Redescription of *Burgessia bella* from the Middle Cambrian Burgess Shale, British Columbia

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Hughes, C.P. 1975 07 15: Redescription of *Burgessia bella* from the Middle Cambrian Burgess Shale, British Columbia. *Fossils and Strata,* No. 4, pp. 415–435, Pls 1– 13, Oslo. ISSN 0300–9491. ISBN 82-00-04963-9.

Previously studied specimens and additional material of *Burgessia bella* from old and new collections have been prepared, and new photographs accompanied by explanatory line drawings are given together with reconstructions in various aspects. The carapace is roughly circular, invaginated posteriorly, and extends back above the trunk leaving only the long unsegmented posterior spine uncovered. The carapace is gently convex sagitally and transversely. No cephalic doublure or ventral plates are present. The body is segmented and appears to have been subcircular in cross-section, with no pleurae. The mouth is ventral. Four appendage-bearing somites lie within the cephalon and the remaining eight in the trunk. A large kidney-shaped gut-caecal system occupies the lateral portion of the carapace, being connected by a wide diverticulum to the alimentary canal at the posterior cephalic somite. The so-called eyes are reinterpreted as attachment areas for muscles connecting the anterior end of the body to the carapace. The anterior cephalic appendages consist of a pair of multijointed uniramous antenna, the second, third and fourth are biramous, consisting of a jointed walking-leg and a whip-like flagellum. All the trunk appendages, except the last, are biramous and consist of a coxa with telopod composed of six segments and terminal claws, and a small lateral, leaf-like gill branch presumed to be attached to the coxa. The posterior appendage is believed uniramous consisting simply of a backwardly curved spike. The telson consists of an anal segment lacking lateral appendages, and a long, tapering unsegmented caudal spine jointed at the base to the anal segment. Dark stains are occasionally associated with specimens and are presumed to represent organic matter squeezed out of the body during compaction. The carapace ranges from four to seventeen mm in maximum width, the size-frequency histogram being unimodal except that the smallest three specimens are somewhat detached. The occurrence within the Phyllopod bed closely matches that of *Waptia, Marrella,* and *Yohoia.*

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A re-investigation of the stratigraphy, palaeontology and palaeoecology of the Burgess Shale was begun in 1966 by the Geological Survey of Canada, with the kind cooperation of the authorities of the Yoho National Park and the Department of Indian and Northern Affairs. Ottawa. Field work was undertaken in 1966 and 1967 (Aitken, Fritz & Whittington 1967, Aitken & Fritz 1968). The author was kindly invited to join the palaeontological investigation by Whittington in 1967. The paper, one of a series devoted to the systematic redescription of the fauna and flora of the Burgess Shale, is concerned with the third most common non-trilobite arthropod, *Burgessia bella.* Although abundant, this species has attracted less attention since Walcott's original descriptions (Walcott 1912, 1931) than some other species, Simonetta (1970) being the only author to give a redescription based on a reappraisal of the original collections. As in the restudy of other forms (Bruton in preparation, Whittington 1971b, 1974, 1975) preparation of previously described specimens together with detailed study of much additional material has revealed new information. Also it is shown that specimens do not lie precisely parallel to the bedding surface, but that different parts of an individual lie at slightly different levels within the rock.

The photographs used herein have been taken using ultraviolet radiation both at high and low incident angles (Whittington 1971b: 1, 2). All previously figured material is refigured, many with accompanying explanatory camera lucida drawings. Since the drawings were made using

a variety of lighting conditions, in some instances they show details not at all clear on particular photographs – any doubts of interpretation may thus only be resolved by examination of the relevant specimen.

Throughout this work I have been greatly aided by discussions with Professor H.B. Whittington and Dr. D.L. Bruton, who together with Drs. W.T. Dean and W.H. Fritz have critically read the manuscript. I am also indebted to Dr. S.M. Manton, F.R.S., for much useful discussion, particularly concerning the function of the appendages. Drs. Porter M. Kier and Richard E. Grant, United States National Museum (USNM), gave every facility for study of the Walcott collections. The figures were prepared by Mr. John Lewis and photographs enlarged by Mr. David Bursill. To all these persons I give my thanks. I am also particularly grateful to the organisers and sponsors of the NATO advanced study institute held in Oslo in July 1973 for the invitation to present the results of this study. Financial support for this study was provided by Natural Environment Research Council grant GR3/285 awarded to H.B. Whittington.

Preservation

Whittington (1971a: 1180 – 1189) has discussed the general nature of the preservation of the Burgess Shale fossils, with specific reference to *Marrella* (see also Whittington 1971b: 19 – 20), and Piper (1972) has postulated a sedimentary model for the deposition of the Burgess Shale. Both the palaeontological and sedimentological evidence suggest that preservation was due to the live entombment in a moving cloud of sediment, presumably in the terminal regions of a turbidity flow, where current velocity and turbulence would be relatively low. The preservation of *Burgessia* supports this, in that, like all other forms so far restudied, the specimens are preserved as a thin, dark apparently carbonaceous film, with individual specimens being preserved at all angles to the bedding plane (Pl. 1: 1, 4, 9), although when the specimen is preserved very obliquely to the bedding, problems of identification arise (Pl. 13: 1). Many specimens are twisted to some extent, and in particular the carapace is commonly pulled forward from over the trunk (Pl. 3: 8, Pl. 4: 1) and in extreme cases nearly pulled completely free of the remainder of the animal (Pl. 7: 1, 2), this presumably reflects the effects of transportation for at least a short distance within the entombing sediment cloud.

