted the presence of a cephalic shield, but Henriksen (1928, p. 9-10) regarded a "carapace" as being absent, and seems to have interpreted the marginal ridge of the cephalic shield as a "spine-like projection from the head." Simonetta (1970, p. 42) writes of a "head tergum" and refers to the "pleural lobes of the cephalic somites" but was uncertain as to whether or not they were fused to each other. I consider that the modes of preservation of the specimens, particularly the original of Plate VIII, figure 1, afford clear evidence of a cephalic shield as described above. Simonetta gave no evidence for his statement that the first pleural lobe "is bent sharply inwards [and] appears to be free and movable," and I find none.

In parallel or slightly oblique specimens (Pl. II, figs. 1-3; Pl. VII, figs. 1, 2; Pl. X, figs. 4, 5; Pl. XI, figs. 5, 6) there is a sub-semicircular median area, and a lateral ovate or subcircular area preserved in front of the anterior, median margin of the cephalic shield. In lateral specimens the median area appears as a pendant, lobate shape, and the lateral area, at its base and adjacent to the margin of the shield, as an elongate, oval area (Pl. I, fig. 1; Pl. VIII, figs. 2, 3; Pl. X, figs. 1-3). As the photographs show, these areas are poorly defined and show no structures; in reflected radiation all three may appear equally reflective (Pl. VII, fig. 2). The median area is here referred to as the median frontal lobe, but nothing can be said about its nature or structure, merely that it is the most anterior part of the cephalon, projecting forward from beneath the dorsal margin of the cephalic shield. It is this structure, seen in lateral aspect (Pl. I, figs. 3, 4), that Walcott (1912, p. 172) interpreted as the antennule. Exactly which structure, seen in dorsal aspect (Pl. II, figs. 1-3), he considered to be the antennule is uncertain; he was presumably referring to the structures here regarded as the great appendages. Størmer (1944, p. 93-94; 1959, p. O36) did not accept the supposed antennule, but seemed to regard the median area as possibly a rostrum. Walcott (1912, p. 172) regarded the lateral area as representing the pedunculate eye, referring to the reflectivity of the area in the original of Plate II, figures 1 to 3. In this specimen, as in others (Pl. VII, figs. 1, 2; Pl. IX, figs. 1, 2; Pl. XI, figs. 5, 6), the lateral area is no more intensely reflective than the median frontal lobe or the alimentary canal, and does not show any distinctive features in either low angle or reflected radiation. The position and shape suggest that it may have been a pedunculate eye, but alternatively it may have been a short, blunt anterior appendage. Because of this uncertainty I have not shown it as an eye in the reconstruction (Textfigs. 2, 5). Simonetta (1970, p. 42, Pl. IX, figs. 1, 2c, 2d) not only shows a large pedunculate eye in his reconstruction, but also a "triangular labrum (or epistomium) . . . whose grooved surface lodges the antennules."

He considered the labrum to be extended forward horizontally or directed vertically. The basis for this view is his illustration (1970, Pl. X, fig. 18) of the original of Plate II, figures 1 to 3, Textfigure 11. I consider that this specimen shows the strongly flexed pair of great appendages, extending forward in front of the cephalic shield, and it is these that Simonetta has interpreted as a single plate, his presumed labrum. I find no sign of antennules, "composed of three articles" (i.e., segments), in this or any other specimen. Thus my reconstruction of the cephalic region (Textfigs. 2, 5) is different from Simonetta's in showing no antennule or compound eye. Whether or not the median frontal area should be termed a rostrum is debatable, and the nature of the lateral area uncertain.

Trunk

This region is composed of 14 somites, the tergites of the anterior 10 somites semitubular in cross-section, laterally extended as pleurae. First tergite (Pl. II, figs. 1-3; Pl. IV, figs. 3, 4; Pl. VI, figs. 1, 2; Pl. X, figs. 1-3) of width (tr.) twice length (sag.), length increases in successive segments, so the tenth tergite has length approximately equal to width. The pleurae are blunt, that of the first somite short (tr.), those of somites 2 to 9 successively longer and extended posteriorly as a short, blunt spine. Pleura of tenth somite (Pl. 11, fig. 4; Pl. VII, fig. 5; Pl. X, fig. 5) shorter (tr.) but extended backward by a spine; pleurae of somites 2 to 9 with narrow median ridge which curves out into the tip of the spine. The pleurae were presumably flat, and directed steeply outward and downward. In parallel specimens (Pl. X, figs. 4, 5) they are spread out on each side of the body. Crushing of the most proximal part (Pl. II, figs. 1-3) gave a superficial appearance of trilobation. In oblique specimens (Pl. II, fig. 5; Pl. VIII, fig. 4), the pleurae on one side were buried approximately parallel to the bedding and so the shape is well preserved. The pleurae on the other side are folded under the tergites, and some traces of them may be impressed through the tergites in compaction. Lateral specimens also show the form of the pleurae of one side (Pl. VII, fig. 6), and their shape and the spaces between them allow a degree of flexibility to this part of the body. In parallel (Pl. X, figs. 4, 5), oblique (Pl. I, fig. 2; Pl. VII, fig. 5) or lateral (Pl. I, figs. 3, 4) specimens, somites 11 to 13 of the trunk appear subrectangular in outline, somites 11 and 12 of similar length to each other and preceding somites, length (sag.) of somite 13 greater. It appears that the exoskeleton of these somites was tubular in form.

The telson is lobate in outline in parallel specimens (Pl. X, fig. 4), the straight sides diverging backward to the maximum width at the rounded tip. The posterior margin bore short spines, two pairs being longer than the intervening two pairs (Pl. VIII, fig. 4). In lateral and oblique specimens (Pl. I, figs. 2-4; Pl. VII, fig. 5; Pl. XI, fig. 1) a narrow band, diminishing in width posteriorly, runs along the straight lateral margin to die out at the rounded tip. Relative to the broad, median flattened portion of the telson, each band is flexed at a slight angle, one in the opposite sense to the other. In occasional specimens (Pl. I, fig. 1; Pl. V, fig. 5; Pl. VII, fig. 1), the lateral bands may lie approximately in the bedding planes, the main body crushed transversely so that it is relatively narrow (tr.) and lying at a steep angle to the bedding planes. In one example (Pl. VI, fig. 5), the telson is flexed steeply posteroventrally relative to the rest of the body, which is oriented approximately parallel. The telson is thus shortened (sag.) and lying at a steep angle across the bedding planes. The surface of the median region is flat, the lateral bands parallel to it. In the light of these observations, I regard the telson as having had narrow, flat, lateral bands in which the dorsal and ventral exoskeletal layers were closely approximated, whereas the median region was probably gently convex on each surface. At the anterior end, the cross-section must have changed in a short distance from subcircular (to fit into the exoskeleton of the 13th postcephalic segment)

to gently biconvex with flat extremities. It will be observed that in lateral specimens the telson may be preserved uncrushed and lobate in outline (Pl. I, figs. 3, 4), or crushed to appear as a narrow band (Pl. V, fig. 5); neither specimen has the body disrupted. I conclude, therefore, that some rotation along the longitudinal axis was possible between somites 10 and 14, i.e. that the paddle-shaped telson could be rotated. It is assumed in the restorations (Textfigs. 2, 5) that the "normal" position of the telson was with the paddle-like blade horizontal.

Each tergite, and the telson, was extended forward by a short (sag. and exs.) articulating flange, which passed beneath the doublure of the preceding tergite, or of the cephalic shield. Compaction of these exoskeletal layers gives a thickened edge, which may appear as a posterior marginal ridge or groove on the median part of the cephalic shield and on each tergite (Pl. I, figs. 1, 3, 4; Pl. II, fig. 4; Pl. VII, fig. 5). Parallel and oblique specimens (Pl. I, fig. 2; Pl. X, figs. 4, 5; Pl. XI, fig. 1) show how the tergites fitted into one another. There may have been a narrow ridge along the margins of the pleurae. However, the appearance that such ridges are present (Pl. I, fig. 3; Pl. VI, figs. 1, 2; Pl. VIII, fig. 1) may result from the compaction of the dorsal exoskeleton against a narrow, sclerotized doublure. My reconstruction of the exoskeleton of the trunk (Textfigs. 2A, 2B) thus differs from that of Simonetta (1970, Pl. IX, figs. 1, 2a) in certain details. In particular, the pleura of the first somite is short (thus allowing considerable flexibility between cephalic shield and trunk), succeeding pleurae have a distal median ridge, and the telson does not have a median rib. One specimen (Pl. II, fig. 5) shows an approximately sagittal groove, which I regard as resulting from compaction, since in other specimens the median region appears flat (Pl. II, figs. 4, 6).

Appendages

As discussed above, I find no evidence for the pair of antennules, composed of three segments, shown in Simonetta's restoration (1970, Pl. IX, figs. 1, 2c, 2d). The great anterior appendage is commonly preserved, presumably because it was relatively heavily sclerotized. Other appendages were presumably much less sclerotized, so that although traces are frequently preserved, their exact nature is not clearly revealed by any specimen. It has been suggested above that the pair of subcircular or elongate areas in front of the anterior margin of the cephalic shield may represent an anterior pair of appendages, or possibly a pair of pedunculate eyes.

The base of the great anterior appendage was attached beneath the anterior part of the cephalic shield, close to the midline (Pl. V, fig. 2; Pl. VI, figs. 1, 2; Pl. VIII, fig. 1), and there was an "elbow" joint at about the midlength, and a distal joint at the base of the four terminal, movable spines. The appendage is preserved in an extended, or a partly or strongly flexed position. In the latter (Pl. I, figs. 3, 4), the tips of the spines are close to the median frontal cephalic lobe. In a parallel specimen (Pl. II, figs. 1-3), the great appendage is folded back at the "elbow" joint; in others (Pl. VI, fig. 5; Pl. IX, fig. 3), and in an oblique specimen (Pl. VII, fig. 5), it is extended. It was this great appendage folded back that Walcott (1912, p. 172, Pl. 29, fig. 9) incorrectly interpreted as the first pair of appendages (terming them "antennules"), and the counterpart of the parallel specimen has been interpreted by Simonetta (1970) as showing the "labrum" and "antennules." The terminal spines may be preserved in a separated (Pl. VII, fig. 5) or closed (Pl. V, fig. 2) position, and are thus considered to have been movable. The exoskeleton is poorly preserved in many specimens, or may show wrinkles (Pl. VI, fig. 2; Pl. VIII, fig. 1), so that further details of joints are not revealed; even the position of the "elbow" joint is rarely preserved. Walcott (1912, p. 172) considered that three joints were visible beyond the "head," and that there were three terminal spines. Simonetta (1970, p. 42, Pl. IX, fig. 1) introduced several features for which I can find no evidence. He

considered that the joint beyond the elbow bore tiny spines on its anterior face, and that there were three distal joints, the proximal two each bearing two large spines, the terminal joint a single large spine, for a total of five. I find no specimen showing more than four large spines (Pl. V, fig. 2; Pl. VI, fig. 2; Pl. IX, figs. 4-6); these spines appear to have a common base, and I have so restored them (Textfigs. 2, 5).

Other cephalic appendages are rarely preserved. Walcott considered that three succeeding appendages, "small jointed legs hanging below the head" (1912, p. 172), were shown by the original of Plate I, figures 3, 4. There appear to be three, preserved as vaguely defined carbonaceous areas in rock layers lying partly on the inner surface of the right pleural region of the cephalic shield. Other specimens (Pl. I, fig. 1; Pl. IV, figs. 3-5; Pl. VI, figs. 1, 2; Pl. VIII, fig. 4; Pl. IX, figs. 4-6) show traces of three appendages in the same position, and they are most clearly preserved in the original of Plate VII, figures 3, 4. The appearance that there are more than three (Pl. IX, figs. 5, 6; Pl. X, figs. 2, 3) may be because both left and right of a pair are visible. In all, the preservation is poor, but each appendage appears broadest proximally, tapering, projecting well below the shield. Joints are obscurely preserved, so that the number and relative length of segments is uncertain, and the distal part of the appendage is not shown. The restoration of these appendages (Textfig. 2) summarizes what little is known, and suggests three pairs of walking (?) legs beneath the cephalic shield. The presence of a fourth, similar pair of appendages, attached presumably to the first postcephalic somite, is suggested by one specimen (Pl. I, figs. 3, 4), and the distal part apparently preserved in another (Pl. VII, figs. 3, 4). The presence of this fourth pair of walking legs is not shown by other specimens, so that they are shown tentatively in the restoration (Textfig. 2). No specimen, except the original of Plate I, figures 3, 4, suggests that such appendages were present on succeeding somites; even in this particular example there are merely vaguely defined carbonaceous bands extending below these segments, without clear margins or suggestions of joints. Walking legs are thus not shown in the restoration beyond the first postcephalic somite.

In many oblique and lateral specimens (Pl. I, fig. 1; Pl. IV, figs. 3, 4; Pl. V, figs. 1, 2; Pl. VI, figs. 3, 4; Pl. X, figs. 1-3), a carbonaceous film is present over an area extending from below the posterior part of the cephalic shield to the ninth or tenth trunk somite, the area being largest beneath somites 1 to 6 or 7. Fine-grained pyrite may be associated with this film, and its position in the rock shows that it is the remains of structures emerging from beneath the exoskeleton. Few specimens show much detail in this area, though many reveal that the film is not a continuous sheet but composed of a series of overlapping elongate-oval plates, one pair per somite. In rare specimens (Pl. III, figs. 1-3; Pl. VI, figs. 1, 2; Pl. VII, figs. 3, 4), the distal part of these plate-like appendages is preserved, and shows a median lobe with a fringe of setae that are short laterally and longer in the distal portion. No further detail is preserved. The most anterior of this type of appendage appears immediately below the first trunk somite; no such traces are clearly preserved beneath the cephalic shield. In most specimens, the last (and shortest) appears to be below the ninth trunk somite, though some suggest that it is below the tenth somite (Pl. I, figs. 3, 4; Pl. X, figs. 1-3). The restoration embodies this uncertainty.

If there was a walking leg on the first trunk somite, then the first lobate appendage branched from it near the base, on the outer side. This implies a biramous appendage on this somite, and one might assume that the appendages were biramous beneath the cephalic shield and on trunk somites 2 to 9 or 10, as did Simonetta (1970, p. 42-43, Pl. IX, fig. 1). However, I do not consider that the specimens afford adequate grounds for such an assumption. Where the walking legs are best preserved (Pl. VII, figs. 3, 4), there is no sign of such legs behind the first trunk somite, nor is there in the originals of Plate I, figure 1 and Plate VI, figures 1, 2. In a specimen (Pl. III, figs. 1-3) in which the lobate appendages of the anterior

part of the trunk, principally the right side, but possibly also the left side, are preserved, segmented walking legs do not appear to be present. Such legs are poorly preserved only beneath the cephalic shield. The original of Plate I, figures 3, 4, is equivocal; the dark carbonaceous strips, vaguely outlined, beneath somites 2 to 8 of the trunk are probably traces of the lobate appendages. Preservation of the appendages is by so thin a layer that preparation is difficult. I have not found it possible, for example, to remove one of the lobate areas in search of a possible walking leg beneath. Specimens broken at a variety of levels, however, do not reveal such legs. Simonetta (1970, p. 43) claimed that the originals of Plate IV, figures 1 to 4, and Plate V, figures 3 and 4, showed clearly a "rod-like exopodite" that branched "off the first visible joint of the leg." He showed (1970, Pl. IX, fig. 1) such an "exopodite" as possibly present on the posterior appendage of the cephalic region, and as present on all trunk appendages. The specimens he refers to are not the best preserved, and study of better preserved examples (particularly the original of Pl. VII, figs. 3, 4) does not reveal any clear evidence of such an "exopodite." The nature of the preservation of the appendages, as described above, militates against the possibility of such evidence being available. I have not found preserved in any specimen the distal segment of the walking leg (the "tiny pretarsus" of Simonetta, 1970, p. 43, Pl. IX, figs. 1, 2b), nor have I been able to discern fringes of setae on the posterior edges of the proximal segments.

Nothing is revealed of the most proximal parts of appendages, for they cannot be followed beneath the exoskeleton. Restoration (Textfigs. 2, 5) of the size and positions of appendages beyond the exoskeleton is based on lateral and oblique specimens. In parallel specimens, only the median frontal lobe and lateral areas and great appendage, in front of the cephalic shield, are preserved—no trace of other cephalic appendages, or the lobate appendages, has been observed outside the pleural regions, presumably because they were concealed beneath the exoskeleton. It may be, because of compaction, that the lobate appendages appear to extend farther ventral to the exoskeleton than they did in life, and have been restored in lateral view as hanging too far below the body. If they did extend as far ventrally as restored, one might expect to see some trace of them in parallel or near parallel specimens.

Internal Features

The alimentary canal may be outlined as a band that appears relatively dark in low-angle radiation (Pl. I, figs. 1, 2) or as a band that reflects strongly in high-angle radiation (Pl. IX, figs. 1, 2; Pl. XI, figs. 3, 6). The band may be slightly raised or depressed relative to adjacent parts of the exoskeleton, and the margin marked by a groove, ridge, or slight change in slope. In one example (Pl. VII, fig. 6), the anterior portion, the stomodaeum, is relatively raised and fine-grained pyrite is associated with it. The band starts at the anterior margin of the cephalic shield and, if reflective, may be continuous with the reflective areas of the median frontal lobe and lateral areas anterior to the shield (Pl. IX, fig. 2; Pl. XI, figs. 3, 6). In the trunk, the band is about one-quarter the width of the tergite, runs medially back to terminate in the anterior part of the telson, indicating the position of the anus (Pl. VI, fig. 1; Pl. IX, fig. 1). In lateral specimens (Pl. I, fig. 1; Pl. VII, fig. 6; Pl. IX, figs. 4–6) the band runs from the upper, anterior part of the shield downwards and backwards to the mid-part of the posterior region. It appears to extend into the lobate area of the median head region and suggests that the mouth is probably situated on the underside of this median head region. The band continues along the trunk in the region where tergite and pleura join, along the ventral side of somites 11 to 13, and to the most anterior, ventral part of the telson. Certain parallel specimens (Pl. IX, figs. 1, 2; Pl. XI, figs. 3, 6) contain features that suggest branches from the alimentary canal, two or three in the posterior area of the cephalic shield and one near the posterior

margin of each trunk somite. These branches are shown indistinctly only by specimens viewed in reflected radiation.

The Dark Stain

An irregular dark-stained area of rock, adjacent to the posterior part of the exoskeleton, is visible in 8 of the samples of 100 measured specimens mentioned above in the section on preservation. The area is small, rarely conspicuous, and occurs adjacent to somites 11 to 13 and the telson (Pl. IV, figs. 3–4; Pl. V, fig. 2; Pl. VIII, fig. 5). In one specimen in which the telson is flexed sharply up over the body (Pl. IX, fig. 3), the stain extends straight back behind the flexure. A larger, more conspicuous stain associated with *Marrella* (Whittington, 1971b, p. 16) is regarded as having been made by organic matter squeezed out of the body after burial. The stain associated with *Y. tenuis* appears to be of the same type.

Size Range

The range in total length of known specimens is summarized in Textfigure 3. Specimens less than 10.0 mm long are rare, and there appears to be no significance in the absence of individuals of 8 to 10 mm long. In contrast to the results obtained from measurements of *Marrella* (Whittington, 1971a, p. 1191–1196, Textfig. 23), no bimodal size distribution is evident. The smallest specimens (Pl. XI, fig. 2, length 7.6 mm; Pl. XI, fig. 7, length 10.8 mm; Pl. XI, fig. 4, length 10.7 mm) do not appear to differ from larger specimens (Pl. I, figs. 3, 4, length 20.3 mm; Pl. IV, figs. 3, 4, length 20.9 mm; Pl. VIII, fig. 4, length 21.1 mm; Pl. VIII, fig. 5, length 20.5 mm) in relative size (Textfig. 4) and shape of parts of the exoskeleton, number of trunk somites, or nature of the great anterior and other appendages (insofar as appendages are shown by the small specimens). The measurements (Textfigs. 3, 4) support the view that a single species, *Y. tenuis*, is represented by the collections, and there is no evidence of sexual dimorphism; early developmental stages are not present.

Habitat, Mode of Life, Function of Appendages

Most specimens of *Y. tenuis* were complete when buried, and are oriented in various directions in the rock, not on one bedding plane. The associated dark stain may result from squeezing out of the body contents. As in the case of *Marrella splendens* (Whittington, 1971b, p. 19–20), it may be argued that the habitat of *Y. tenuis* was benthonic after the animal had attained an exoskeletal length of 6.0 mm, and that part of a living population was catastrophically overwhelmed by suspended sediment and buried as the sediment settled. The animal (Textfigs. 2, 5) is thus thought to have swum or drifted near the sea bottom. Beneath the cephalic shield were three pairs of apparently uniramous jointed appendages, the nature of the distal segments being unknown. These, together with the possible similar branch of the appendage of the first trunk somite, may have functioned as walking legs, enabling the animal to poise with the body extended above the water–sediment interface. The pair of great anterior appendages, with their four distal spines, are preserved extended or flexed, always projecting straight in front of the cephalic region, approximately parallel to each other. At maximum retraction, the tips of the spines could be brought close to the mouth, which was situated beneath the median frontal cephalic lobe. This pair of appendages could have been used to capture and carry food particles to the mouth, and may also have had a sensory function. The distal spines could have served to entangle food particles for, since they all appear to have been movable, they did not constitute a cutting or crushing device. The function of the short, lobate pair of appendages situated beside the median

frontal lobe is uncertain. It is doubtful whether they were pedunculate eyes; they may have assisted in transferring food from the tips of the great appendage to the mouth. Lobate appendages, fringed with setae which were longest distally, were borne by the first nine or ten somites of the trunk. If a walking leg was present on the first of these somites, then the lobate appendage branched from it; walking legs have not been observed on succeeding somites. To and fro movements of the lobate appendages, combined with some rotation, would have enabled the animal to swim. Possibly these appendages, the exoskeleton of which appears to have been thin, also functioned as gills. Because there were pleurae to act as lateral valves, and perhaps the distal setae also acted to form valves, metachronal movements of these appendages (Textfig. 5) may have served to draw in water laterally on the forestroke and expel it on the backstroke, as described for *Hutchinsoniella* (Sanders, 1963, p. 10, Fig. 8). Such activity would have propelled the animal forward, and may have created a current along the midventral line to the mouth, thus aiding in feeding.

Yohioia tenuis is thus considered to have swum near the sea bottom and to have fed on particulate debris, conveyed to the mouth in part by the pair of great anterior appendages, and in part by currents of water along the midline of the body. Metachronal movements of the lobate appendages created these currents and also enabled the animal to swim forward. Possibly the lobate appendages also functioned as gills. Flexure of the body to give a rapid downward and forward flip of the telson may have enabled the animal to dart backward. The flexibility of the posterior part of the body and its ability to rotate suggest that the paddle-like telson was also used in steering when swimming forward. Walcott (1912, p. 172) considered the anterior appendage to be the male clasper, but this does not seem a probable interpretation of an appendage present in most specimens. Walcott's statement (1912, p. 172) that there was a short, blunt antennule, and Simonetta's claim (1970, p. 42, Pl. IX, figs. 1, 2c, 2d) that the antennule was slim and three-jointed are, as explained in the description, based on misinterpretations. *Yohioia tenuis* apparently lacked a long, multijointed sensory appendage of the type seen in many, but not all, Burgess Shale arthropods.

Discussion

The view that there are five somites in the cephalon (Walcott, 1912, p. 172), or "four posterior segments" (Henriksen, 1928, p. 9), appears to have been based on Walcott's Plate 29, figures 12, 13. The original of these figures (Pl. I, figs. 3, 4) and many other specimens show the three transverse ridges on the lateral part of the cephalic shield, the first at the anterior margin. The part of the shield posterior to the third ridge is relatively longer (exs.) than the parts between the three ridges. The description by Henriksen (1928, p. 9) of a "triangular, spine-like elongation" extending downward from the anterior and posterior ends of the head appears to have been based on a misinterpretation of Walcott's (1912) Plate 29, figure 13. This figure was taken in reflected light, and may have been retouched; Henriksen is referring to apparently darker areas at the anterior and posterior edges of the pleural region of the shield. As the present illustrations show, these areas are not separate from the rest of the cephalic shield. If the small, lobate area in front of the cephalic shield is an appendage rather than a pedunculate eye, then there are five pairs of appendages in the cephalic region, so that the cephalon includes at least this number of somites, but is not necessarily "composed of five somites" (Simonetta, 1970, p. 42) only.

The trunk consisted of 13, not 12 (Walcott, 1912; Størmer *in* Moore, 1959), somites and the telson. The first of these somites bore a short (sag. and exs.) tergite with narrow (tr.) pleura. It was first recognized by Simonetta (1970, p. 42, Pl. IX, figs. 1, 2c, 2d), but incorrectly described by him as similar in dimensions and form to those of succeeding somites. The

exoskeleton of somites 11 to 13 appears to be cylindrical, without pleurae, while that of the tenth somite may bear a short (tr.) pleura which is drawn out into a posterior spine. This tenth somite may or may not bear a pair of lobate appendages. Because of this and other uncertainties, I do not use the terms "thorax" and "abdomen," as they are applied to Crustacea, to denote subdivisions of the body. I term the 14th trunk somite the telson, because the anus appears to have been situated in it. The telson was a paddle-shaped plate; Walcott (1912) apparently interpreted the marginal bands of this plate as a pair of "caudal rami."

The body of *Y. tenuis* was presumably subcircular in cross-section, the pleurae directed downward and outward, probably steeply (Pl. V, fig. 2). In lateral or slightly oblique specimens (Pl. I, figs. 3, 4; Pl. VII, fig. 6; Pl. VIII, figs. 1-3), there is no evidence of a longitudinal groove or other clear division between tergite and pleura. Because of compaction, parallel specimens (Pl. II, figs. 1-3; Pl. IX, fig. 3; Pl. XI, fig. 4) may show an apparent trilobation in the body; the part of the pleura adjacent to the tergite is crushed vertically, the distal part spread out horizontally. I therefore do not accept that the body was "distinctly trilobate" (Størmer, 1944, p. 93), a description that Størmer (*in* Moore, 1959, p. O35) later abandoned.

The appendages of *Y. tenuis* are not trilobite-like, in that there is no long, multisegmented antennule followed by a series of similar biramous appendages; only the appendage of the first trunk somite is doubtfully biramous. The lobate appendages of the trunk apparently do not bear marginal flattened filaments, but rather fine setae, and the form of the appendage proximally is unknown. Only in the most general way may the distal portion be compared to the distal segment of the trilobite gill branch (Størmer, 1939, Fig. 27). The lobate appendage with its fringe of setae is not like the gill branch of *Marrella* (Whittington, 1971b) or the "abdominal limb" of *Waptia* (Walcott, 1931), each of which has a multijointed, tapering shaft bearing fine filaments.

Størmer (*in* Moore, 1959, p. O36) considered that *Y. tenuis* "may represent a larval stage of *Opabinia* or a related form." The largest known specimens of *Y. tenuis* are considerably smaller than any known of *Opabinia*, and the morphology of the latter does not encourage the notion that *Yohoia* is a developmental stage of it. It does not seem likely that *Y. tenuis* is a larval stage of any other species from the Burgess Shale.

Affinities

Earlier authors (Fedotov, 1925, p. 385, 389; Raymond, 1920, p. 109-110; Henriksen, 1928, p. 9-10) agreed with Walcott (1912) in placing the genus in the Order Anostraca of the Branchiopoda. Henriksen considered that the presence of pleurae justified the erection of a separate family, which Hutchinson (1930, p. 13) placed in his Suborder Palaeanostraca of the Anostraca. Raymond (1935, p. 227) placed *Yohoia* in his Order Pseudanostraca, which he considered ancestral to Anostraca. Størmer's work (1944; *in* Moore, 1959) has led him to erect a separate class, Trilobitoidea, for the Burgess Shale and other arthropods; he is uncertain of the position of the Yohoiidae in this class. Simonetta (1970, p. 44) considered this animal to have been similar to a typical crustacean and remarked on its "caridoid aspect." He believed that antennules were present, that the appendages were similar on cephalon and trunk and that they bore two outer branches, the lobe-shaped "epipodite" and a "rod-like exopodite" (1970, p. 43). The evidences for such an interpretation are questioned here and, using the definition in Moore (1969, p. R93) of "caridoid facies," it is doubtful whether *Yohoia* exhibits any of the characters defining this facies. The "caridoid aspect" is superficial, and the relationships of *Yohoia* remain to be clarified.

Class MALACOSTRACA Latreille, 1806?
Subclass PHYLLOCARIDA Packard, 1879?
Order and Family uncertain
Genus *Plenocaris* n. gen.

Type species. *Yohioa plena* Walcott, 1912

Diagnosis. Elongate body subdivided into cephalic region and trunk, latter composed of 13 somites, the last being the telson, with which was articulated a furca composed of two lobate rami; cephalic region bearing pair of uniramous antennae, other features unknown; apparently somites 2 to 4 of trunk each with one pair of uniramous, elongate appendages; somites 5 to 12 lacking appendages. Carapace-like structure loosely covering dorsally and laterally cephalic region and anterior part of trunk; a spiniform rostral plate apparently present.

Geological horizon. Middle Cambrian, Stephen Formation, Burgess Shale Member, *Bathyriscus-Elrathina* Zone, British Columbia.

Plenocaris plena (Walcott, 1912)
Plates XII-XVI, Plate XVII, figures 1, 2; Plate XVIII, figures 2-4, 6; Textfigures 6-8, 24-30

1912	Walcott, p. 173, Pl. 29, fig. 14.
1928	Henriksen, p. 10.
1944	Størmer, p. 93, Fig. 18b.
1958	Tiegs and Manton, upper left figure only of group in Fig. 14e.
1959	Størmer, in Moore, 1959, p. O36.

Holotype. USNM 57700, Plate XII, figure 1, original of Walcott, 1912, Plate 29, figure 14.

Other material. USNM 182530 to 182557, 28 specimens, Walcott collection, figured or measured herein, seven with counterparts. In addition the collection includes nine poorly preserved specimens (USNM 182558 to 182566), considered below under Preservation, and nine fragments.

Locality and stratigraphical horizon. Middle Cambrian, Stephen Formation, Burgess Shale Member, *Pagetia bootes* faunule of *Bathyriscus-Elrathina* Zone, situated on ridge between Wapta Mountain and Mount Field, at an elevation of about 7,500 feet, 3 miles north of Field, southern British Columbia (see Fritz, 1971, for an account of the stratigraphy of the shale).

The present material presumably includes the "better specimens" mentioned by Walcott, and an additional fragment labelled 35k/10 (i.e., from the Raymond quarry) is indeterminate. No specimens were collected by the GSC party, not even any which, in outline or size, might be considered to be the isolated carapace. The USNM specimens are on small pieces of shale, one of which contains, in addition, one valve of an inarticulate brachiopod, another a fragment of the alga *Morania*. These occurrences afford no clue to the level or levels in the Phyllopod bed at which *P. plena* may occur.

Preservation

The carapace is preserved in 28 of the 38 selected specimens; considerably displaced in eight (e.g., Pls. XIII, XIV), approximately in place in the others (Pl. XV, figs. 3, 6; Pl. XVIII, figs. 3, 4, 6). The outline of the carapace may be sub-oval (Pl. XVIII, figs. 3, 4, 6) or subtriangular (Pl. XV, fig. 3); in these latter, and when irregular (Pl. XV, fig. 5; Pl. XVI, fig. 5), showing obvious signs of crushing. Particularly judging by the original of Plate XIV, where the two free edges are partially visible, the sub-oval outline is the lateral aspect of the carapace. In such specimens (Pl. XVI, fig. 3; Pl. XVIII, figs. 3, 4, 6), the trunk has one edge straight or

concavely curved, the other more strongly and convexly curved, the width (tr.) greatest at about one-third the length from the anterior. I consider such specimens to be oriented in a *lateral* position, the sagittal plane parallel to the bedding planes. In specimens (Pl. XV, figs. 3, 6) in which the carapace is subtriangular in outline, the trunk outline is bilaterally symmetrical, and widest (tr.) at about one-third the length. Such specimens appear to be oriented *parallel*, with the sagittal plane at right angles to the bedding. Other specimens (Pl. XII, figs. 1, 5; Pl. XVI, fig. 4) appear to be at an *oblique* angle approximating to one or other of these positions. Parts of the specimens are preserved at slightly different levels or angles to one another (Textfigs. 24–30), particularly the two rami of furca. The exoskeleton of the trunk is preserved as an exceedingly thin, apparently carbonaceous layer, with which fine-grained pyrite may be associated (e.g., Textfig. 26). No convexity is preserved, and there are no pleurae with external ridges, so that there is no indication, as in *Yohioia tenuis*, of which surface of the trunk exoskeleton is visible in a particular specimen. In the sample of 38 specimens, antennae are preserved in 20, traces of other appendages in 13. Apart from separation of the carapace from 10 of the 38 specimens, they appear to have been complete when entombed, antennae being present in examples in which the carapace is missing (e.g., Pl. XV, figs. 1, 2, 4; Pl. XVI, figs. 1, 2). The manner of preservation appears to be similar to that deduced for *Marrella* (Whittington, 1971b, p. 19–20).

Description

Cephalic Region

This region, visible in specimens in which the carapace is displaced or missing, appears as an irregular carbonaceous area (Pl. XIV, figs. 1–4; Pl. XV, figs. 1, 2; Pl. XVI, figs. 1, 2). In two examples (Pl. XIII; Pl. XVII, figs. 1, 2) there is a distinct, convexly curved antero-ventral outline, the shape of the region appearing subtriangular (apex downward) in lateral aspect. The reconstruction (Textfig. 6B) is based on these specimens. The antenna was attached to the anterodorsal area of the region, and appears to have been stout, tapering slightly distally, and composed of about 12 segments (Pls. XIII, XIV; Pl. XVII, figs. 1, 2). The proximal segments expanded distally, and bore setae at the anterior margin; distally the segments became relatively longer and cylindrical in shape, and the most distal bore setae at the tip. The flexible antennae are preserved directed forward and curved, or may appear from beneath the carapace directed forward or backward and downward (Pl. XII, fig. 1; Pl. XVI, fig. 5).

Trunk

One specimen (Pl. XIII, figs. 1, 2) shows the trunk to be composed of 13 somites including the telson, which bears a furca. A few additional specimens (Pl. XII, fig. 2; Pl. XVII, figs. 1, 2) show the second and/or third somite of the trunk; these and other specimens show the fourth to twelfth somites and the telson. In parallel specimens (Pl. XV, figs. 3, 6), the trunk appears approximately symmetrical, the sixth or seventh somites the widest (tr.), the somites reduced progressively in width to anterior or posterior of this level. In lateral specimens (Pl. XII, fig. 2; Pl. XVII, figs. 1, 2; Pl. XVIII, figs. 4, 6), the trunk is deepest at the fifth and sixth somite. If the trunk is extended, the outline of the dorsal side is straight, while that of the ventral side is curved convexly. Somites 4 to 7 or 8 thus appear to have been ovate in cross-section; successively posterior somites may have approximated to the probably circular cross-section of the telson. Measurements of sagittal length of somites (Textfig. 7) show that the anterior somites were the shortest, and somites 10 to 12 the longest. There were no abrupt changes in length between members of the series, but instead a gradation, so that this criterion affords

no evidence for a subdivision of the trunk. Examination of the length (sag.) of the 12th somite (Textfig. 8) shows that it increases in proportion to increase in the total length of somites 4 to 13, i.e., within the known size range it increased in length at the same rate as the trunk. In the majority of specimens, the trunk is extended straight back, but it was evidently flexible (Pl. XIII) and in one example (Pl. XVIII, fig. 2) it was curved through about 130 degrees.

In the original of Plate XIII, figures 1, 2, the ventral margin of the exoskeleton of somites 1 to 4 appears to have been thickened. The two margins are not co-incident in this example, apparently because the orientation is not exactly lateral; the same seems to be true of the original of Plate XVII, figures 1, 2. The dorsoventral dimension (depth) of the exoskeleton of somites 1 to 4 increases progressively posteriorly, suggesting that the exoskeleton was an inverted U-shape in cross-section, and that there was a ventral membrane extending between the margins. The appendages of the trunk appear to have belonged to these somites; these appendages are poorly preserved in all examples, visible as narrow, elongate carbonaceous strips, but showing no joints (Pl. XII, fig. 1; Pl. XIII, fig. 2; Pl. XV, figs. 1, 2; Pl. XVI, fig. 5; Pl. XVII, figs. 1, 2). The number of pairs of appendages is uncertain; it may be four, but not more than three can be observed with any certainty.

No appendages have been observed on somites 5 to 12. At the boundary between the exoskeleton of these somites there is a darker band (Pl. XII, fig. 2; Pl. XIII; Pl. XVI, fig. 5). This suggests a doublure at the posterior margin, beneath which extended the exoskeleton of the succeeding somite. The alimentary canal may be preserved in this part of the trunk as a sediment-filled band, flattened ovoid in cross-section (Pl. XII, figs. 4, 5) or less clearly as a darker strip (Pl. XVI, fig. 5). It extends sagittally from somite 4 or 5 to the posterior margin of the telson. In the few specimens showing anterior somites, the position of the canal cannot be seen, so that its course is not shown in this region in the restoration (Textfig. 6).

The telson was presumably subcircular in cross-section, since the width (tr.) appears similar in parallel or lateral specimens; the length (sag. and exs.) in most individuals was less than that of somite 12 (Textfig. 7). Each ramus of the furca appears sub-oval in outline in parallel specimens, the width (tr.) greatest at about one-third the length (Pl. XII, fig. 6), the tip broadly rounded. The rami are preserved in various positions, from slightly (Pl. XII, fig. 5; Pl. XVI, fig. 4) to widely divergent (Pl. XII, fig. 1) and, in one example (Pl. XV, fig. 5), are widely divergent and rotated, so that each lay at an angle to the bedding planes. In slightly oblique-lateral examples (Pl. XIII; Pl. XVII, fig. 1), the two rami are preserved with one partly overlapping the other, and may appear relatively narrow (tr.). Presumably, therefore, each ramus, while sub-semicircular in cross-section at its insertion into the telson, became rapidly thinner and blade-like distally (Textfig. 6B), and in the slightly divergent position the blades partially overlapped proximally.