Compaction has been considerable, and one effect has been to rotate the walking-legs so that the anterior-posterior surfaces lie parallel to the bedding (this has also been demonstrated in *Olenoides* (Whittington 1975) and is almost certainly the case in other forms). The gill branches, however, appear to have retained their approximate life-attitude in specimens preserved approximately parallel to the bedding, which is to be expected. Gill branches have not been identified in obliquely preserved specimens where they may have been rotated, or possibly more likely crumpled due to their fragile nature.

Virtually no decomposition of the specimens has taken place and the ventral cuticle appears to have been intact during transportation and compaction since in not one specimen are the appendages displaced relative to the body or each other.

In his redescription of *Yohoia,* Whittington (1974) has shown that the preservation of *Yohoia*, and by inference, that of many other Burgess Shale fossils, is such that part and counterpart specimens are not directly comparable with those of more common types of preservation, which might, for example, show the outer surface of the exoskeleton and a mould of the outer surface, or if the shell has been dissolved away, moulds of the internal and external surfaces. Rather he showed that in *Yohoia* the split has occurred within the exoskeleton and not along either the inner or outer surface. The situation is further complicated by the fact that the surface along which the rock splits jumps from one level to another on which different portions of the specimen are preserved. Though it is more difficult to be certain that this is the case in *Burgessia* since the carapace is smooth, there is no reason to suspect that it is any different. The full nature and significance of this type of preservation is not fully understood at present. Since it is impossible to say in a particular specimen whether one is seeing the inside, outside, or some internal surface of the exoskeleton, counterpart specimens preserved in lateral or oblique views are simply referred to as lateral or oblique; the prefixes left and right or dorsal and ventral are not used. In parallel preserved specimens, if the carapace is nearer the exposed surface than the appendages, then the specimen is referred to as being a dorsal view, whereas if the reverse is the case, then it is referred to as a ventral view. Since in oblique preservation the carapace becomes wrinkled, the terms forward and backward as applied to *Marrella* by Whittington are not employed.

Terminology

As advocated by Whittington (1971b) descriptive terms such as 'walking-leg' and 'gill branch' have been used in preference to terms such as 'exopodite' and 'endopodite', since they have the advantage of not being the same as applied in either the trilobite or crustacean literature, and so carry no implication of possible phylogenetic relations. However, there are certain terms used in arthropod studies that can be usefully employed, and in general such terms are used as defined by Moore & McCormick (*in* Moore 1969: 90 – 103), e.g. 'segment' for an individual component of a limb, connected by a movable 'joint' with the adjoining segment. A few terms (see below) are not used strictly acccording to their definitions, either because they are defined in terms of specifically modern arthropod morphological terms, or because sufficient details of morphology are not known in *Burgessia.* A few terms are used in a restricted sense. Terms relating to the gut-caecal system are based on those of Öpik (1961). Terms relating to the attitude of the specimens within the rock have been discussed above (*Preservation*).

Antennae: Anterior pair of uniramous, multisegmented appendages.

Carapace: This term is restricted to the dorsal, slightly sclerotized surface of cephalic cuticle. The unsclerotized cuticle forming the underside of the fold of cephalic exoskeleton is not included.

Endite: Ventrally positioned lobe of coxa or of any walking-leg segment.

Flagellum: Slender, outer branch of post-antennal cephalic appendage. Not known whether it is multisegmented.

Explanation of symbols on Plates and Figures.

a = antenna
ad = anterior diverticulum
al = anterior lobe of gut
al c = alimentary canal
an = anus
ap = appendage (branch not specified); suffix denotes somite number following antenna
c = caecum
ca = carapace
cl = claws
cn = caecal node
co = coxa
coe = coxal endite
d = diverticulum
ds = dark stain
e = endite
fl = flagellum
g = gill branch, suffix denotes trunk somite number
hj = hinge joint
j = joint
icn = intercaecal node
l = prefix indicating left side
m = mouth
ma = muscle attachment area
mc = margin of unsclerotized cuticle
ms = muscle strands
ob = outer branch of cephalic appendages, suffix denotes somite number following antenna
pd = posterior diverticulum
pj = pivot joint
r = prefix indicating right side
s = segment
se = seta
t = telson
w = walking-leg, suffix denotes somite number following antenna
1–11 = suffixes denoting the number of the appendage numbering from the first post-antennal biramous appendage, except for the gill branches which are numbered from the first trunk somite.

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

GENUS *BURGESSIA* WALCOTT, 1912

SYSTEMATIC ATTRIBUTION. – Family Burgessiidae Walcott, 1912. [*nom. corr.* Størmer 1959 (*ex* Burgessidae Walcott, 1912)].

TYPE SPECIES. – *Burgessia bella* Walcott, 1912 by original designation.

DIAGNOSIS. – Subcircular carapace extending back over trunk with wide invagination posteriorly, no compound eye, no well-developed sclerotized labrum. One pair of antennae with twenty to thirty segments, three post-antennal biramous cephalic appendages with inner branch a walking-leg, outer branch a flagellum. Trunk of eight segments without pleurae, each, except the last, with a pair of biramous appendages, inner branch a walking-leg, outer branch a gill-branch, eighth somite with short uniramous appendages. Telson of anal segment, without lateral appendages, and long unsegmented, single, caudal spine. Large gut-caecal system fills most of carapace, connected to alimentary canal at posterior cephalic somite by a large diverticulum.

GEOLOGICAL HORIZON. – Middle Cambrian, Stephen Formation, Burgess Shale section, *Bathyuriscus – Elrathina* Zone, British Columbia.