Carapace

A carapace extended over the anterior part of the body (cephalic region and somites 1 to 5 of the trunk), loosely covering this part dorsally and laterally, including the proximal parts of the antennae and trunk appendages, but only part of trunk somite 5. In lateral aspect (Pl. XIV; Pl. XVI, fig. 3; Pl. XVIII, figs. 3, 4, 6), the outline was sub-oval, the dorsal and posterior margins almost straight, the latter directed downward and slightly backward. The outline anterolaterally appears to have been truncated by a short, straight edge running downward and forward (Pl. XIV, fig. 4). In parallel specimens (Pl. XII, fig. 4; Pl. XV, figs. 3, 6), the outline is subtriangular, widest posteriorly, and it is surmised that this reflects original shape, i.e., that the sides of the carapace diverged posteriorly (Textfig. 6A). Compaction in parallel and oblique specimens has crushed and folded the carapace, so that the

nature of the hinge line cannot be seen. In two lateral specimens (Pl. XII, figs. 2, 3; Pl. XIV), an elongated, spine-like object is preserved adjacent to the anterolateral part of the carapace. This is presumed to represent the rostral plate, but its shape and relation to the rest of the carapace is conjectural. In the original of Plate XIV, figures 1 to 4, the free anterior, ventral and posterior margins of the carapace show a narrow thickened rim, and a carbonaceous strip inside the rim which represents the doublure. While in most specimens the carapace is in place, it may also be displaced (Pl. XII, figs. 2, 3; Pls. XIII, XIV) or absent (Pl. XV, figs. 1, 2; Pl. XVI, figs. 1, 2, 4). How it was attached to the body, and whether or not adductor muscles were present, is not known.

Size

Because of the crushing or displacement of the carapace, and the incompleteness of the furcae distally, it is not possible to give more than an approximate size range, expressed as sagittal length. This range is 7 (Pl. XV, fig. 5) to 17 mm, slightly larger specimens than the original of Plate XVII, figure 1, being known. Textfigures 7 and 8 are based on more precise measurements of somites of the trunk, and Textfig. 8 shows that somites 4 to 13 (excluding the furca) have a total length of approximately 4 to 10 millimetres.

Habitat

Since the mode of preservation is like that of *Marrella* (Whittington, 1971b), then the habitat was presumably benthonic. The sediment-filling of the alimentary canal (Pl. XII, figs. 4, 5) suggests a deposit-feeding habit. There were no appendages to aid in swimming on the median and posterior part of the trunk; however, swimming and steering may have been accomplished by movements of the flexible trunk and blade-like furcae.

Discussion

The single figure and brief description by Walcott (1912) constitute the only information previously available on this species. As Henriksen (1928) observed, and the present investigation confirms, there are no pleurae on the trunk. This character distinguished the species from *Yohioia tenuis*, as does the telson with furca and the far fewer pairs of trunk appendages. Furthermore, *Y. tenuis* has a cephalic shield apparently formed of fused tergites and pleurae. *Plenocaris plena*, however, has a structure which loosely covers laterally and dorsally the cephalic region and anterior trunk somites; this structure is carapace-like, if not a true carapace, and is so called here. The carapace, ovate in outline, the posterior part of the trunk without appendages, and the telson with furca, resemble such Cambrian phyllocarids as *Hymenocaris* and *Canadaspis* (Rolfe, in Moore, 1969, p. R315, R323). For these reasons *Plenocaris* is regarded as probably a phyllocarid, and thus presumably a malacostracan crustacean. However, it does not exhibit all the characters of Phyllocarida as defined by Rolfe (in Moore, 1969, p. R312). Though there may have been a rostral plate, evidence of an adductor muscle is lacking in *Plenocaris*. The trunk is not divisible into thorax and abdomen; it consisted of 13 somites rather than 15, and appendages were present only on somites 2 to 4. *Hymenocaris* is poorly known, but the peculiar characters of the telson and caudal spines seem to distinguish it. *Canadaspis* has not yet been studied in detail, but it seems to represent a quite different species and genus, having distinctive trunk appendages.

Waptia fieldensis (Walcott, 1912, p. 181–182, Pl. 27, figs. 4, 5; 1931, p. 20–24, Pl. 18, figs. 2–5; Pls. 19, 20, Pl. 21, fig. 2) had a carapace similar in shape to that of *Plenocaris*, and Walcott claimed that a small rostral plate was present. However, on the anterior part of the

trunk there are five pairs of jointed, uniramous appendages, and on the eight succeeding somites there are appendages similar to the trilobite gill branch (exopodites of Walcott, 1931, Figs. 6, 7). The six succeeding somites were longer (sag.) than they were wide, lacked appendages, and the lobate rami of the caudal furca were segmented. In material of *W. fieldensis* now being studied by C. P. Hughes are two specimens respectively 13.6 mm (Pl. XVIII, figs. 1, 5) and approximately 19.5 mm (Pl. XVII, figs. 3, 4) long (sag.), that is, within and slightly above the known size range of *P. plena*. The "exopodites," elongate posterior trunk segments, and segmented caudal rami were present in these small *Waptia*, so that they were quite distinct from *Plenocaris*.

These considerations lead to the view that the species *plena* cannot be retained in *Yohioia*, and that it is not congeneric with *Canadaspis* or *Waptia*. It is made the type of a new genus, and the appendages do not suggest that it is a trilobitoid. It is placed tentatively in Phyllocarida, order and family uncertain (Rolfe, in Moore, 1969, p. R323-8), because it is like some fossil forms placed in this group, though at the same time the trunk does not exhibit all the typical phyllocarid characteristics.

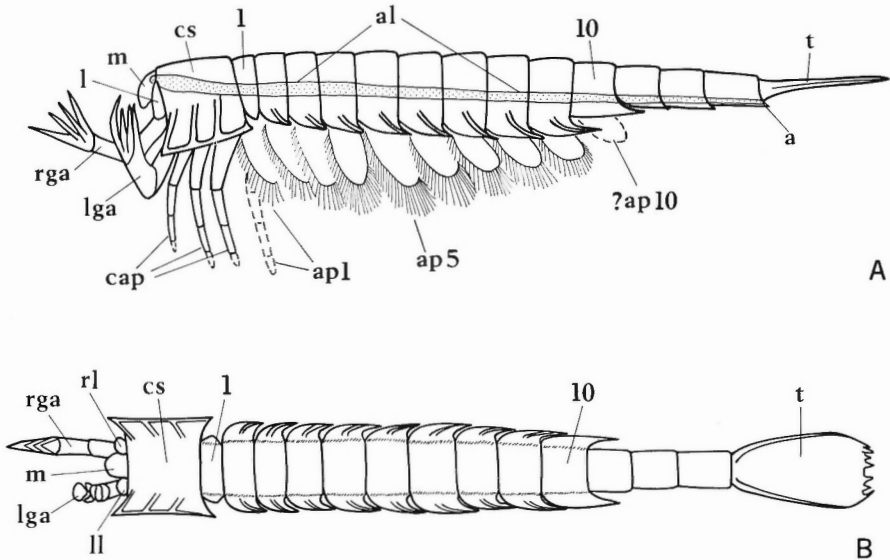
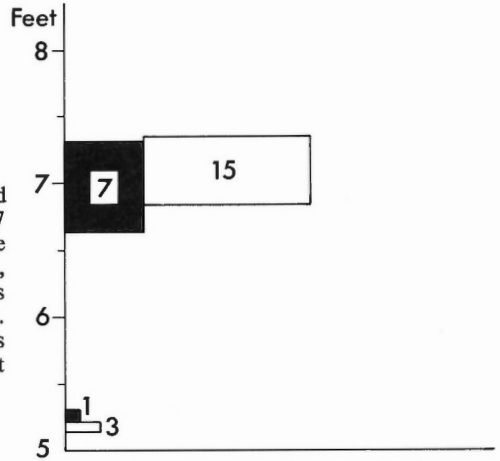
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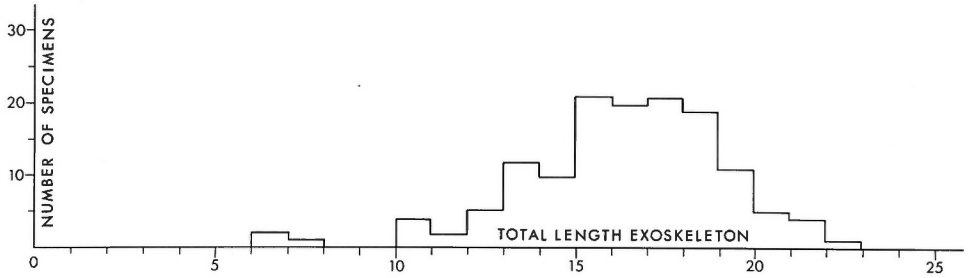
TEXTFIGURES 1-8

TEXTFIGURE 1

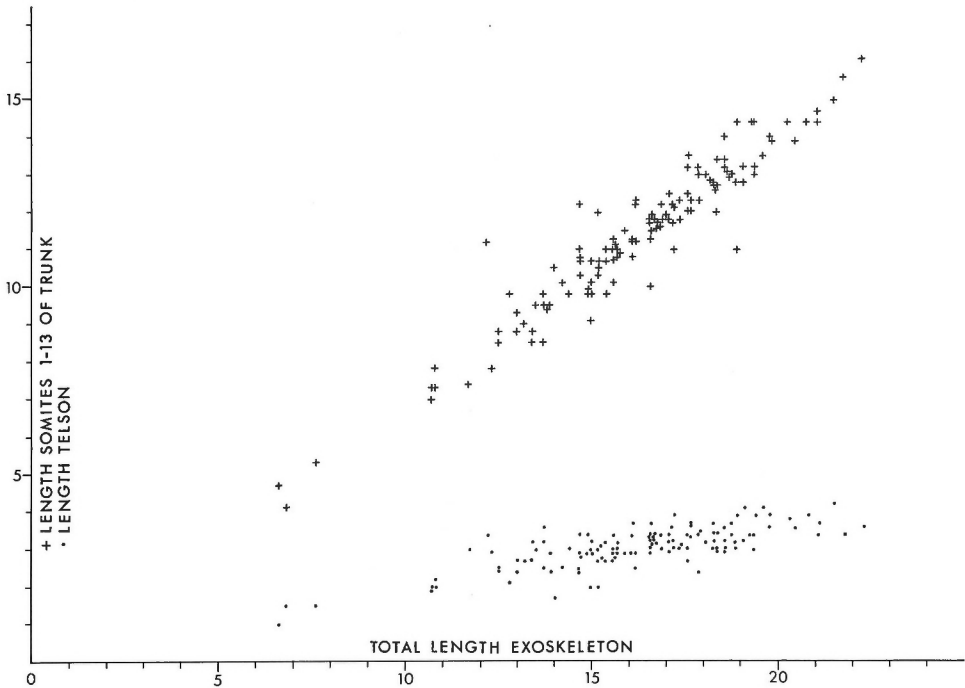
Numbers of specimens of *Yohoia tenuis* collected by GSC party in 1966 (solid black) and 1967 (open rectangle) from levels indicated in the Phyllopod bed, Walcott quarry. See Whittington, 1971a, Fig. 3, for photograph of quarry with levels indicated; level 5 feet is base of Phyllopod bed. Compare Whittington, 1971a, Fig. 5, for numbers of specimens of *Marrella splendens* collected at similar levels.



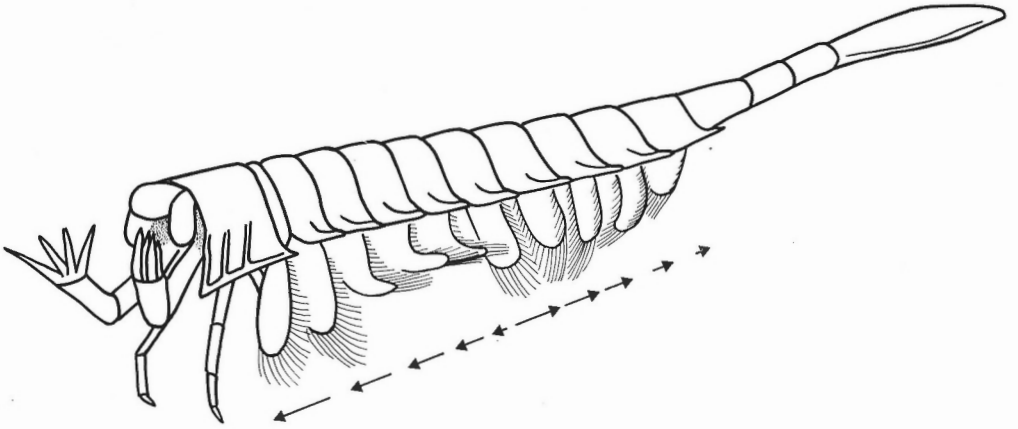
TEXTFIGURE 2. *Yohoia tenuis* Walcott, 1912. Restorations in left lateral (A) and dorsal (B) views. A, showing left and right great appendages, other appendages only of left side; stippled area indicates position of alimentary canal. B, showing only appendages of cephalic region; shading indicates proximal margins of pleurae. ca. x7 mean size.



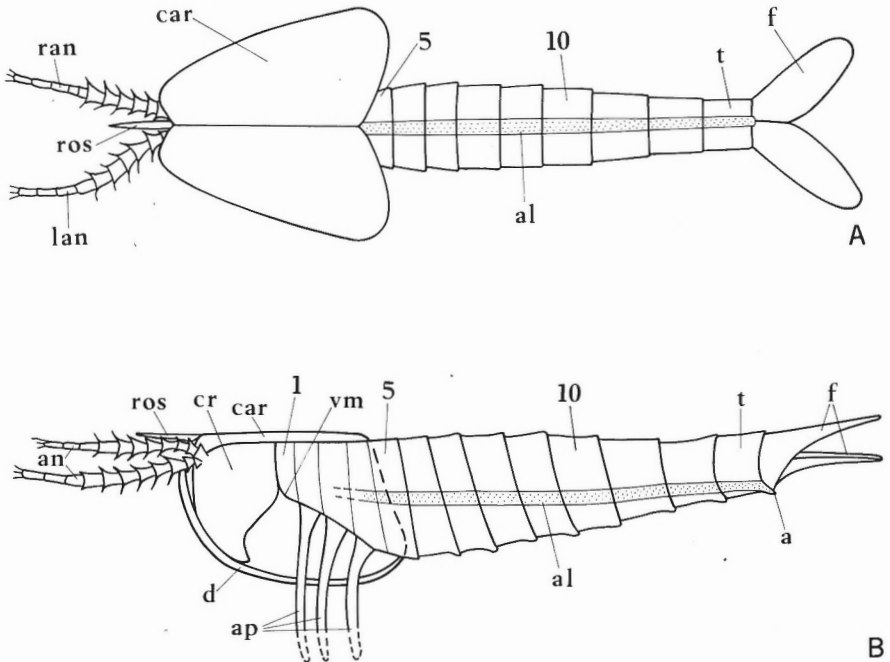
TEXTFIGURE 3. *Yohioia tenuis* Walcott, 1912. Size-frequency histogram of total length of exoskeleton in millimetres. Measurements of extended specimens made in straight line, of flexed specimens along arc. $N = 138$; mean = 16.3; var. = 8.13. Sample includes USNM 57694, 57697 to 57699 (Walcott's 1912 specimens), USNM 155603-605, 155608-610, 155613, 155617, 155619, 155620 (studied by Simonetta), USNM 179008, 179010, 179011, 179015, 179016, 179019 to 179128, and GSC 31133, 31134, 31136 to 31141.



TEXTFIGURE 4. *Yohioia tenuis* Walcott, 1912. Plots of total length exoskeleton (E) against length of somites 1-13 of trunk (B) and against length telson (T). Bivariate statistics, E:B. Mean E (var. E) = 16.22 (8.157); mean B (var. B) = 11.34 (4.496); α (var. α) = 1.06 (0.0008); a (var. a) = 0.74 (0.0004); r (r_e) = 0.96 (0.96); $N = 125$. Bivariate statistics, E:T. Mean E (var. E) = 16.22 (8.223); mean T (var. T) = 3.05 (0.307); α (var. α) = 1.03 (0.0037); a (var. a) = 0.19 (0.0001); r (r_e) = 0.76 (0.76); $N = 124$. Plots and bivariate statistics by Dr. C. P. Hughes. Measurements in millimetres, of extended specimens in straight line, of flexed specimens along arc. Sample includes USNM 179008, 179010, 179011, 179015, 179016, 179019 to 179128, and GSC 31133, 31134, 31136 to 31141 (USNM 179083 not used for E:T because T is incomplete).

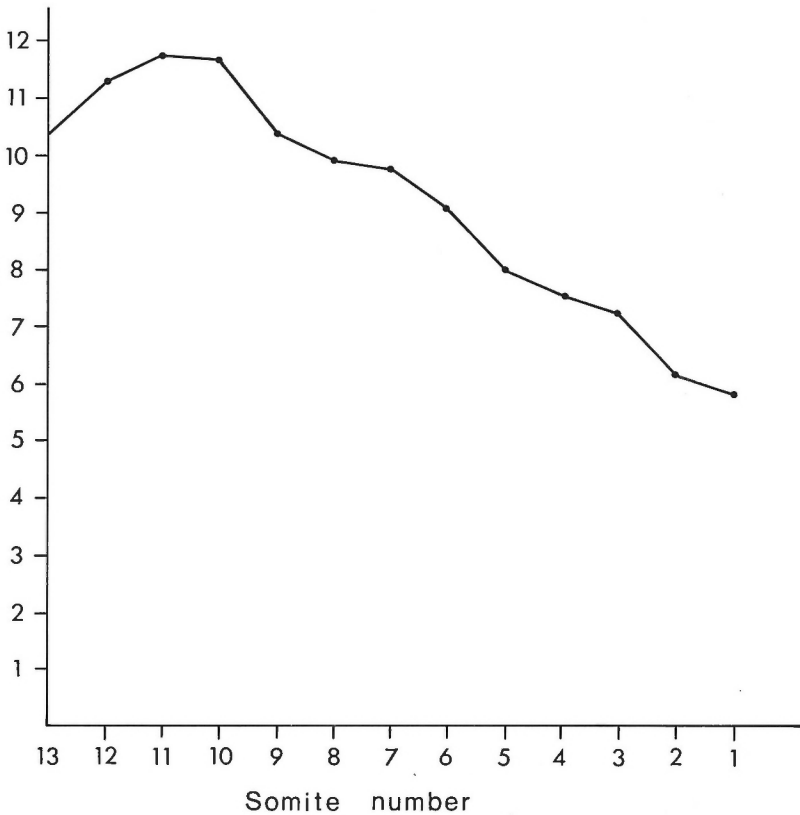


TEXTFIGURE 5. *Yohioia tenuis* Walcott, 1912. Restoration in oblique view, swimming, cephalic appendages 2, 3, and ?4 trailing and partly or completely concealed by lobate appendages. Latter shown on left side only, in metachronal movement. Lobate appendages 1-5 shown in stages of forward stroke when water is being drawn in laterally; 6-10 in stages of backward stroke, when water is being forced out laterally (cf. Sanders, 1963, Fig. 8). Length of arrows is proportional to length of stroke completed.



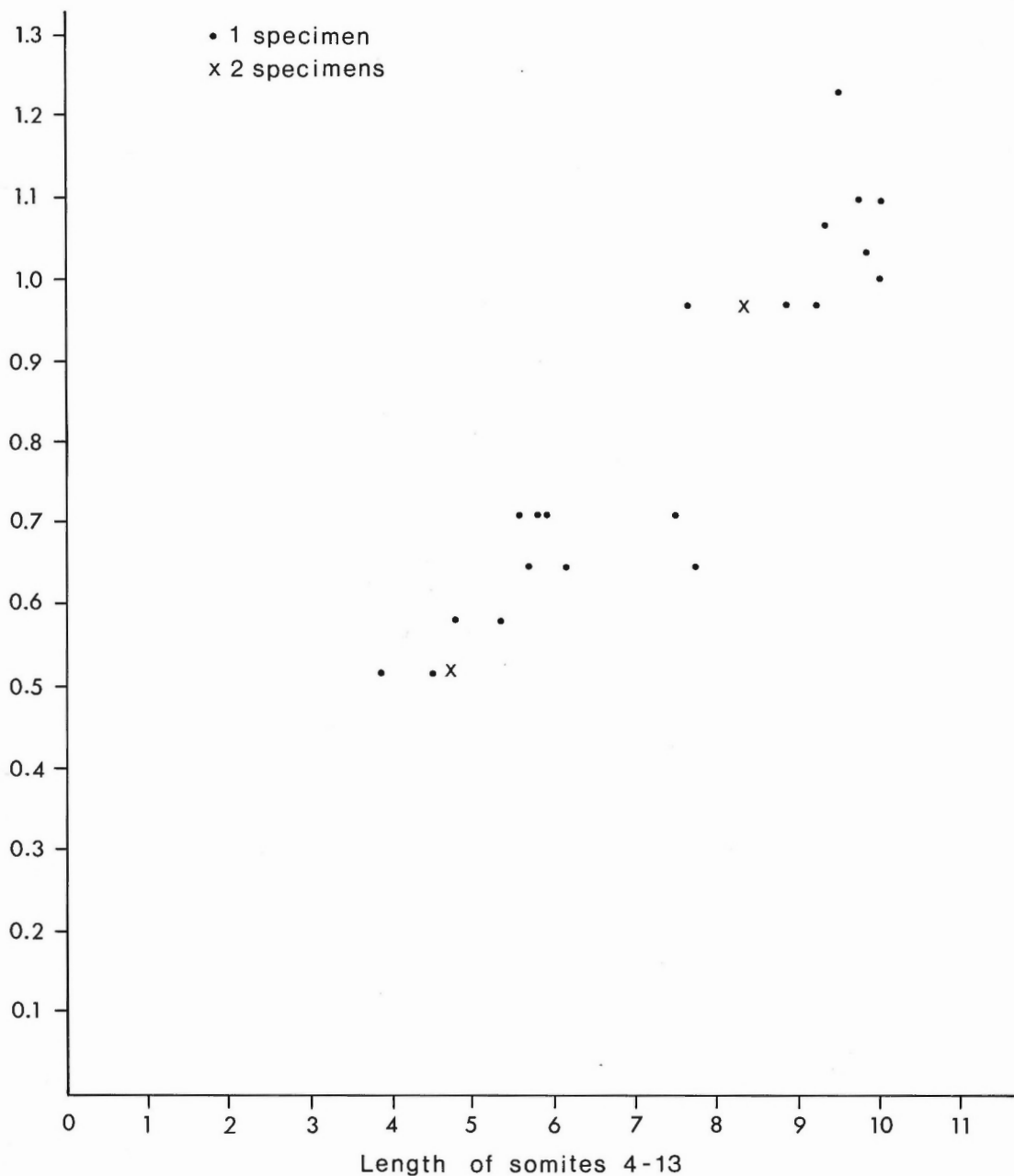
TEXTFIGURE 6. *Plenocaris plena* (Walcott, 1912). Restorations in dorsal (A) and lateral (B) views. Left and right antennae shown, other appendages only of left side, approximately x7.

Length somite as percentage
of length somites 4-13



TEXTFIGURE 7. Measurements of sagittal length of somites of trunk of 24 specimens (USNM 182530-31, 182533-35, 182537, 182539-541, 182543-44, 182545-557) of *Plenocaris plena*. Plot shows length of each somite as an average percentage of the total length of somites 4-13 (excluding length of furca). Total length of somites 4-13 used because this is the largest group of somites preserved in every specimen.

Length of
somite 12



TEXTFIGURE 8. Measurements in millimetres of sagittal length of somites of trunk of 24 specimens (those used for Textfig. 7) of *Plenocaris plena*. Length of somite 12 selected to plot against total length of somites 4-13 of trunk (excluding furca).

Explanation of Plates I–XVIII and Textfigures 9–30

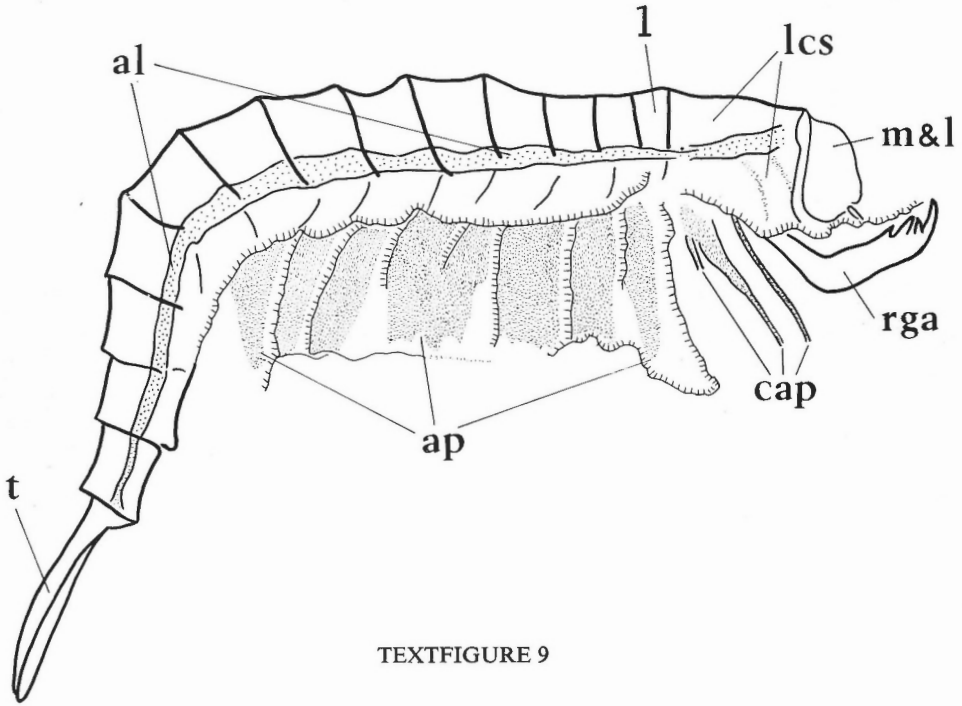
The photographs have been taken on panchromatic film in ultraviolet radiation, after focussing in ordinary light. The radiation has been directed at 30 degrees to the horizontal, and the direction from which it came is given as west, northwest, et cetera, relative to the margins of the plate. Photographs referred to as reflected (Whittington, 1971b, p. 1) 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 planes is given as parallel, lateral, or oblique (*see* sections on preservation) and, for *Yohoia tenuis*, the particular exoskeletal surface (inner, outer, left or right side) exposed is noted. Textfigures 9–30 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 textfigures 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. Certain specimens have been illustrated previously by Walcott (1912, P1. 29, figs. 7–13) and Simonetta (1970, P1. X, figs. 5–19); for brevity, only the author and figure number is given.

The items explaining individual figures on the plates are arranged in the following order: depository and specimen number; orientation of specimen and surface exposed; direction of radiation; magnification; reference to previous illustration; comment and/or reference to textfigure; locality and horizon in terms explained in Fritz, 1971 and Whittington, 1971a.

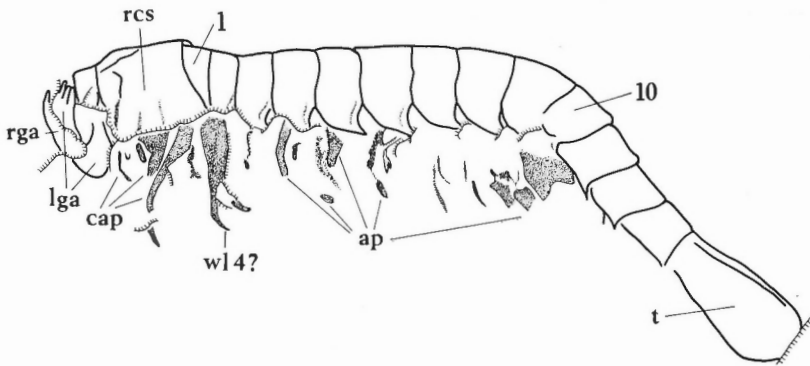
PLATE I

Yohioia tenuis Walcott, 1912
Phyllopod bed, Walcott quarry

- Figure 1. USNM 57694, lateral, inner surface of left side; west; x10; original of Walcott, Fig. 7; Simonetta, Fig. 5; see Textfig. 9.
 Figure 2. USNM 57695, oblique of flexed trunk; west; x5; original of Walcott, Fig. 8; Simonetta, Fig. 7.
 Figures 3, 4. USNM 57699, lectotype, lateral, inner surface of right side; northwest and reflected respectively; x5; original of Walcott, Figs. 12, 13; Simonetta, Fig. 8; see Textfig. 10.



TEXTFIGURE 9



TEXTFIGURE 10

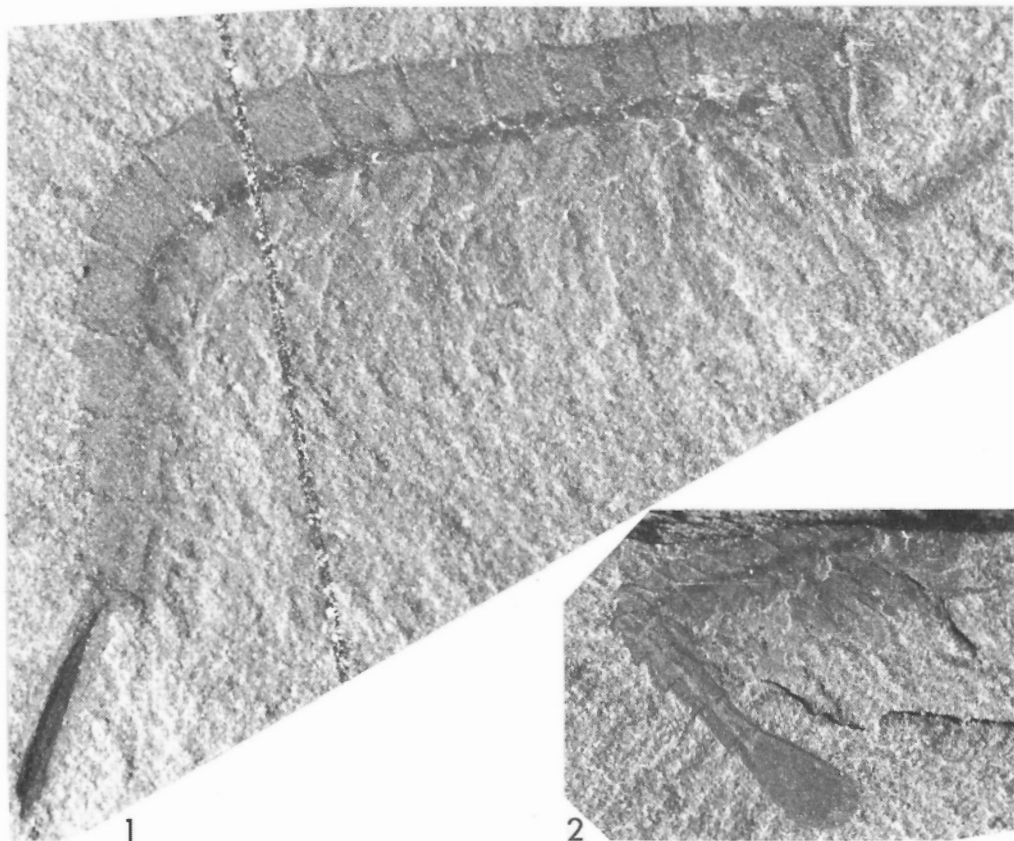
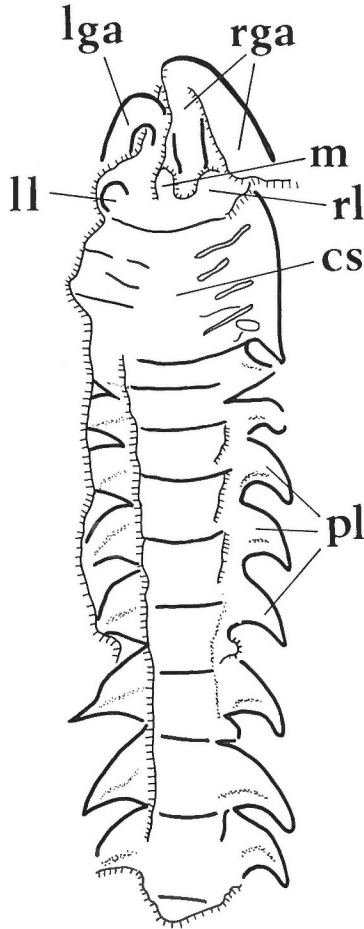


PLATE II

Yohoia tenuis Walcott, 1912
Phyllopod bed, Walcott quarry

- Figures 1-3. USNM 57696, parallel, incomplete, part and counterpart; Figs. 1, 2, inner surface; north and reflected respectively; Fig. 3 (USNM 155609), outer surface; northwest; x10; original of Walcott, Fig. 9; Simonetta, Figs. 10, 18; see Textfig. 11, which is drawn with the outer surface of the exoskeleton exposed, based on Fig. 3.
- Figure 4. USNM 57697, parallel, outer surface; west; x5; original of Walcott, Fig. 11; Simonetta, Fig. 9.
- Figure 5. USNM 155613, oblique, outer surface; west; x5.
- Figure 6. USNM 179008, left oblique; inner surface of right side; west; x5.



TEXTFIGURE 11

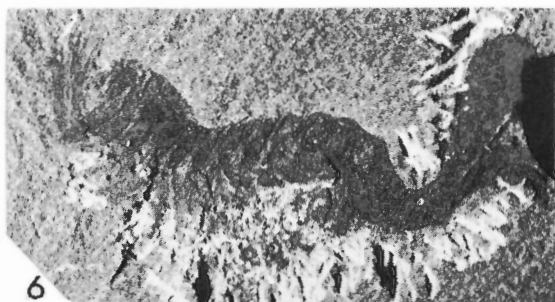
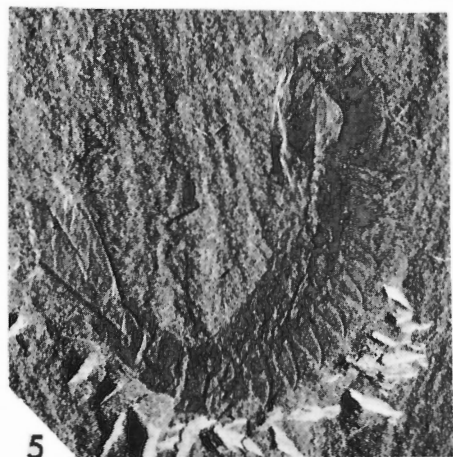
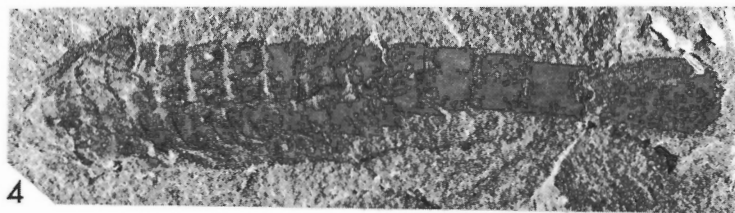
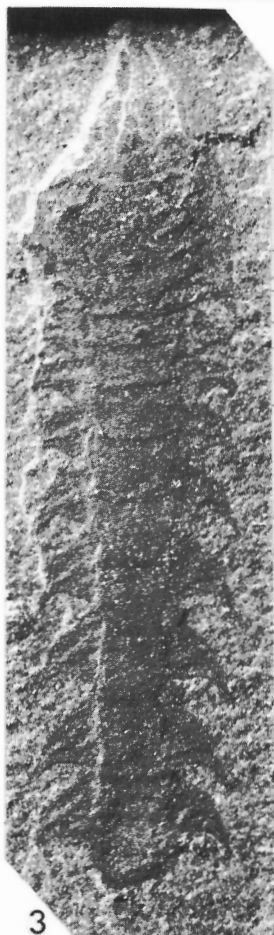
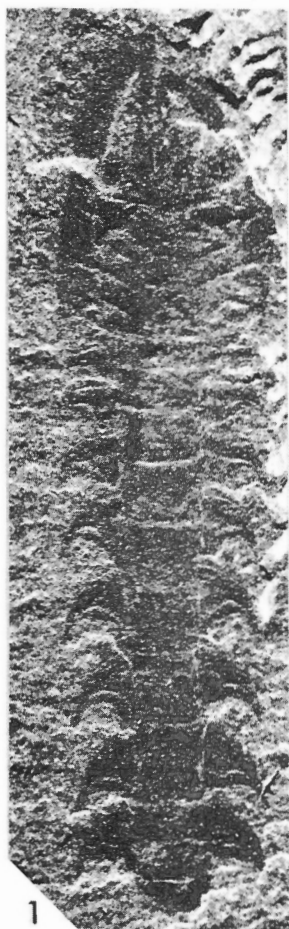
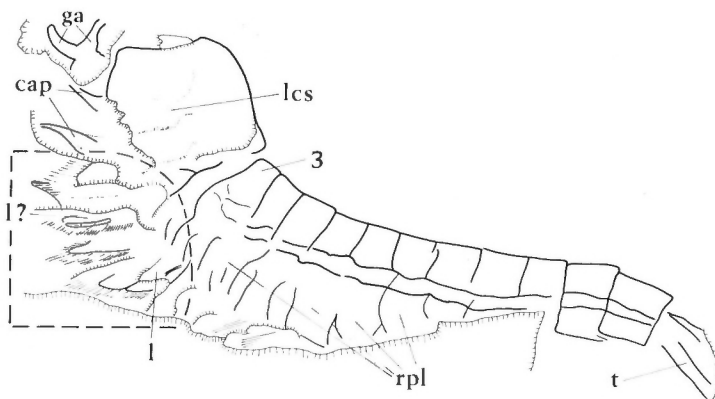


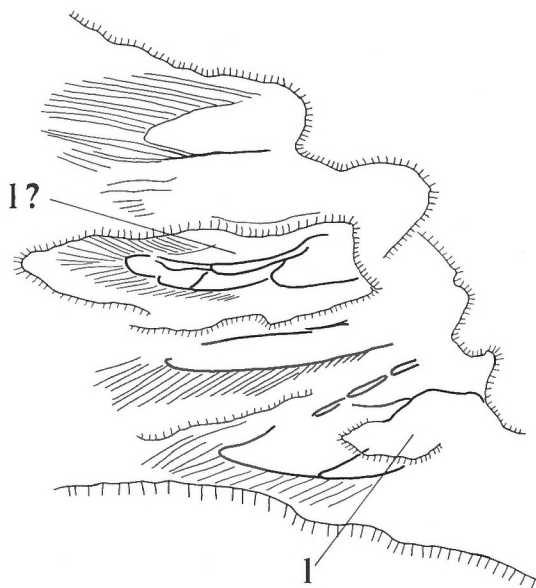
PLATE III

Yohioia tenuis Walcott, 1912
Phyllopod bed, Walcott quarry

Figures 1-3. USNM 155601, left oblique, part of left external surface of cephalic shield, remainder is internal surface of right side; Figs. 1, 2, respectively reflected, northeast, x5; see Textfig. 12. Fig. 3, enlargement of part of Fig. 2; west; x15; see Textfig. 13 for drawing of trunk appendages of area within dashed line of Textfig. 12, also shown in lower left portion of Fig. 3; original of Simonetta, Fig. 12.