BURGESSIA BELLA WALCOTT, 1912

Plates 1 – 13, Figs. 1 – 35

SYNONYMY. – □ 1912 Walcott: 177–180, Pl. 27: 1–3; Pl. 30: 3. (*non* Pl. 30: 4 which is *Waptia fieldensis*). □ 1920 Raymond: 108–109. □ 1925 Fedotov: 385, 386, 389. □ 1928 Henriksen: 11–13. □ 1930 Beurlen: 501. □ 1931 Walcott: 15–20, Figs. 3–5, Pl. 15: 4–7; Pl. 16; Pl. 17; Pl. 18: 1. □ 1932 Richter: 855, 866, Fig. 44B. □ 1939 Størmer: 232, 236, 237, Fig. 30c. □ 1944 Størmer: 98, 99, Figs. 19, 1–4, 25. □ 1949 Størmer *in* Grassé: 204, Fig. 30. □ 1958 Tiegs & Manton: 291–293, 313, 316, Fig. 6C. □ 1959 Størmer *in* Moore: O32, Fig. 21, 1–5. □ 1970 Simonetta: 41, 42, Pl. 28: 1–3, 5–10; Pl. 29; Pl. 30: 1–3; Pl. 32: 1–4.

LECTOTYPE. – USNM 57676, Pl. 1: 2, 3, 8, Figs. 11, 12; original of Walcott 1912, Pl. 27: 1, designated herein. Also figured Richter 1932, Fig. 44B; Simonetta 1970, Pl. 28: 1.

OTHER MATERIAL. – USNM 57677 – 57678, 57680 (erroneously recorded as USNM 57679 by Walcott 1912, explanation Pl. 30: 3), originals of Walcott 1912, Pl. 27: 2, 3; Pl. 30: 3, and Simonetta 1970, Pl. 28: 2, 5, 3 respectively: USNM 83947 a–o, originals of Walcott 1931, Pl. 15: 4–7; Pl. 16: 1–6; Pl. 17: 1–4; Pl. 18: 1: USNM 83947h is also original of Størmer *in* Grassé 1949, Fig. 30: USNM 114243, 155623, 155624, 155626, 155630, 155632, 155661, 155665, 155667, 155669, 155676, 155680 (erroneously recorded as USNM 155678 by Simonetta 1970, explanation Pl. 28: 6), originals of Simonetta 1970, Pl. 28: 10; Pl. 30: 1, 3; Pl. 28: 9; Pl. 32: 1; Pl. 28: 8; Pl. 30: 2 (erroneously recorded as USNM 155661 by Simonetta 1970, explanation Pl. 30: 2, counterpart specimens are numbered 114240 and 155678 in USNM collections); Pl. 32: 4 (erroneously recorded as Fig. 7 by Simonetta 1970, explanation Pl. 32), 2; Pl. 28: 7; Pl. 32: 3; Pl. 28: 6 respectively. USNM 155625, 155627–155629, 155631, 155633, 155634, 155664, 155666, 155668,155670–155675, 155677, 155679, studied but not figured by Simonetta. Major additional collections in USNM and GSC, both including material figured and measured herein. Fifty-four additional specimens collected by P.E. Raymond are present in the Museum of Comparative Zoology, Harvard University (Rolfe 1962: 6).

LOCALITY, STRATIGRAPHICAL HORIZON, NUMBERS OF SPECIMENS, SIZE. – Middle Cambrian, Stephen Formation, Burgess Shale section, *Pagetia bootes* faunule of *Bathyuriscus – Elrathina* Zone, situated on the ridge between Wapta Mountain and Mount Field at an elevation of approximately 2,300 m (7,500 ft), longitude 116°28'30", latitude 51°26'50", 4.8 km (3 miles) north of Field, southern British Columbia (see Fritz (1971) for geology and stratigraphy and Piper (1972) for a description of the sediments).

Burgessia bella occurs only in the lower half of that part of the Burgess Shale referred to as the 'Phyllopod bed' by Walcott (1912). The base of this bed 2.3 m (7'7") thick corresponds

approximately with the 5 ft level on the scale used to record levels at which fossils were obtained in 1966 and 1967 (see Whittington 1971a, Fig. 3). Fig. 1 shows the numbers of specimens collected from the various levels in the 1966 and 1967 collections. In both collections the bulk of specimens come from around the 7 ft level, 21 specimens from an 8 inch band (6'7½" to 7'3½") in 1966 (84% of total in collection) and 21 from a 6 inch band (6'10" to 7'4") in 1967 (60% of total in collection from the main quarry). There are about 1800 specimens in the U.S. National Museum, although this figure almost certainly includes some unidentified counterparts. All specimens collected by Walcott are labelled '35k', i.e. the 'Phyllopod bed' in the Walcott quarry, but there is no indication from which particular layer individual specimens came. Fig. 1, however, suggests that there are relatively few layers in the 'Phyllopod bed' in which *Burgessia* occurs, and comparison with Whittington (1971a, fig. 5) indicates that these may well correspond to the main *Marrella*-bearing levels. From the new collections it is known that *Marrella* occurs in the same bedding surface as *Burgessia* as do the following genera: *Canadia, Elrathina, Ottoia, Ptychagnostus, Scenella, Selkirkia, Waptia* and *Yohoia.* Walcott (1912: 152–153) also recorded *Amiskwia, Miskoia, Molaria, Mollisonia, Naraoia, Opabinia, Pikaia, Wiwaxia* and *Yohoia (= Plenocaris) plena* with *Burgessia* from his bed 12 (only 1½" thick) at the base of the phyllopod bed.