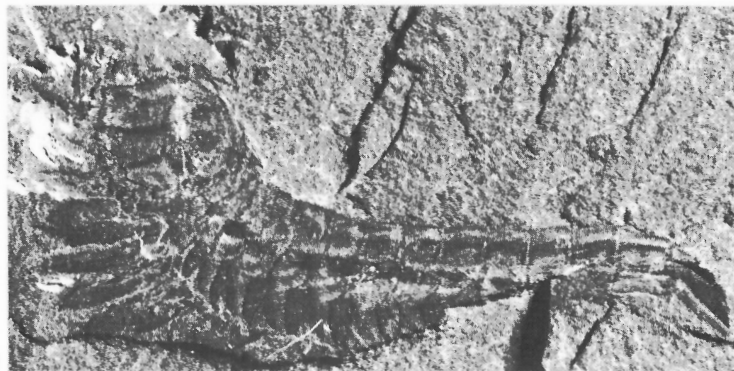
TEXTFIGURE 12



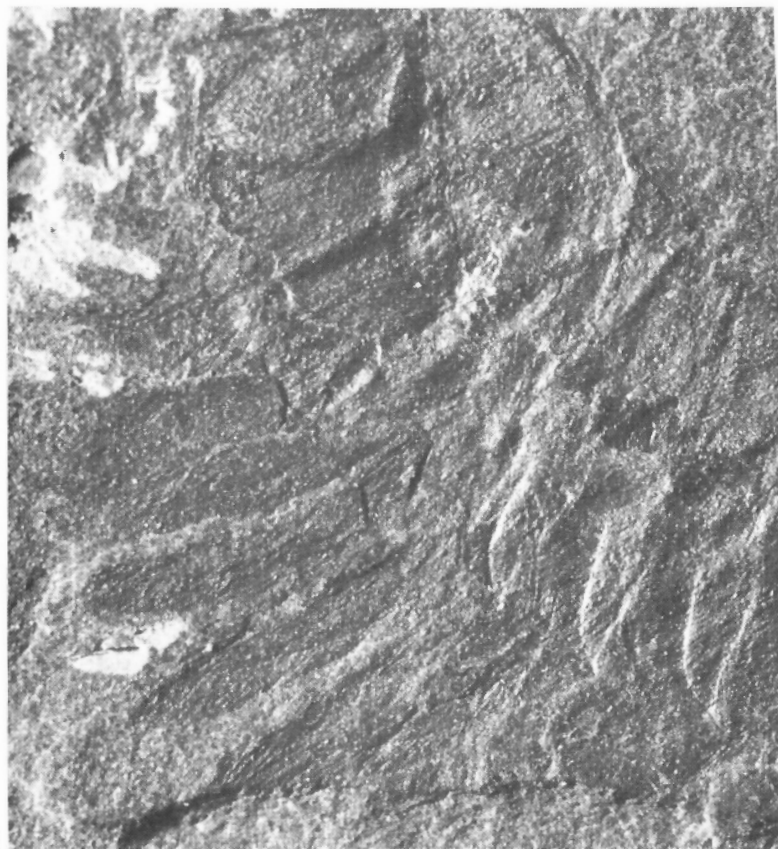
TEXTFIGURE 13



1



2

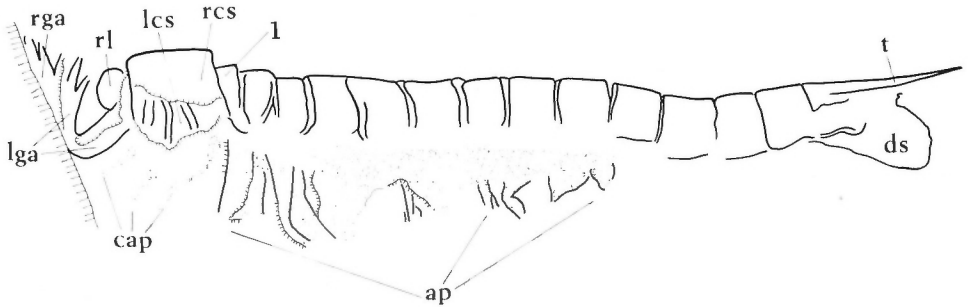


3

PLATE IV

Yohioia tenuis Walcott, 1912
Phyllopod bed, Walcott quarry

- Figures 1, 2. USNM 155604, left lateral, inner surface of right side; respectively reflected, x5, west, x10; original of Simonetta, Fig. 14.
- Figures 3, 4. USNM 155619a, b, counterparts; lateral, inner surface of right side, part of outer, right side of cephalic shield; respectively west, east; x5; originals of Simonetta, Figs. 16a, 16b; see Textfig. 14. Dark stain extends above most posterior part of specimen in Fig. 4.
- Figure 5. USNM 155606, right lateral, external surface; west; x10; showing great appendage and traces of other appendages beneath cephalic shield.



TEXTFIGURE 14

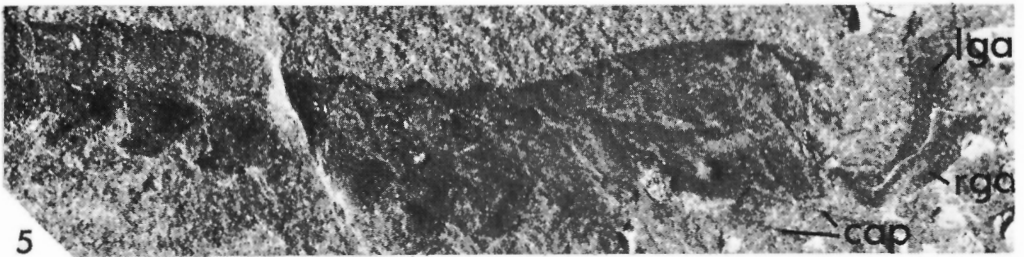
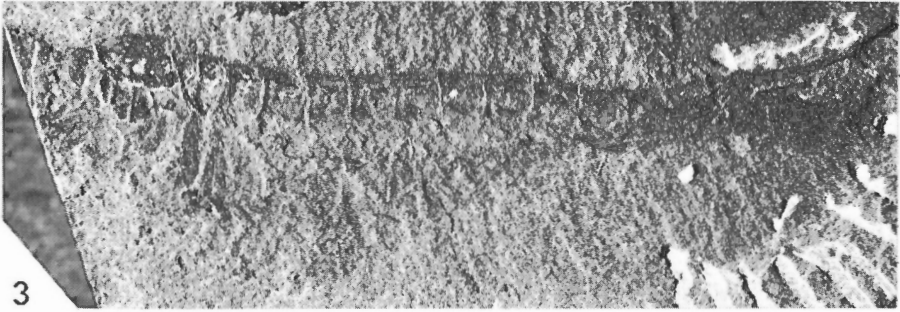
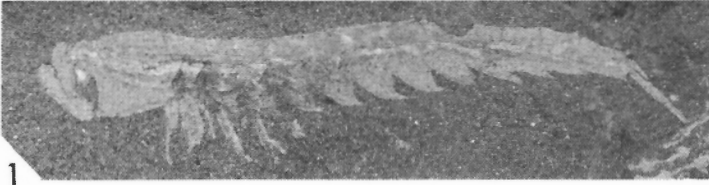
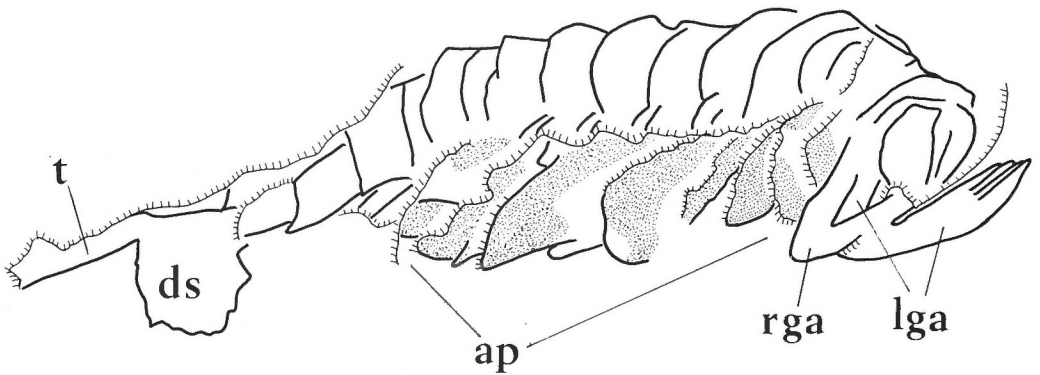


PLATE V

Yohoia tenuis Walcott, 1912
Phyllopod bed, Walcott quarry

- Figure 1. USNM 155610, oblique right, left side of exoskeleton; north; x10; original of Simonetta, Fig. 10; showing carbonaceous areas representing appendages.
- Figure 2. USNM 155616, oblique right, left side of exoskeleton; southwest; x10; *see* Textfig. 15. Tergites and cephalic shield crushed so that details cannot be deciphered.
- Figures 3, 4. USNM 155605, right lateral, left side of exoskeleton; reflected, west; x5; original of Simonetta, Fig. 15.
- Figure 5. USNM 155608, left lateral; west; x5; original of Simonetta, Fig. 11; showing left side of exoskeleton and great appendage.



TEXTFIGURE 15



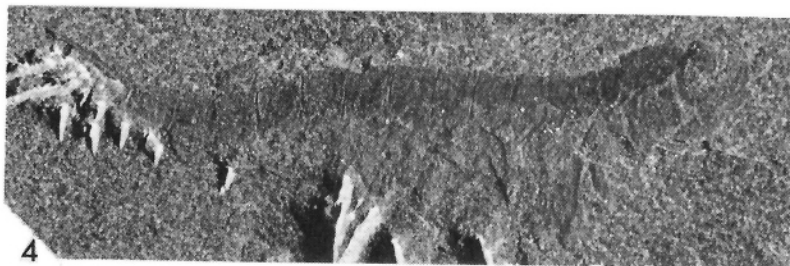
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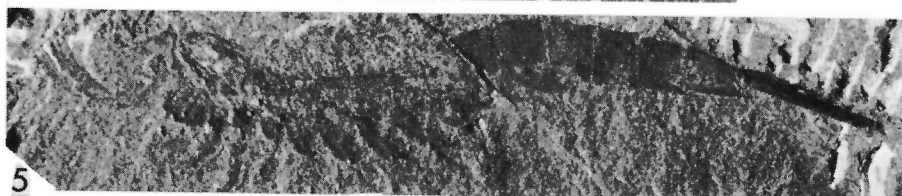
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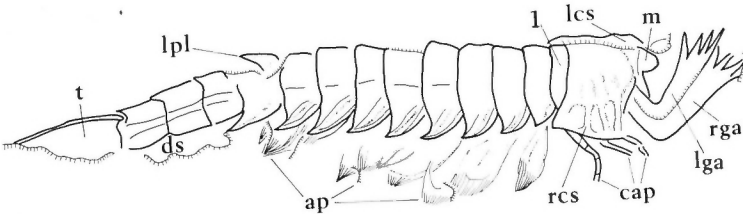


5

PLATE VI

Yohioia tenuis Walcott, 1912
Phyllopod bed, Walcott quarry

- Figures 1, 2. USNM 155621, oblique right, external surface of exoskeleton; respectively north, x5; west, x12; see Textfig. 16.
- Figures 3, 4. USNM 155618, left lateral, external surface of exoskeleton; respectively reflected, west, x5; original of Simonetta, Fig. 13; showing great appendage and carbonaceous areas representing other appendages emerging from beneath exoskeleton.
- Figure 5. USNM 179009, parallel, showing inner surface of exoskeleton; northwest; x5; great appendage (g) extends in front of cephalic shield, telson (t) is flexed ventrally and shortened.



TEXTFIGURE 16

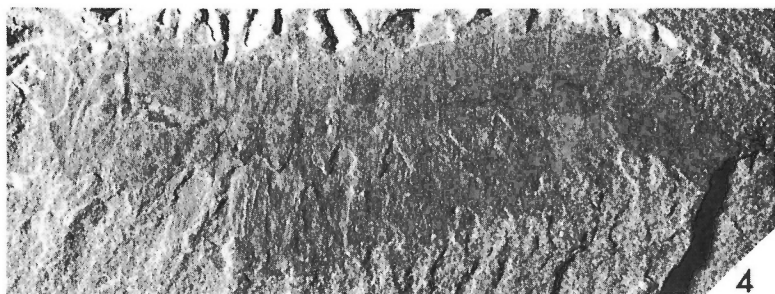
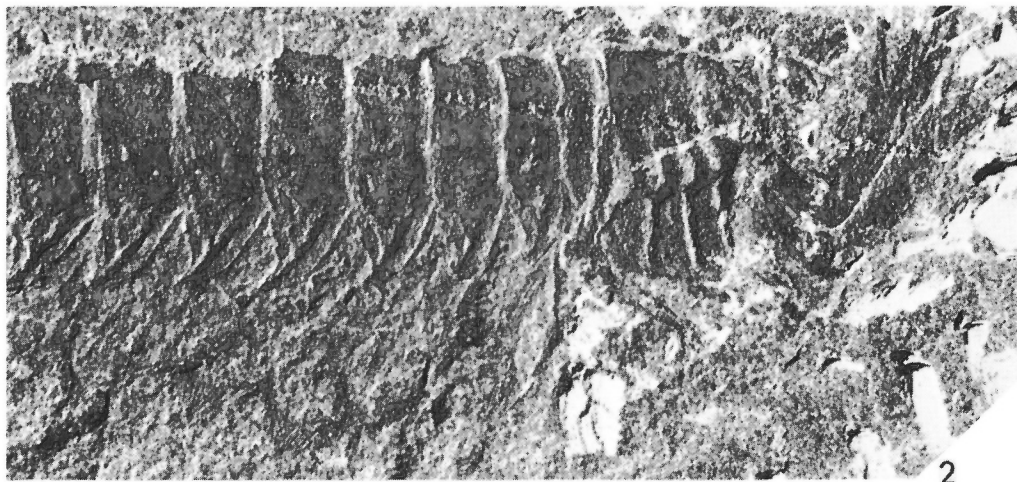
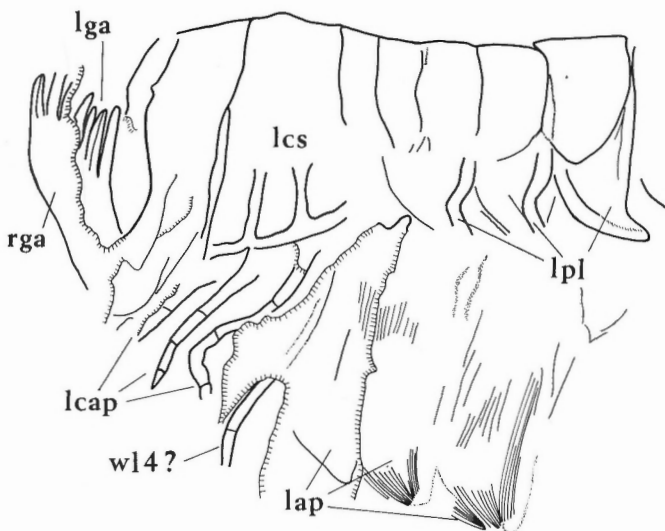


PLATE VII

Yohioa tenuis Walcott, 1912
Phyllopod bed, Walcott quarry

- Figures 1, 2. USNM 179010, oblique, external surface; respectively north, x5, reflected, x10; showing median (m) and lateral (l) areas at anterior margin of cephalic shield.
- Figures 3, 4. USNM 155614, left lateral, external surface of exoskeleton; respectively reflected, x10, north, x12; original of Simonetta, Fig. 17; see Textfig. 17.
- Figure 5. USNM 179011, oblique, external surface of exoskeleton; north, x5, showing great appendage and right pleurae.
- Figure 6. USNM 179012, right lateral, external surface of trunk exoskeleton, left internal surface of cephalic shield; west, x5.



TEXTFIGURE 17

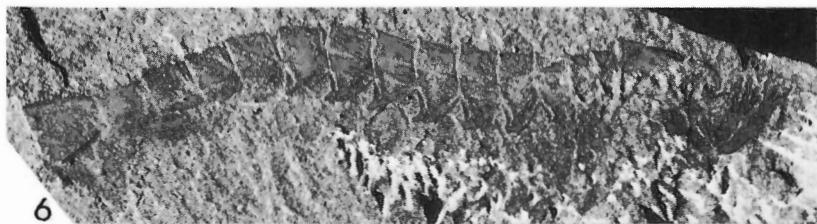
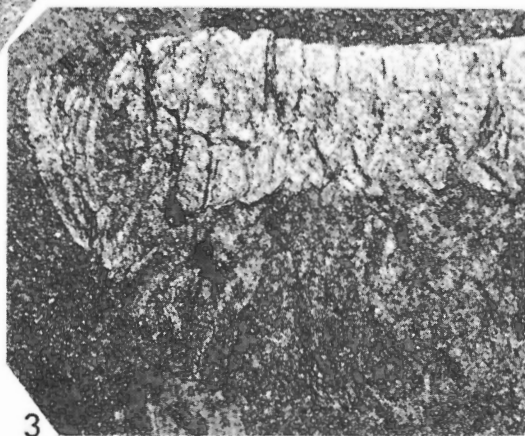
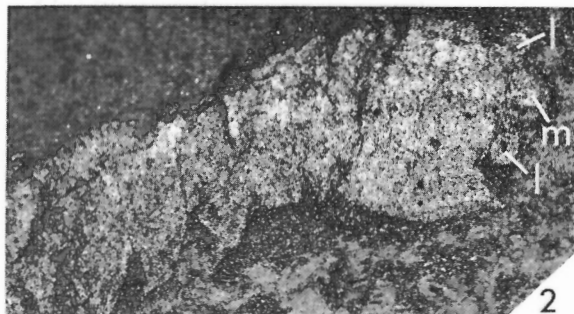
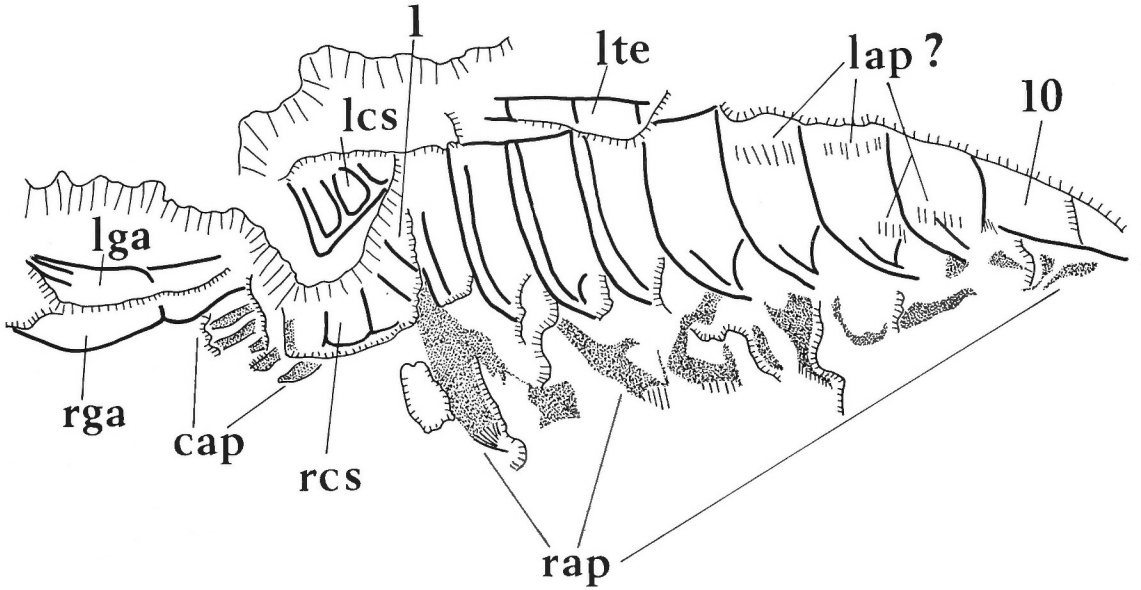


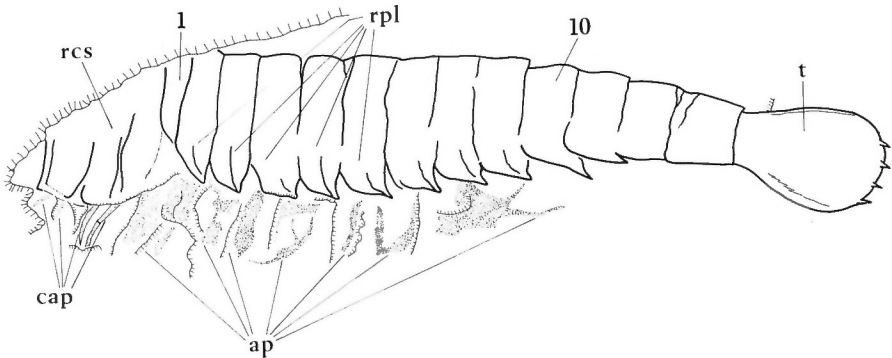
PLATE VIII

Yohoia tenuis Walcott, 1912
 Phyllopod bed, Walcott quarry

- Figure 1. USNM 179013, oblique, lateral; left outer and right inner surfaces of cephalic shield, right inner of trunk; west; x10; see Textfig. 18.
 Figures 2, 3. USNM 179014, left lateral; respectively reflected and northwest; x10; showing median (m) cephalic region and inner surface of right side of exoskeleton.
 Figure 4. USNM 179015, left oblique, inner surface of right side of exoskeleton; northwest; x5; see Textfig. 19.
 Figure 5. USNM 179016, oblique, showing dark stain adjacent to posterior part of body; southwest; x5.



TEXTFIGURE 18



TEXTFIGURE 19

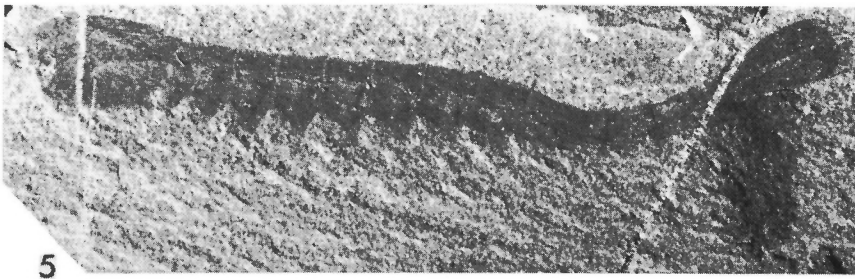
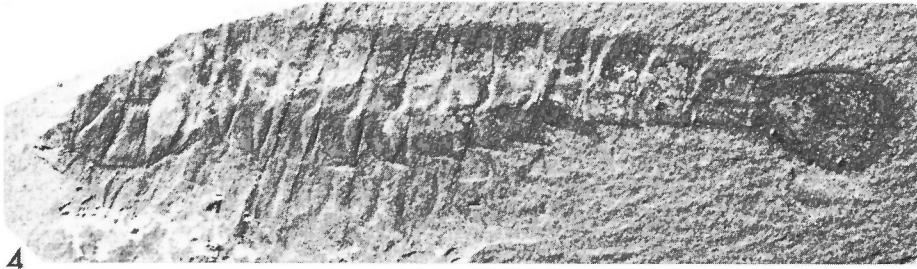
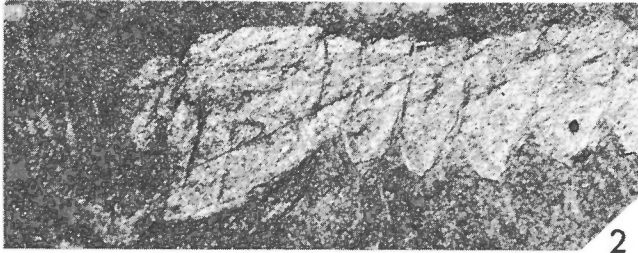
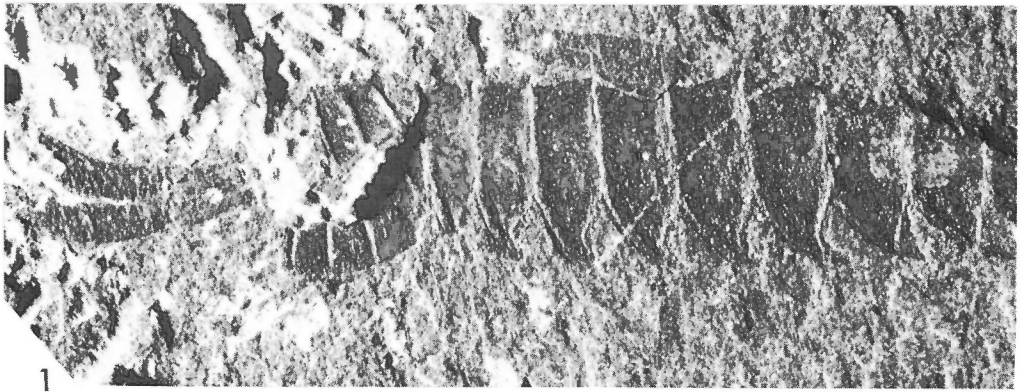
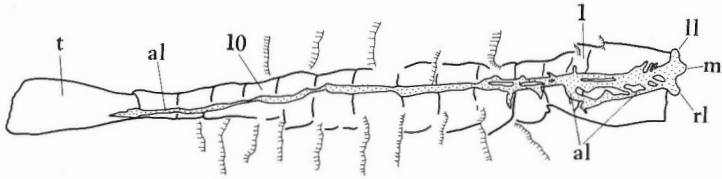


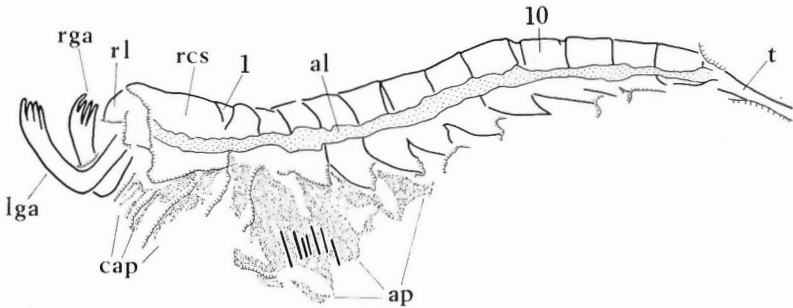
PLATE IX

Yohioia tenuis Walcott, 1912

- Figures 1, 2. USNM 179017, parallel; reflected; x5, x10; showing median frontal lobe, lateral area and alimentary canal, *see* Textfig. 20, in which these areas are stippled; Phyllopod bed, Walcott quarry.
- Figure 3. USNM 179018, parallel, inner surface of exoskeleton; northwest; x5; telson (t) is flexed forward dorsal to rest of body, and dark stain (ds) extends posteriorly; Phyllopod bed, Walcott quarry.
- Figures 4, 5, 6. GSC 31131, lateral counterparts; respectively west, x5; northwest, x10; northwest, x10; *see* Textfig. 21. Walcott quarry, level 6 ft. 7½ in. to 7 ft. 3½ in.



TEXTFIGURE 20



TEXTFIGURE 21

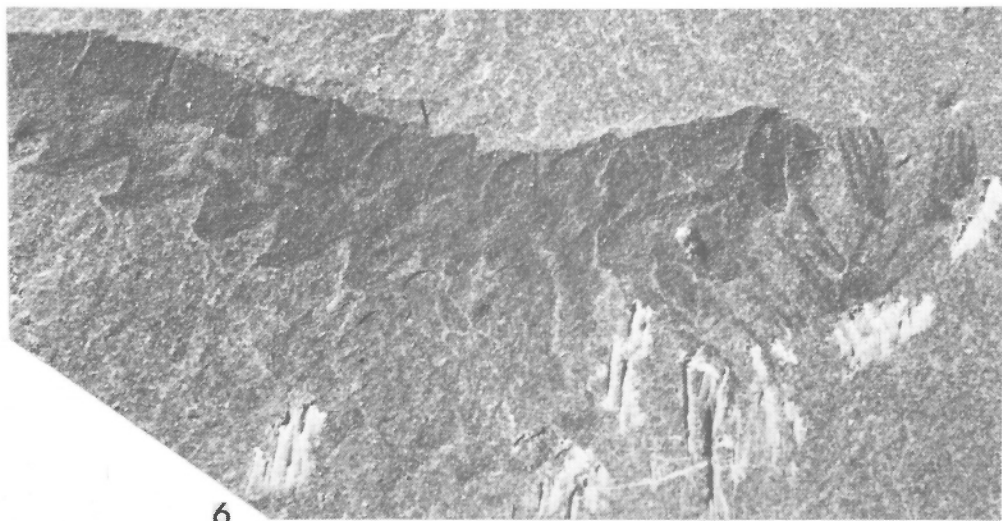
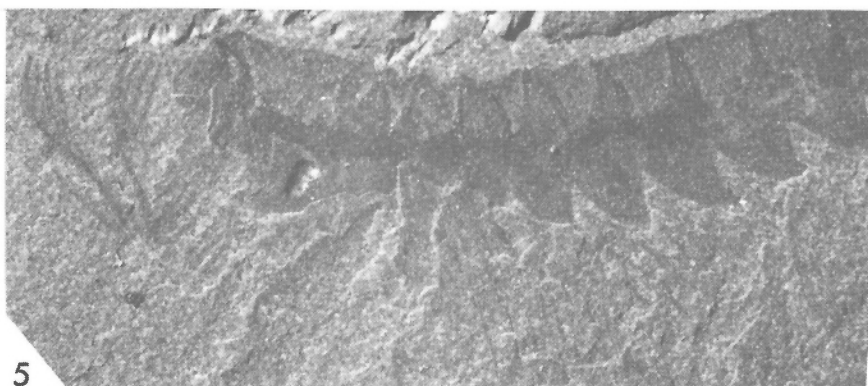
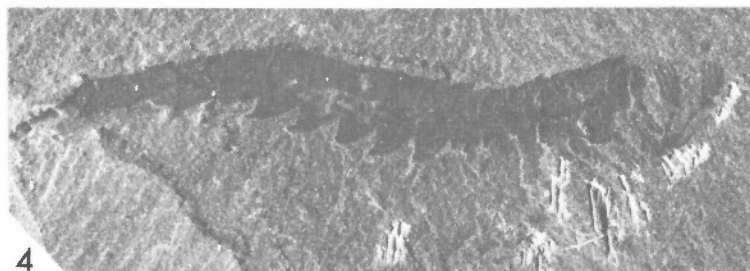
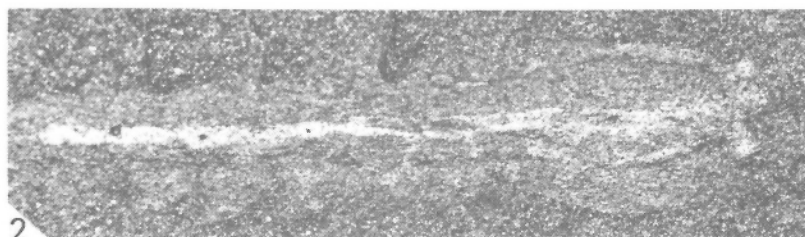
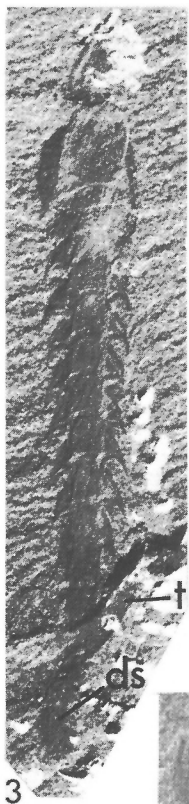
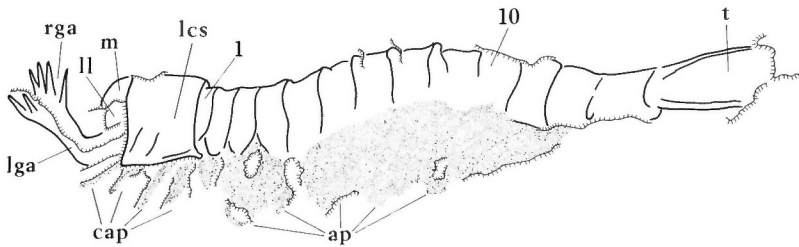


PLATE X

Yohoia tenuis Walcott, 1912

- Figures 1-3. GSC 31132, lateral, counterparts; respectively reflected, x5; west, x10; west, x10; see Textfig. 22; Walcott quarry, level 6 ft. 7½ in. to 7 ft. 3½ in.
Figures 4, 5. GSC 31133, parallel, dorsal surface of exoskeleton; respectively northeast, x5; northeast x10; showing median frontal lobe (m) and lateral area (l); Walcott quarry, level 6 ft. 11 in. to 7 ft. 0 in.



TEXTFIGURE 22

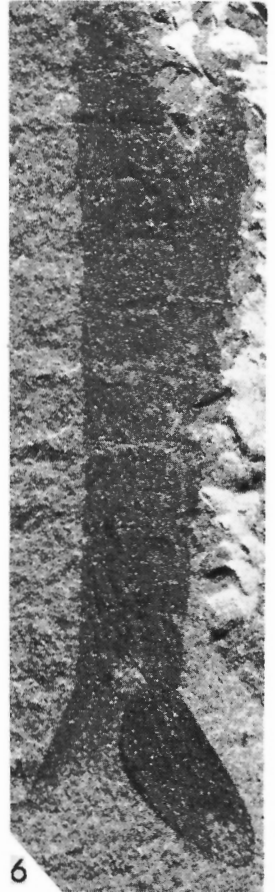
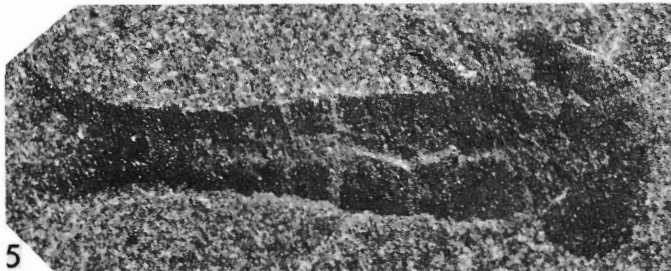
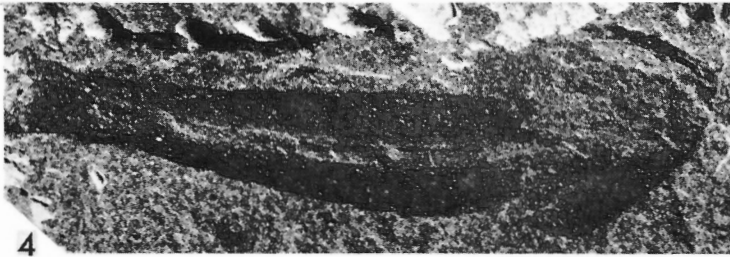
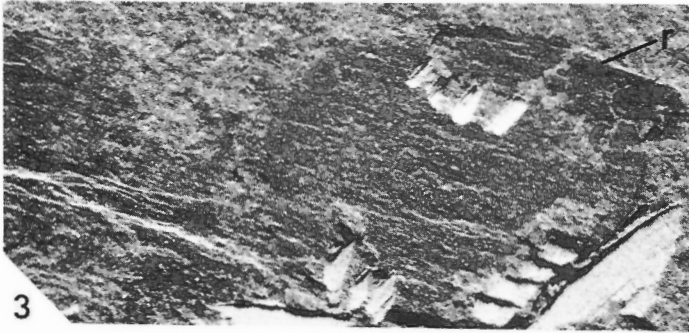
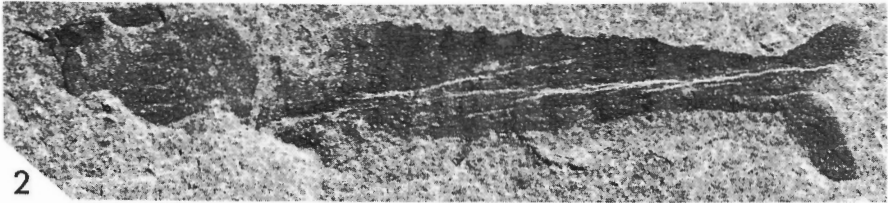
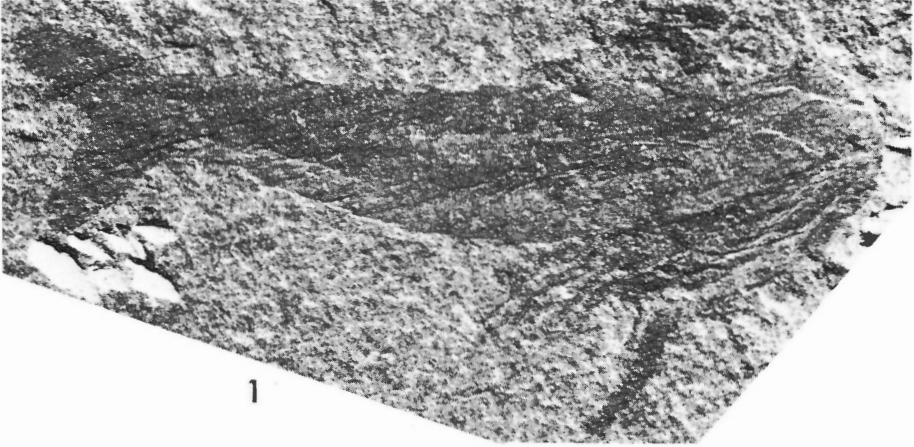
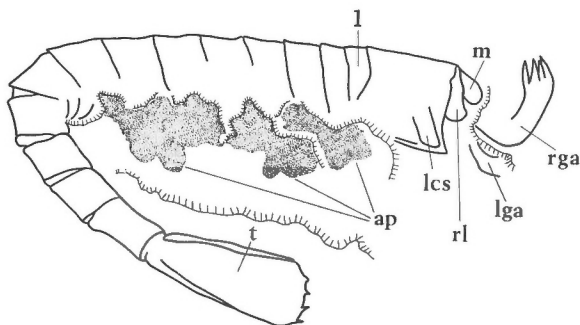


PLATE XI

Yohioia tenuis Walcott, 1912

- Figure 1. USNM 197019, right oblique, internal surface of left side; northwest; x5; see Textfig. 23. Phyllopod bed, Walcott quarry.
- Figure 2. USNM 197020, small individual, oblique, external surface; northeast; x10. Phyllopod bed, Walcott quarry.
- Figure 3. GSC 31134, oblique; reflected; x10; anterior portion showing alimentary canal and branches in cephalic region. Walcott quarry, level 6 ft. 10 in. to 7 ft. 2 in.
- Figure 4. USNM 197021, parallel, inner surface of exoskeleton; northwest; x10; part of great appendage (g) preserved. Phyllopod bed, Walcott quarry.
- Figures 5, 6. GSC 31135, oblique, outer surface of exoskeleton; respectively northeast, reflected; x10; showing median frontal lobe (m) and lateral area (l). Figure 6 shows reflective bands of alimentary canal and branches. Walcott quarry, level 6 ft. 7½ in. to 7 ft. 3½ in.
- Figure 7. USNM 197022, small individual, oblique; northwest; x10; great appendage (g) preserved. Phyllopod bed, Walcott quarry.