Measurements of maximum carapace width were made to the nearest 0.5 mm on 154 specimens in which the carapace was preserved more or less symmetrically. The width ranged from 4.0 to 16.5 mm (Fig. 2), though no specimen less than 7.0 mm wide was observed showing more than the outline of the carapace and digestive system. This range is in good accord with Walcott's (1931:17) figures for length, excluding the caudal spine, and those of Simonetta (1970:41). Width measurements were used since this allowed a greater number of specimens to be measured. The smallest identified specimen (Pl. 9: 1) is of the order of 3 mm wide. The significance of the gap in the size-frequency curve between 4.5 and 7.0 mm is uncertain. Its presence might invite the interpretation that the small individuals represent an early instar. The fact that no

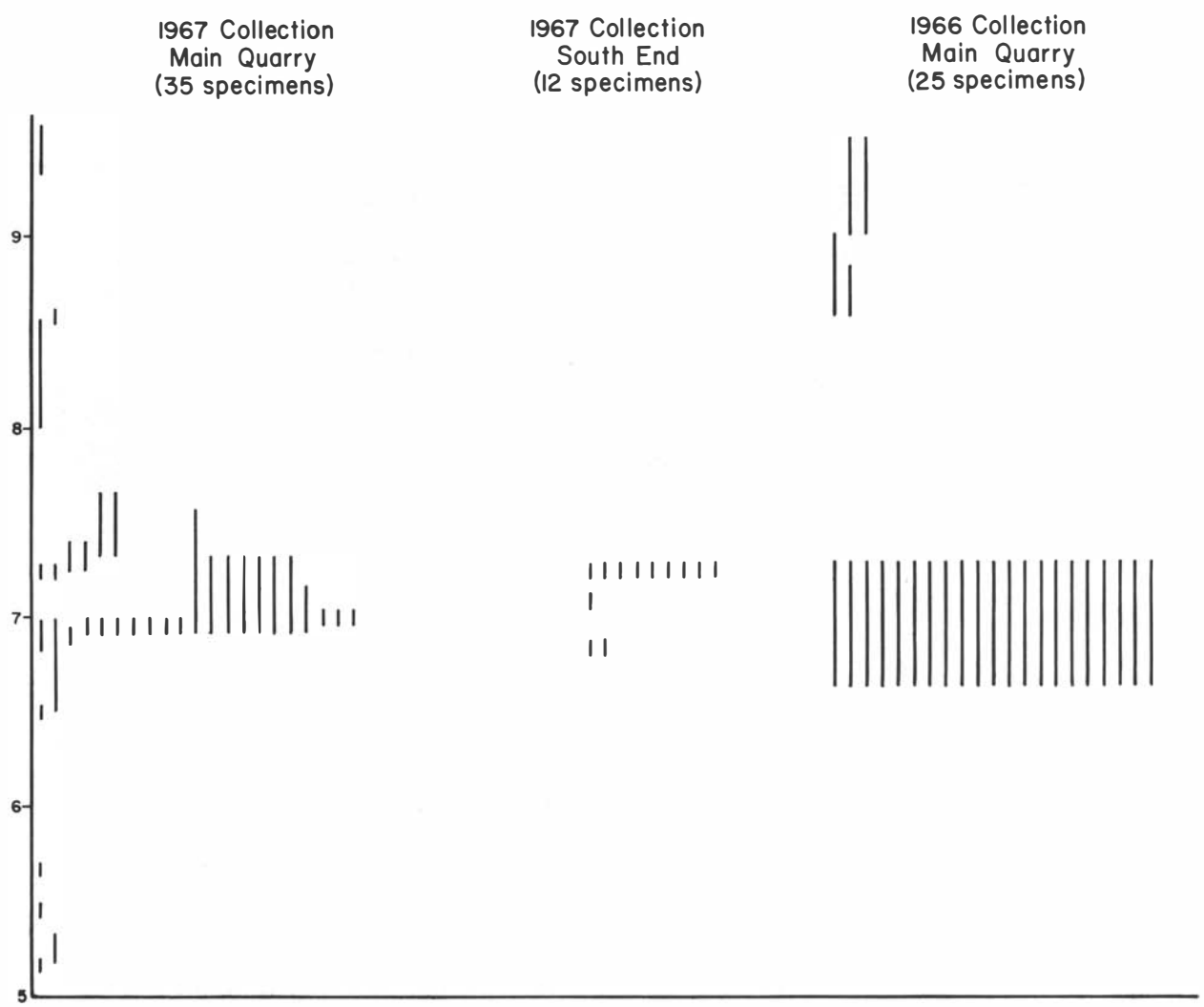

Fig. 1. Distribution within the Phyllopod bed of *Burgessia bella* from the 1966 and 1967 Geological Survey of Canada collections. Each line represents one specimen.

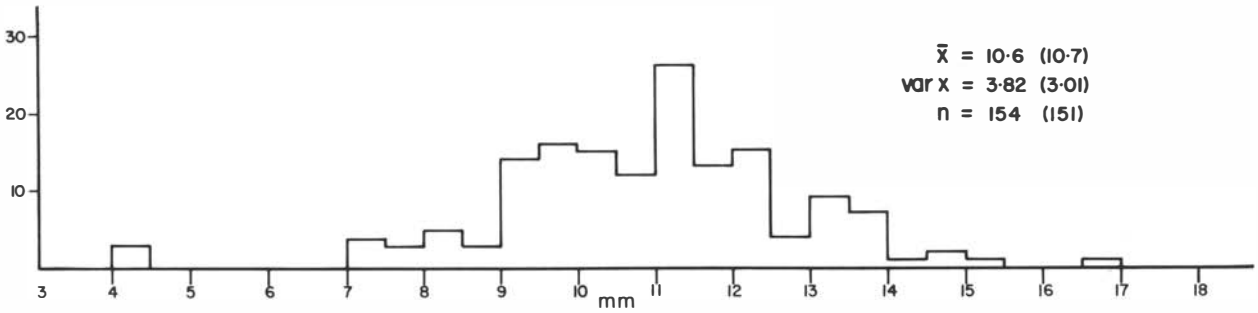

Fig. 2. Size-frequency histogram for 154 specimens of *Burgessia bella*. Size measured as the maximum carapace width. Summary statistics in brackets based on the sample less the three smallest specimens.

trace of appendages or caudal spine has been seen in these small specimens might even suggest that they represent a late larval stage, though the absence of such details in so tiny and fragile specimens could easily be attributed to the preservation, and in fact some larger specimens show little else other than the carapace. The details of the carapace, body and digestive system are, as far as can be determined, the same as in larger specimens. Specimens in the collections made in 1966 and 1967 are not sufficiently abundant to investigate the changes in size-frequency distributions in different levels in the succession as in *Marrella splendens* (Whittington 1971a: 1193–1196).

DETAILED DESCRIPTION

Carapace

The carapace is subcircular, elongate sagittally with a wide relatively large posterior invagination. Although entirely flattened in the majority of specimens, a few obliquely and laterally preserved specimens give some indication of an original convexity (Pl. 1: 9, 10, Pl. 6: 3, 4), the transverse convexity being by far the greater. Many laterally compressed specimens show how easily the carapace could become wrinkled and distorted (Pl. 3: 4, 8, Pl. 4: 1, Pl. 6: 2), this, coupled with the fact that the details of the underlying digestive organs are clearly seen, suggests that the carapace was extremely thin and only weakly sclerotized. Most laterally compressed specimens indicate that many of the somites are free, since the carapace is clearly above and separate from them (Pl. 1: 4–7, 9, 10, Pl. 4: 1, 3). It is inconceivable that the diverticulum (see *Digestive system*) of the fourth appendage-bearing somite should be unenclosed like 'aircraft wing struts', and this, together with the specialisation of the anterior four pairs of appendages (see *Antenna* and *Post-antennal cephalic appendages*) is believed to be strong grounds for considering these anterior somites to form the cephalic region and the dorsal cuticle to form a true carapace extending back over the trunk as a fold of the cephalic cuticle.

Unsclerotized cuticle

Very little is seen of this, the only direct evidence being seen in specimens such as USNM 83947c (Pl. 2: 3) and USNM 83947m (Pl. 5: 4). When these are viewed in high angle illumination they show a silvery line 'cutting-off' a small region of the carapace (mc on Fig. 15). This has in the past been interpreted as the anterior margin of a labrum (Walcott 1931: 17; Pl. 15: 6; Pl. 17: 3). However, since such lines may be present in other quadrants of the carapace (Pl. 9: 3, Pl. 10: 7, where it is present around about two-thirds of the margin), this interpretation is believed to be in error (see also *Labrum*). This silvery line is here thought to be the outer edge of the unsclerotized cuticle forming the underside of the carapace, where it has pulled away from the rim of the weakly sclerotized dorsal carapace upon compaction, since assuming the ventral surface to be approximately flat, the flattening of the gently convex carapace on compaction would cause the unsclerotized cuticle either to stretch or pull away from the rim at some point. If this is correct, then there is no ventral doublure to the carapace, as suggested by Walcott (1931: 17), because there was no ventral sclerotization.

Body

Walcott (1912, 1931) made very little mention of the form of the body, apart from stating it to be segmented. In his reconstruction (1931, Fig. 5) he showed this clearly and also indicated that the alimentary canal tapered rapidly in the anterior portion and that in the trunk it occupied approximately one third of the width of the body. Simonetta (1970) believed all the trunk segments (which included three now believed to be cephalic) to possess small pleural lobes, though he gave no indication as to which specimen(s) showed this. In the present study I have found no convincing evidence for the presence of any pleural structures, and it is believed that the trunk body region tapered posteriorly and was segmented. It might be argued that the slightly 'stepped' outline of the trunk region in USNM 83947c (Pl. 2: 3) is due to small pleurae: however, it is believed equally possible that this is simply a result of the compaction of an annulated body. In cross-section the body is though most likely to have been oval.

Labrum

Walcott (1912: 178) originally believed the labrum to be a small narrow plate covering the central portion of the stomach anteriorly and that it was the cause of the apparent bifid anterior of the stomach. At this time he clearly did not fully realise the significance of the mode of preservation in determining whether a specimen was exposed in dorsal or ventral aspect, since he believed USNM 57676 (Pl. 1: 2) and USNM 57677 (Pl. 1: 1) to be seen in dorsal and ventral aspect respectively. However, as may be seen from Plate 1, they are both preserved in dorsal view. In his subsequent redescription (1931: 17, Fig. 3) he considered the labrum to be a much larger structure covering the entire width of the gut and extending back to cover the anterior part of the mouth, which he believed lay between the first pair of cephalic walking-legs (his mandibles). As has been shown above, the feature considered by Walcott to be the anterior edge of the labrum is now thought to be the torn-away edge of the ventral cuticle. No evidence has been found for the pair of short lateral furrows shown on the labrum by Walcott (1931, Fig. 3) and claimed by him to be present on USNM 83947m (Pl. 5: 1, 3, 4; Pl. 6: 1). Any wrinkling on this region of this specimen and also on GSC 35455 (Pl. 10: 5, 8) is thought to be explained by the compaction of the downturned, rearward facing anterior portion of the anterior end of the gut with the mouth at its termination (see *Digestive system*). The general highly reflective region, interpreted by Walcott as representing the main body of the labrum, is thought to be the result of compaction of the filled anterior region of the gut. The apparent lack of evidence for a labrum in many specimens was explained by Walcott as being due to it being very thin, readily distorted and rarely preserved. In view of the general completeness of specimens in all other respects (see *Completeness of specimens*) it is thought unlikely that if it were developed it should be preserved in so few specimens. Simonetta (1970, Pl. 30: 3, Pl. 32: 3) considered the labrum to be even bigger than that described by Walcott, claiming that there was a wide triangular labrum (his epistomium) along the margins of which the antennae were inserted. Restudy of these specimens does not substantiate this (Pl. 7: 6, 7; Pl. 7: 3, 5 respectively).