TEXTFIGURE 23

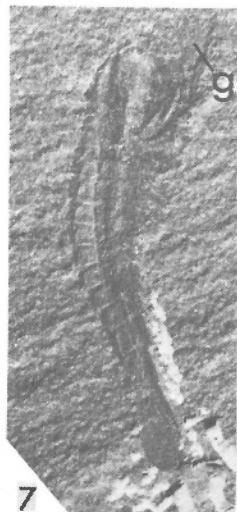
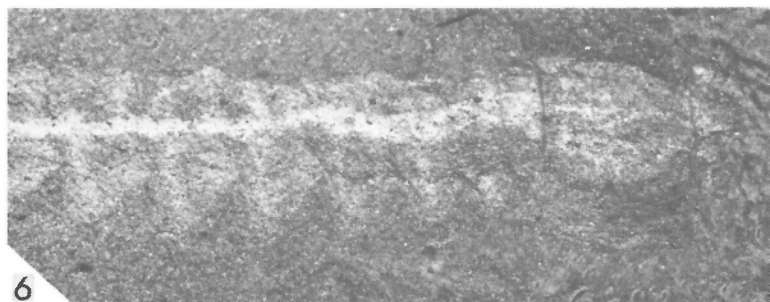
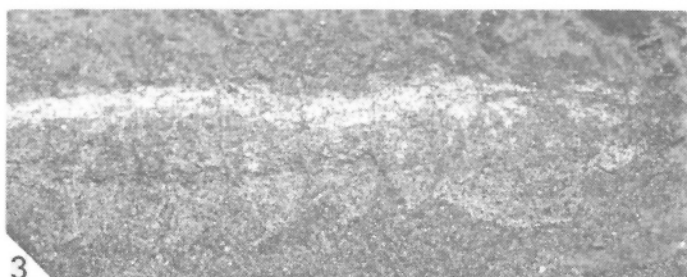
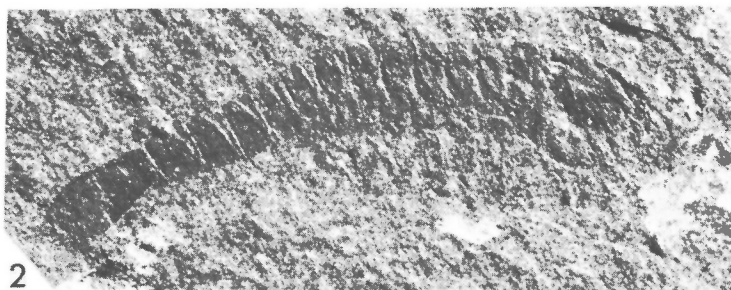
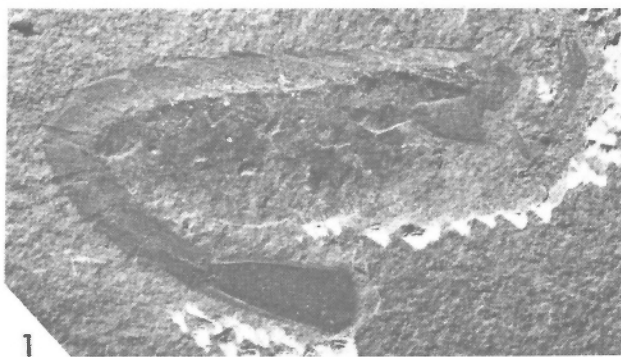
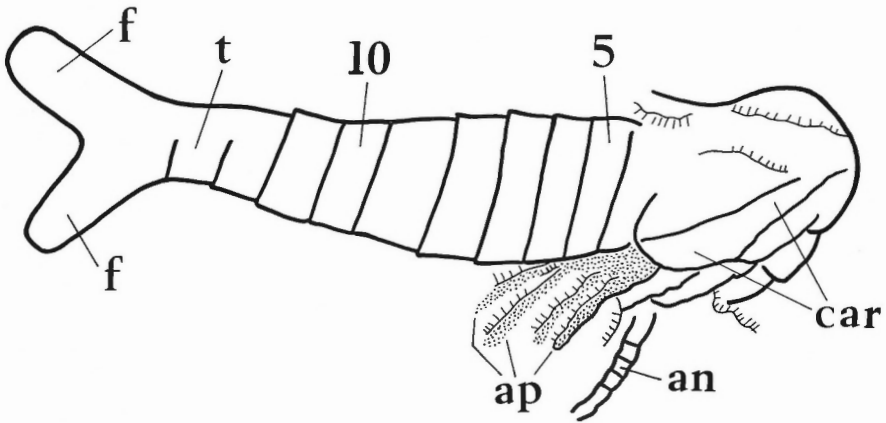


PLATE XII

Plenocaris plena (Walcott, 1912)
Phyllopod bed, Walcott quarry

- Figure 1. USNM 57700, holotype, oblique, northeast, x10; original of Walcott, Fig. 14; see Textfig. 24.
- Figures 2, 3. USNM 182530, lateral, carapace displaced; Fig. 2, southwest, x5; Fig. 3, part of counterpart, north, x10; rostral plate (r) may be preserved.
- Figure 4. USNM 182531, parallel; northeast; x10; showing sediment-filled alimentary canal.
- Figure 5. USNM 182532, oblique; northeast; x10; showing sediment-filled alimentary canal.
- Figure 6. USNM 182533, oblique, south; x10; part of trunk of specimen with carapace missing, showing outline of ramus of furca.



TEXTFIGURE 24

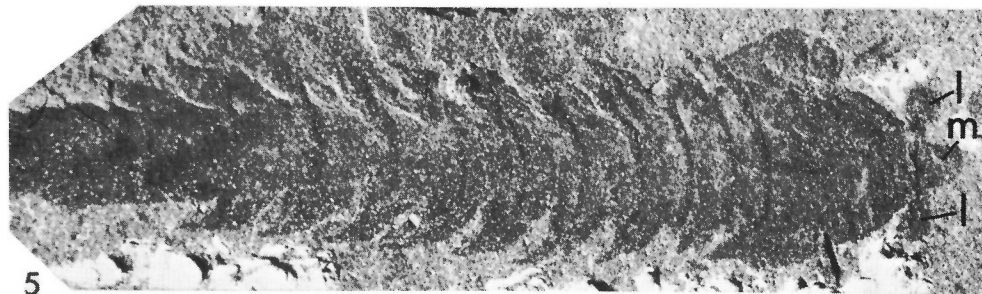
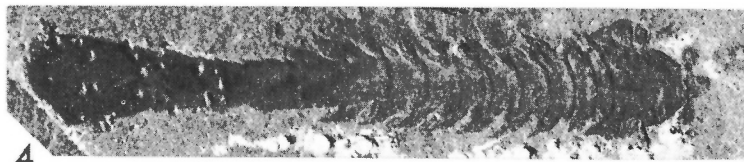
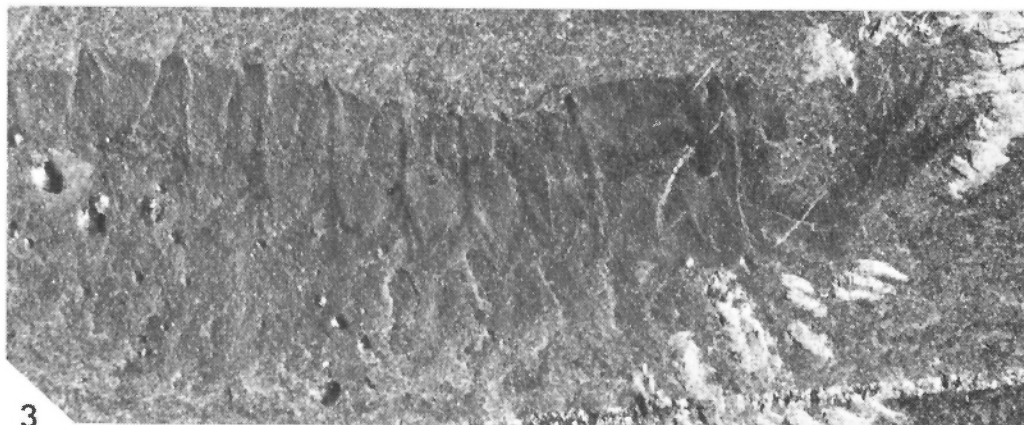
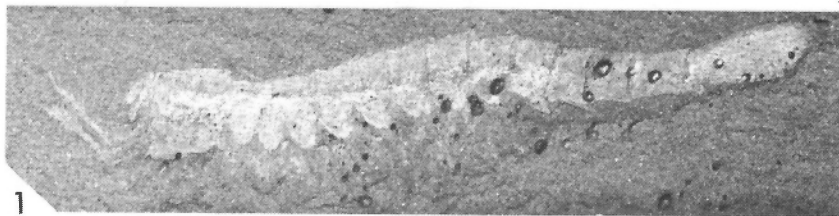
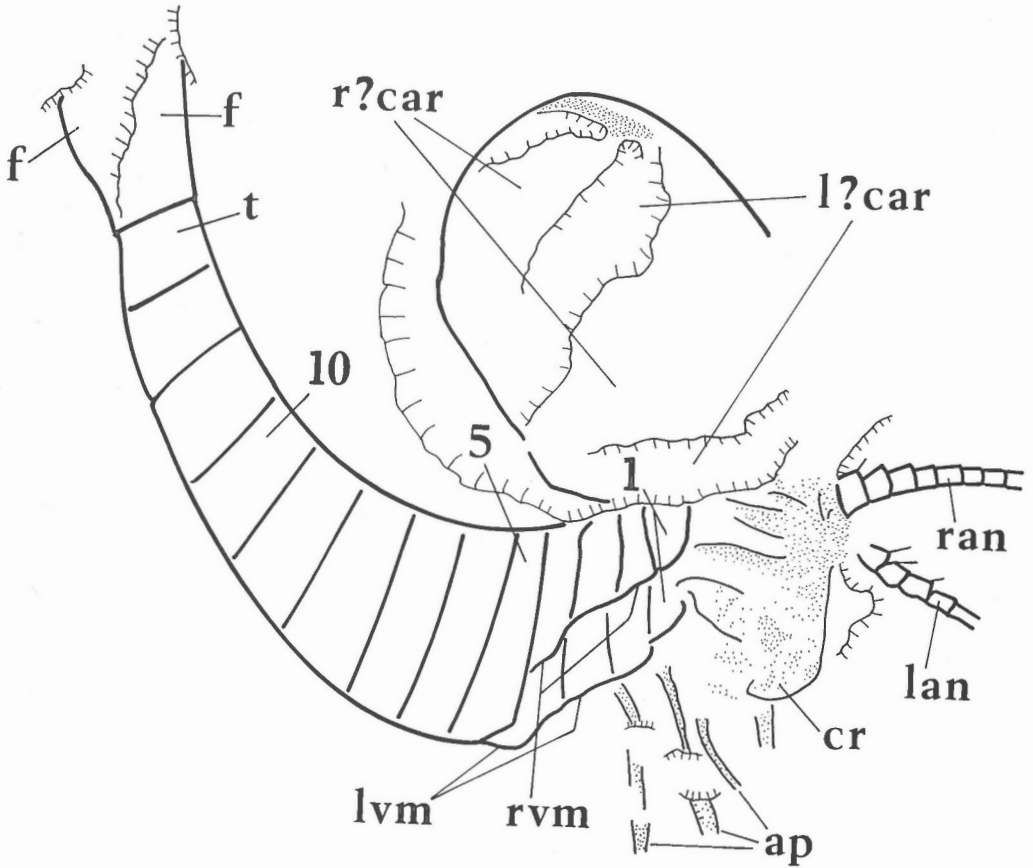


PLATE XIII

Plenocaris plena (Walcott, 1912)

Phyllopod bed, Walcott quarry

Figures 1, 2. USNM 182534, lateral, part and counterpart, carapace displaced; Fig. 1, east, Fig. 2, southwest; x10; see Textfig. 25.



TEXTFIGURE 25



1



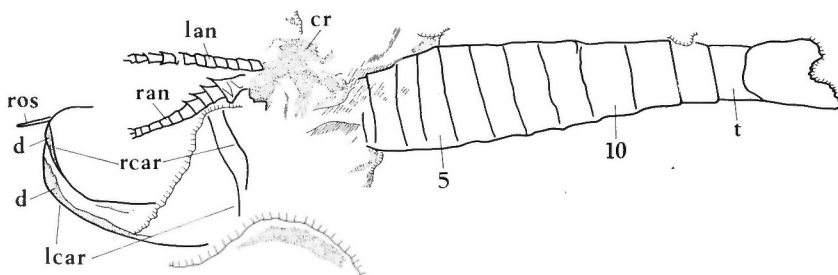
2

PLATE XIV

Plenocaris plena (Walcott, 1912)

Phyllopod bed, Walcott quarry

Figures 1-4. USNM 182535, lateral, part and counterpart, carapace displaced; Figs. 1, 2, east, x5; west, x10; Figs. 3, 4, counterpart, east, x5; northeast, x10; see Textfig. 26; possibly trunk rotated through about 180 degrees relative to cephalic region so that ventral side is upwards in figures.



TEXTFIGURE 26

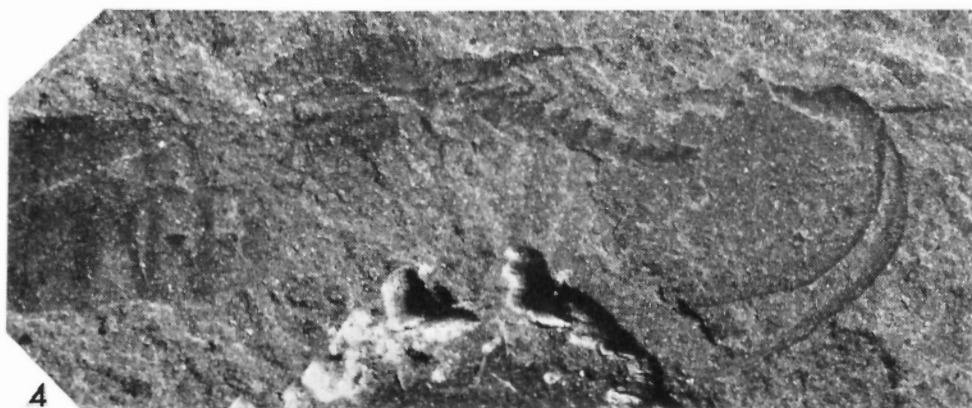
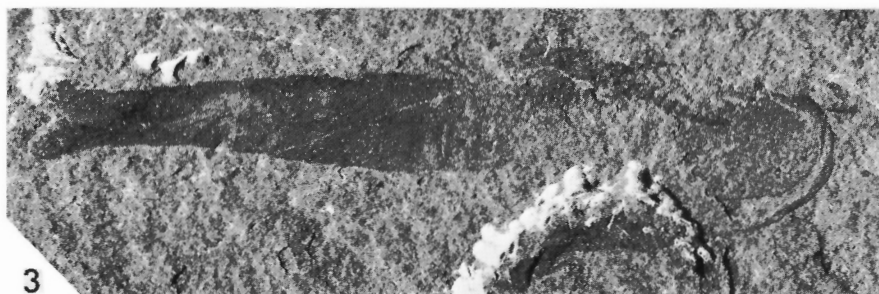
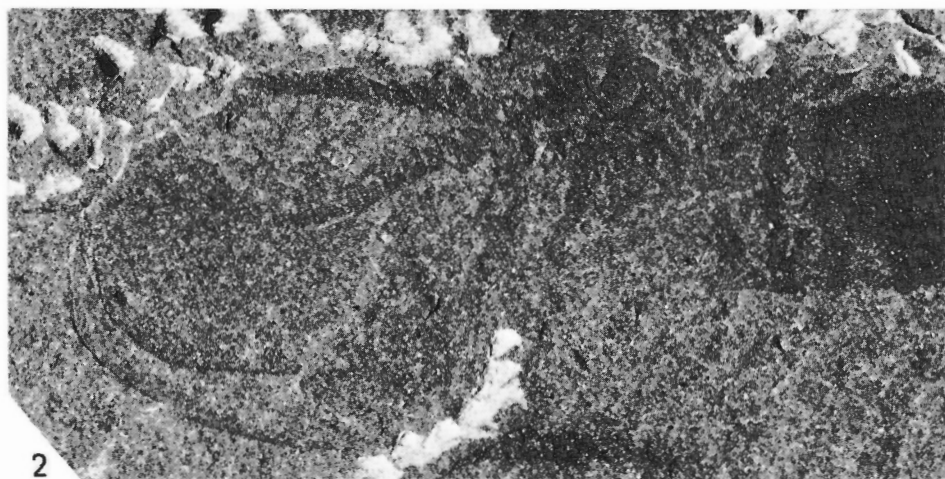
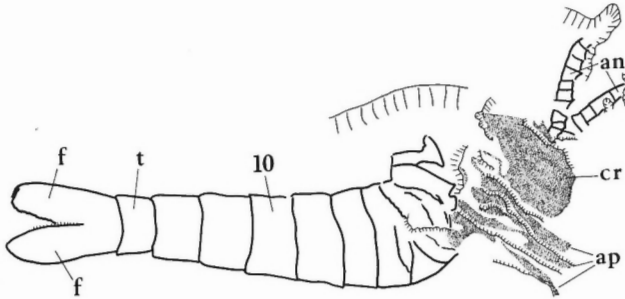


PLATE XV

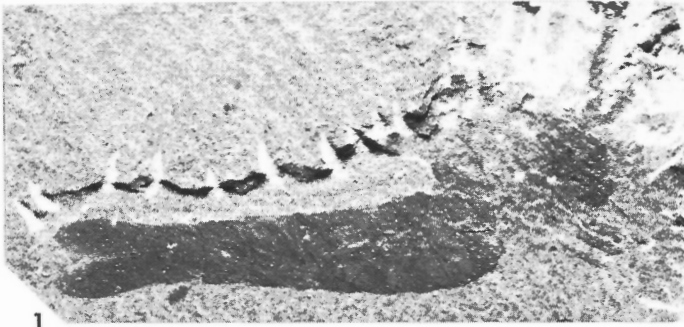
Plenocaris plena (Walcott, 1912)

Phyllopod bed, Walcott quarry

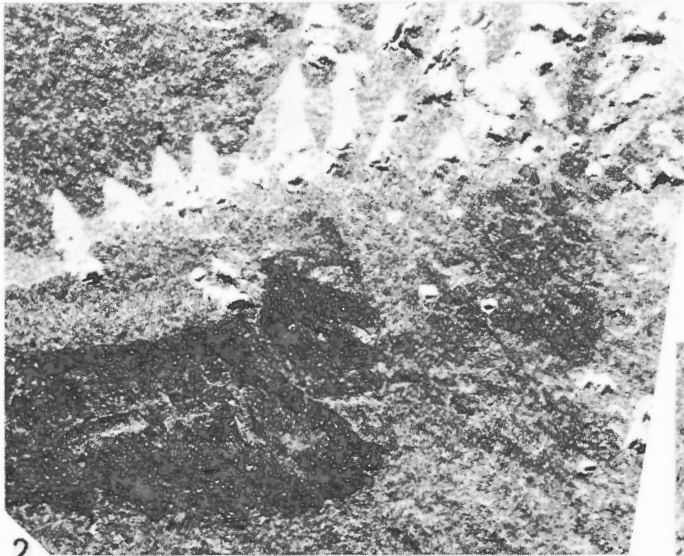
- Figures 1, 2, 4. USNM 182536, oblique, carapace missing; north, x5; south, x10; reflected, x5; see Textfig. 27.
Figure 3. USNM 182537, parallel; north; x10.
Figure 5. USNM 182538, oblique; southwest; x10; rami of furca widely divergent and sloping across bedding.
Figure 6. USNM 182539, parallel; northwest; x10.



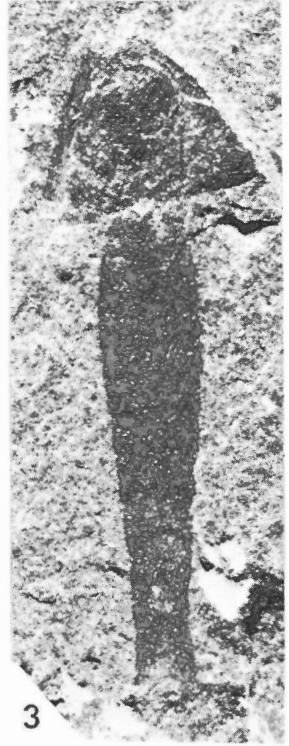
TEXTFIGURE 27



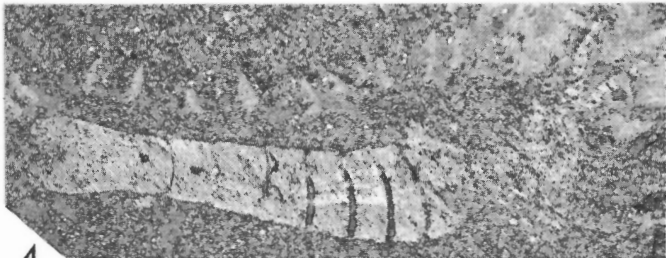
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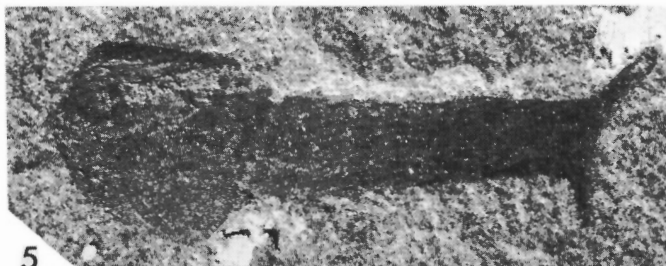
2



3



4



5



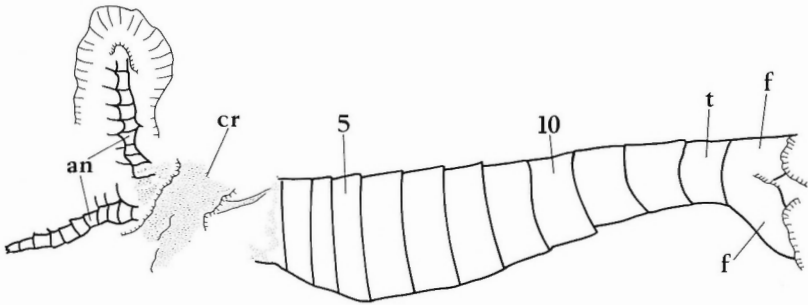
6

PLATE XVI

Plenocaris plena (Walcott, 1912)

Phyllopod bed, Walcott quarry

- Figures 1, 2. USNM 182540, lateral, west, x5; southwest, x10; carapace missing, see Textfig. 28.
Figure 3. USNM 182541, lateral; south; x10; carapace in place.
Figure 4. USNM 182542, oblique; northwest; x10; ap, appendages.
Figure 5. USNM 182543, lateral; northwest; x10; an, antennae; ap, appendages.



TEXTFIGURE 28

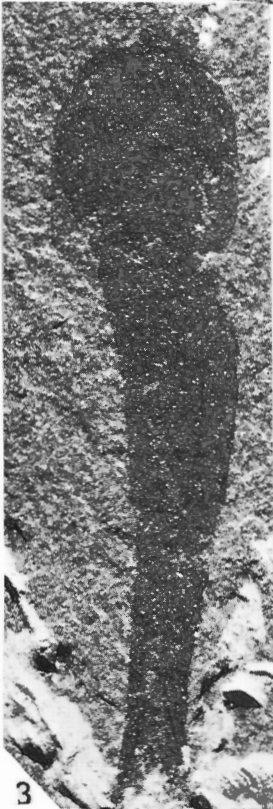
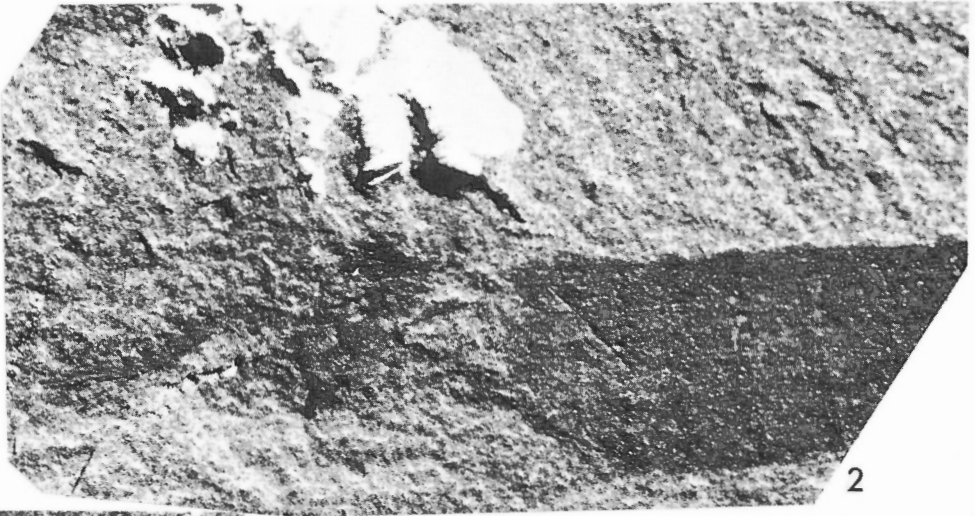
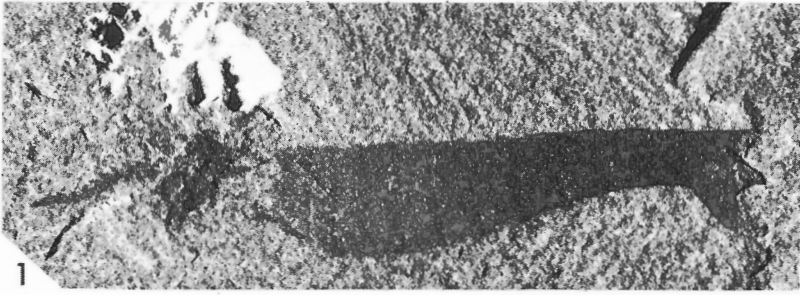


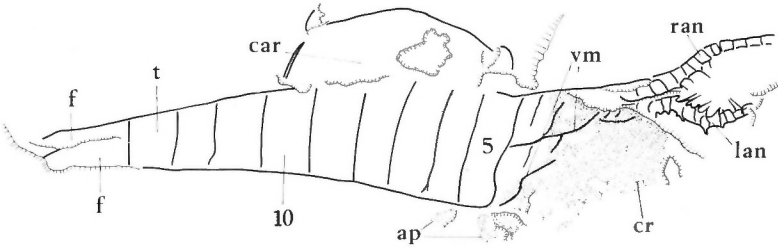
PLATE XVII

Plenocaris plena (Walcott, 1912)
Phyllopod bed, Walcott quarry

Figures 1, 2. USNM 182544, lateral; west, x5; southwest, x10; carapace displaced, *see* Textfig. 29.

Waptia fieldensis Walcott, 1912
Phyllopod bed, Walcott quarry

Figures 3, 4. USNM 182567, Fig. 3, oblique, southeast, x5; Fig. 4, part of specimen, northwest, x10; ex, "exopodites" with lamellae, trunk sharply flexed, rami of furca segmented.



TEXTFIGURE 29

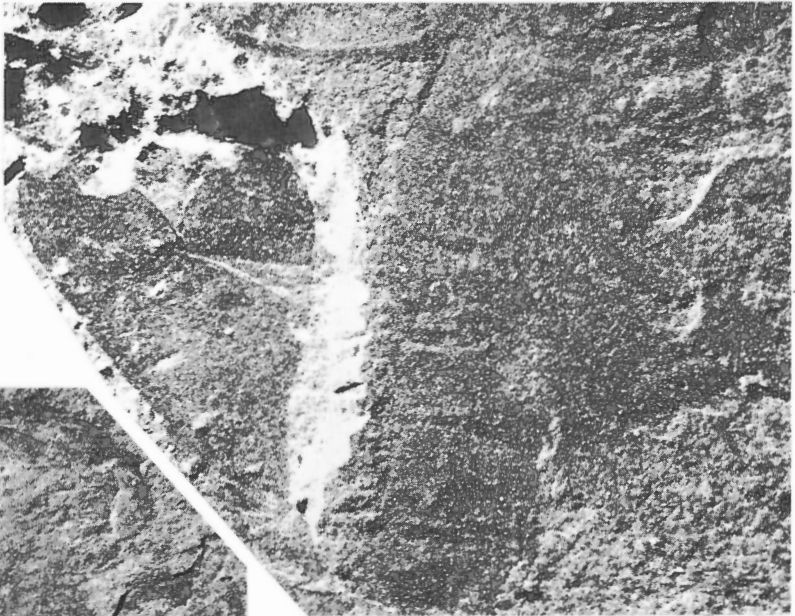
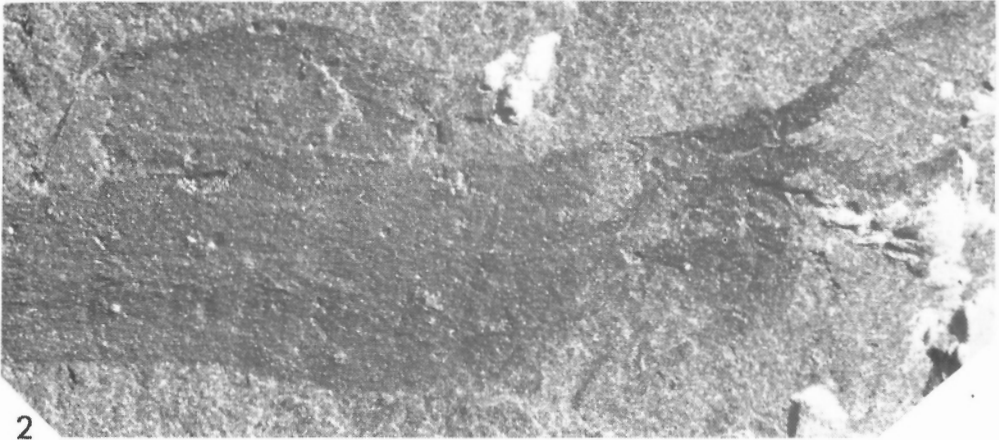
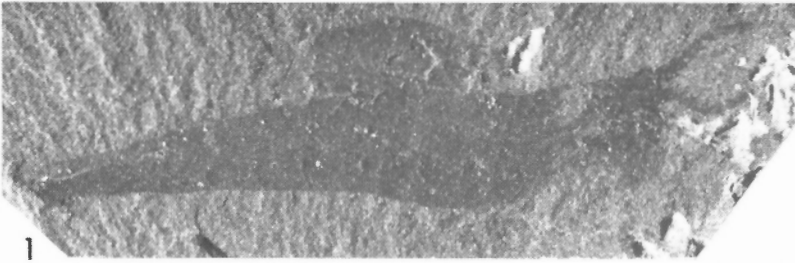


PLATE XVIII

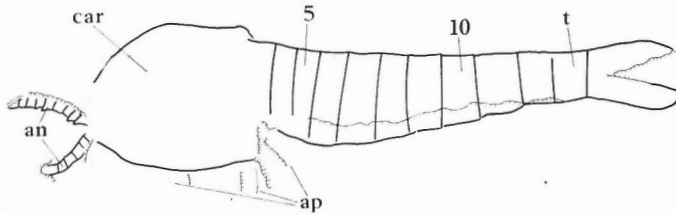
Waptia fieldensis Walcott, 1912
Phyllopod bed, Walcott quarry

Figures 1, 5. USNM 165229, oblique; west, x5; south, x10; showing "exopodites" on right side, somites of trunk and segmentation of rami of furca.

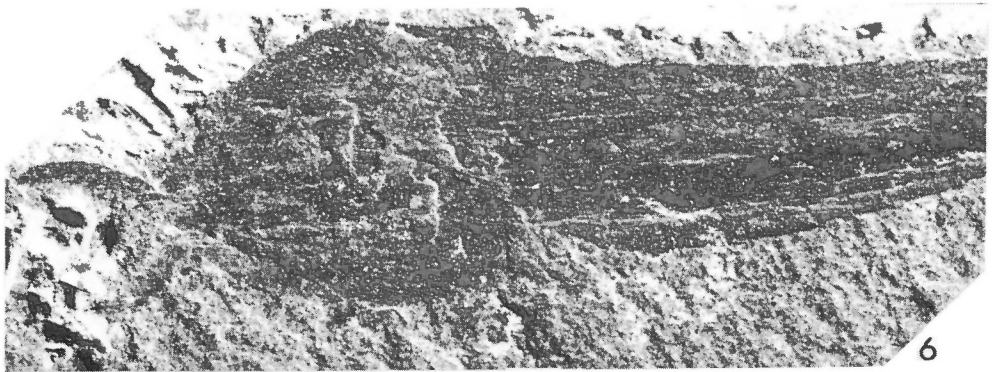
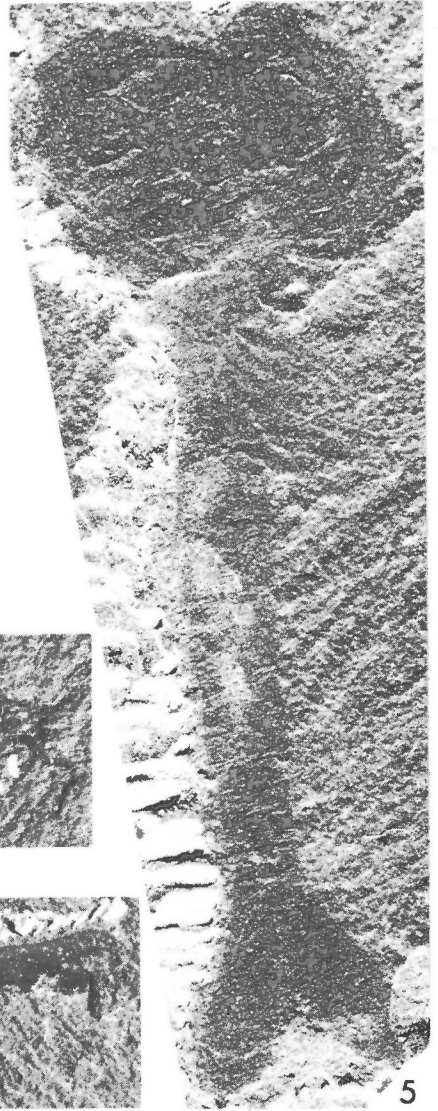
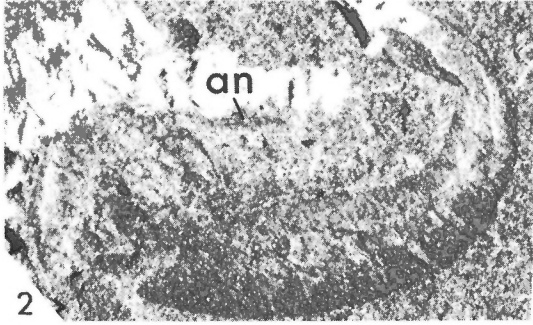
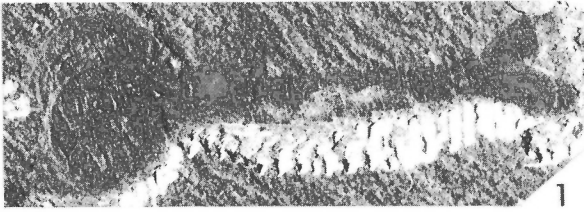
Plenocaris plena (Walcott, 1912)
Phyllopod bed, Walcott quarry

Figure 2. USNM 182545, oblique; northeast; x5; an, antenna, trunk flexed through ca. 130 degrees.

Figures 3, 4, 6. USNM 182546, lateral, part and counterpart; Figs. 4, 6, west, x5; southwest, x10; Fig. 3, counterpart, northwest, x5; see Textfig. 30.



TEXTFIGURE 30



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Geological Survey of Canada

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Some recent titles are listed below (Information Canada No. in brackets):

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- 201 Archaeocyatha from the Mackenzie and Cassiar Mountains, Northwest Territories, Yukon Territory and British Columbia, *by* R. C. Handfield, \$2.00 (M42-201)
- 202 Faunas of the Ordovician Red River Formation, Manitoba, *by* D. C. McGregor, *et al.*, \$2.00 (M42-202)
- 203 Geology of lower Paleozoic formations, Hazen Plateau and southern Grant Land Mountains, Ellesmere Island, Arctic Archipelago, *by* H. P. Trettin, \$3.00 (M42-203)
- 204 Brachiopods of the Detroit River Group (Devonian) from southwestern Ontario and adjacent areas of Michigan and Ohio, *by* J. A. Fagerstrom, \$2.00 (M42-204)
- 205 Comparative study of the Castle River and other folds in the Eastern Cordillera of Canada, *by* D. K. Norris, \$2.00 (M42-205)
- 206 Geomorphology and multiple glaciation in the Banff area, *by* N. W. Rutter, \$2.00 (M42-206)
- 207 Geology of the resurgent cryptoexplosion crater at Mistastin Lake, Labrador, *by* K. L. Currie, \$2.00 (M42-207)
- 208 The geology and origin of the Faro, Vangorda and Swim concordant zinc-lead deposits, Central Yukon Territory, *by* D. J. Tempelman-Kluit, \$3.00 (M42-208)
- 209 Redescription of *Marrella splendens* (Trilobitoidea) from the Burgess Shale, Middle Cambrian, British Columbia, *by* H. B. Whittington, \$3.00 (M42-209)
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- 212 Lower Cambrian trilobites from the Sekwi Formation type section, Mackenzie Mountains, Northwestern Canada, *by* W. H. Fritz, \$4.00 (M42-212)
- 214 Classification and descriptions of copper deposits, Coppermine River area, District of Mackenzie, *by* E. D. Kindle, \$4.00 (M42-214)
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