Eyes

Walcott (1912: 178; 1931: 17) considered a pair of eyes was present, represented by the small highly reflective spots seen on each side of the dorsal median axis near to the anterior margin in many specimens when viewed with high angle illumination (Pl. 4: 5; Pl. 9: 3, 7; Pl. 10: 5). These spots are now thought to represent muscle attachment areas for muscles supporting the anterior end of the body from the dorsal carapace (see *Musculature*). Simonetta (1970, Pl. 29: 1a, 1d) shows two large oval regions, ?presumably representing eyes, on the lateral portions of the carapace. However, he makes no reference to these in the text or plate explanations, and no structure on which they may have been based has been detected in the present study.

Antenna

This is clearly seen in the majority of specimens and consists of a uniramous appendage tapering distally, which projects in front of the carapace and is variously outwardly curved and clearly

flexible. In some specimens the curvature is such that the distal portion lies beneath the antero-lateral part of the carapace (Pl. 7: 3; Pl. 10: 3). A few specimens clearly show, particularly when viewed with high angle illumination, that the antenna is attached to the body just posterior to the anterior lobes of the gut (Pl. 2: 3; Pl. 9: 5, 8). Several other specimens, while not being conclusive in themselves, clearly support this interpretation (Pl. 7: 4, 6, Pl. 9: 3, Pl. 10: 1). No specimen shows any structure that could be interpreted as a second branch to the antenna (see also *Post-antennal cephalic appendages).* The length of the antenna is generally about equal to that of the carapace (Pl. 2: 3; Pl. 4: 2; Pl. 9: 5, 8).

Previous descriptions and reconstructions of *Burgessia* have indicated that the antenna consists of many segments, but no specimens have been figured in support of this, nor has any statement been made regarding the number of segments present. Walcott, in his reconstruction (1931, Fig. 3) showed seventeen segments, whereas Simonetta (1970, Pl. 29: 1c) showed about eighty-five. Specimens USNM 204715 and 204718 (Pl. 13: 2, 4, 5) do, however, show some segmentation of the antenna. USNM 204715 shows ten segments clearly over about two-thirds of the visible portion. Although this specimen is a little distorted, it is believed that this structure must be the antenna despite its unusually straight attitude. The associated fossil at about its mid-point is a small specimen of *Marrella splendens.* In USNM 204718 there can be no doubt of the identity of the antenna, but in this instance the segmentation is not so clearly preserved. However, the length of the segments discernible suggests that the total number of segments present is probably between twenty and thirty. The disparity in the number of segments between the two specimens may, in part at least, be due to more of the proximal portion being hidden beneath the carapace in USNM 204715, but the segments visible are apparently relatively much shorter in specimen USNM 204718, and so there may be some variation between individuals, or the preservation may be such as not to reveal all the joints present. Neither of these specimens shows any trace of the presence of setae at the joints as are known in *Marrella, Waptia,* and some other genera.

In his original description, Walcott (1912: 178) stated that some specimens showed a second pair of antenna-like appendages. His description is, however, ambiguous. He stated (: 178) that the specimen figured by him on Pl. 27: 2 (this paper Pl. 1: 1) showed slender antennae (labelled a' on his Plate). He then stated,'Others show a second shorter, smaller pair that is nearer the median line and probably represents the antennules.' Then in describing the specimen illustrated on Pl. 27: 3 (this paper Pl. 2: 6, 9), he stated,'A flattened specimen of the underside of the head shows the basal joints of the first five pairs of appendages. An antenna may be traced to the second joint.' In this case he labelled it a" on his plate. Raymond (1920) accepted the two pairs with the smaller as the antennules. From Walcott's description it might be concluded that his a" referred to the antennules. However, Henricksen (1928: 12) considered Walcott intended a" (A_2 of Henricksen) to be the antennae with a smaller pair being the antennules, and Henricksen considered that by comparison with the development of these structures in *Apus* (=*Triops*) that the terms should be interchanged. Fedotov (1925: 385) was not convinced of the presence of antennules. Walcott's later, fuller description and reconstruction (1931: 15–20) makes no reference to antennules and presumably he was of the opinion then that his earlier interpretation was in error and that the apparent differences were caused by differences in the incident angle of illumination and/or preservation in slightly different attitudes within the rock, the view also held by the present author. Simonetta (1970: 41) made no specific reference to the possible existence of antennules, although he did hint at the possibility that some small appendages might be hidden beneath an 'epistome'. No structure has been found in the present study that is interpreted as an antennule. The varying length and position of emergence of the antenna from beneath the carapace is believed to be accounted for simply by a difference in direction of compaction of the specimen, which thus affects the relative positions of the carapace and the cephalic and subcarapace structures. Further, since it is believed that no labrum or 'epistome' was developed, it is felt that there is little possibility of any pairs of appendages being hidden by any ventral skeletal structure as suggested by Simonetta.

Post-antennal cephalic appendages

Originally Walcott (1912: 178) believed there to be three pairs of post-antennal appendages anterior to the diverticulae, and these he termed cephalic appendages. Since he initially believed there to be antennules as well as antennae to be developed, this made a total of five pairs of cephalic appendages. This was accepted by Raymond (1920), Fedotov (1925), and Henriksen (1928), although, as mentioned above, Fedotov was not entirely convinced over

the presence of antennules. The only change made by Walcott in his later paper (1931: 17) was to delete the antennules, thus reducing the number of cephalic appendages to four. Størmer (1944: 133, Fig. 25) tentatively suggested, mainly on theoretical grounds, that there might be a fourth pair of post-antennal cephalic appendages. The most recent reconstruction (Simonetta 1970: 41, Pl. 30) suggests that the cephalon was abnormally short and contained no post-antennal appendages.

The present study shows that Walcott's original conclusion that there were three pairs of post-antennal cephalic appendages was correct. In 1912 Walcott gave no details of the structure of these cephalic appendages, although he did note that distally they were very slender and one at least ended in two fine filaments. It is thought likely that he was in fact referring to the outer branches of these appendages which are developed as flagella (see Simonetta 1970: 41, and below). Rather strangely Walcott (1931), having concluded that there were ten pairs of walking-legs, retained the three post-antennal cephalic appendages, the structure of which he knew very little about, and placed all ten walking-legs in the post-cephalic region, thus increasing the number of trunk somites above his 1912 figure of eight. He apparently ignored the possibility that the more anterior of the walking-legs might be cephalic appendages. Walcott's 1931 interpretation was accepted by subsequent authors without much question until Simonetta (1970) found no evidence of any post-antennal appendages and again considered all the walking-legs to belong in the post-cephalic region.

As has already been discussed the cephalon is believed to extend back to include the somite from which the diverticulae arise. Evidence of the presence of some cephalic appendages is to be found in numerous specimens (Pl. 2: 6, 9; Pl. 9: 3, 7; Pl. 11: 2, 5, 6, 7) and suggests the presence of three pairs of appendages anterior to the diverticulae, the anterior one being the antennae. At least one of these (Pl. 11: 2, 7) suggests that there is also a pair of appendages attached to the somite bearing the diverticulae. This is confirmed by a unique specimen (USNM 204716, Pl. 9: 8) which when viewed with high angle incident light, clearly has an appendage base beneath the diverticulum, with a further three in front. This is supported further by specimens such as USNM 204703 (Pl. 9: 4, 6) which clearly show no obvious break in the spacing of appendages from the cephalic to trunk regions.

There can be little doubt from the evidence of specimens such as those illustrated (Pl. 11: 2, 5, 6, 7; Pl. 12: 7, 9) that these cephalic appendages are the three most anterior walking-legs, and not as Walcott believed some entirely separate type of appendage. Unfortunately no known specimen shows any detail of the structure of these appendages. Although numerous specimens (Pl. 3: 4, 5, 8, 9; Pl. 4: 1–4; Pl. 5: 6, 7; Pl. 6: 2, 5; Pl. 8: 8; Pl. 11: 2, 7) suggest that there is little or no difference between the cephalic walking-legs and those of the trunk, only two specimens show their structure in any detail. In one (Pl. 11: 3) it is difficult to determine to which somite the legs belong, although it is almost certain that some of the cephalic legs are visible, and distally at least they appear to have the same form as more posteriorly positioned legs. The second specimen (Pl. 5: 2, 5), from which most of the known detail of the trunk walking-legs is derived, shows only the distal part of the third cephalic walking-leg. Again there appears to be little difference from the distal part of subsequent walking-legs. Thus, since contrary evidence is lacking, it is presumed that the detailed structure of the cephalic walking-legs is similar to those of the trunk region (see below), although it is possible, if not probable, that structures, such as the large cuspidate endite on segment one (Fig. 3), concerned with feeding or grasping (see *Function of appendages*) may well be modified on the cephalic appendages due to their proximity to the mouth.

A relatively small number of specimens show another set of cephalic appendages, namely fine flagella. These are probably the structure that Walcott (1912) thought were the distal ends of the cephalic appendages, which he believed to be uniramous. The form of these structures is best seen in USNM 155624 (Pl. 7: 4, 6, 7) where there are clearly three flagella developed, the second and third looking as if they possibly fuse together just outside the carapace margin. Other specimens (Pl. 3: 2, Pl. 7: 3, 5) also show the presence of a flagellum, but in both instances only one is visible. Apart from Walcott's possible reference to these structures, Simonetta was the first to make any reference to them. He considered them to be the outer branches of the first two walking-legs (considered by him to belong to the trunk), though rather oddly in light of specimen USNM 155624, interpreting the more anterior one to bifurcate distally. While accepting that the bifurcate nature of one of the flagella is a possible interpretation, it is preferred to consider that there are three separate structures each being the outer branch of one of the three post-antennal cephalic appendages and to consider the apparent bifurcation in USNM 155624 the result of an accident of preservation in which two flagella are crossed. A further possibility might be that one or more of the flagella represent a uniramous, biramous or even triramous antennule. This can, however, be discounted since USNM 83947c (Pl. 2: 3, 7, Fig. 15)

shows a single flagellum joining the basal portion of an appendage immediately posterior to the antenna in a position that has already been shown to be occupied by the anterior most walking-leg. It is not known whether the flagella are segmented or not.

Trunk appendages

The anterior seven trunk somites, that is all but the most posterior of the appendage-bearing somites, each bear a pair of biramous appendages, the inner branch being a walking-leg and the outer a gill. This broadly agrees with previous authors' interpretations (e.g. Walcott 1931, Fig. 3; Simonetta 1970, Pl. 29: 1c). The most fundamental difference in the present interpretation is in regard to the total number of biramous trunk appendages. This arises to some extent as a consequence of the recognition that the three most anterior pairs of walking-legs are cephalic appendages.

Several specimens (Pl. 3: 4, 5; Pl. 8: 8; Pl. 9: 6) clearly show ten pairs of walking-legs (excluding the posterior-most short appendage). Others, however, (Pl. 4: 1 – 4; Pl. 5: 6, 7; Pl. 8: 5) show fewer, commonly eight or nine. It is considered that those specimens with less than ten pairs of walking-legs visible may be explained by preservational differences, and that all individuals had a total of ten walking-legs, seven of which belonged to the trunk. The segmentation of the trunk offers little evidence, for although there is clearly one walking-leg to each segment (Pl. 4: 1, 3; Pl. 13: 6, 7), no specimen shows the body segmentation sufficiently clearly to be able to count the number of segments with any certainty, though specimens such as USNM 83947h (Pl. 4: 5, 6) indicate that a total of eight segments would be likely in the trunk.

It is clear from the majority of specimens showing the legs, that there is a progressive diminution in size posteriorly (Pl. 3: 1, 4, 5; Pl. 4: 2, 4; Pl. 6: 2, 5). It is also apparent that the more distal segments of each appendage are more slender than the proximal ones (Pl. 4: 2, 4, Pl. 6: 2, 5; Pl. 13: 6, 7). Very few specimens show any detail of the segments and joints (Pl. 4: 2, 4; Pl. 5: 2, 5; Pl. 6: 8, Fig. 24; Pl. 11: 1, 3) and only two of these show any detailed information regarding the structure of the walking-legs. In USNM 83947i (Pl. 5: 2, 5) the seventh, eighth and ninth walking-legs are particularly well preserved, although even in this specimen certain important features cannot be discerned. The specimen is exposed from the ventral side and the legs have been rotated on compaction through 90°, so that the segments are seen in anterior view. Proximally there appears to be a basal segment (coxopodite of Walcott 1931: 18) to which he believed the outer branch (exopodite) was attached, although he admitted that he had very little direct evidence for this. Simonetta (1970: 41, Pl. 29: 1e) also considered this segment to represent the coxa, but in addition believed a short precoxa was developed, possibly immovably jointed to the body, from which the outer branch arose. As may be seen from Pl. 5: 2, no details are visible of the proximal end of the presumed coxa, nor are they on any other specimen. Thus from the available evidence it is impossible to deduce the presence of a pre-coxa, and Simonetta's interpretation remains purely conjectural. The place of attachment of the outer branch is discussed more fully below, but is believed to be to the coxa. In the reconstruction given here (Fig. 3), it will be noted that in addition to the endital swelling clearly visible on the underside of the distal portion of the coxa, a dorsal flange-like structure is proposed to join the segment to the body. No specimen shows any detail of the coxa-body joint, but this flange-like extension is postulated in order to make a more feasible arrangement for the musculature which, without such an extension, would be very inefficient, or surprisingly complex. Such functional arguments may explain Simonetta's postulated pre-coxa. The walking branches of the seventh and eighth post-antennal somites (fourth and fifth trunk appendages) consists of six segments and some terminal claws, and, in the absence of contrary evidence (see above) it is presumed that the other walking-legs are of similar construction.

The first segment of inner branches 7 – 9 (fourth – sixth trunk appendages) (Pl. 5: 2) has a very pronounced cuspidate endite particularly clearly seen on the eighth appendage. The second segment, best seen on the seventh walking-leg, has a smaller endite surmounted by a pair of bristles or setae. Segments three and four appear basically similar to one another, being subcylindrical, expanding slightly distally with at least one strong seta present at the joint between them (Pl. 11: 3). The fifth and sixth segments are basically similar to the third and fourth, but are considerably slimmer, a seta is present at the joint between them, and between the fourth and fifth segments. Two or three terminal claws to the sixth segment are just discernible in two specimens (USNM 83947j (Pl. 5: 6), USNM 204719 (Pl. 11: 1, 3)). The type of joint between segments varies and is thought to be of the pivot type (Manton *in* Moore 1969, Figs. 1,

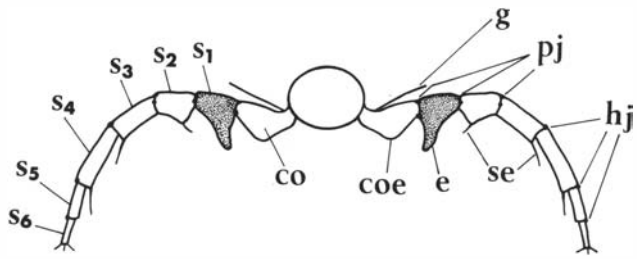

Fig. 3. Diagram showing the basic structure of the trunk appendages of *Burgessia bella* in probable life-attitude. First segment of walking-leg stippled showing strong cuspidate endite which acted as a 'pincer' with the coxal endite.

2) between the coxa and first, first and second and second and third segments and a hinge joint between the fourth and fifth and more distal segments. The type of joint between the third and fourth segments is more uncertain, but is possibly more likely to be of pivot type. The evidence for this interpretation is seen in the specimens figured on Pl. 5: 2, 5; Pl. 11: 1, 3 where the segments pivot-jointed are both the same depth at the joint, whereas in those hinge-jointed the distal depth of the more proximal segment is greater than that of the proximal depth of the more distal segment, which dorsally is in line with the previous segment, but ventrally fits within the segment.

This interpretation of the walking-leg differs from those of Walcott (1931) and Simonetta (1970) in a number of features. Although the original of Pl. 5: 2 was figured by Walcott (1931, Pl. 16: 5), his reconstruction (Fig. 3) shows progressively more segments with an endite expansion on the more posteriorly placed legs, with the inner five segments being so expanded on the last four pairs. The evidence of Pl. 5: 2 does not support this. It is possible that Walcott considered specimens such as the original of his Pl. 16: 1 (herein Pl. 3: 4, 5, 7, 9) as indicating the higher number of expanded segments. Walcott's photograph is considerably retouched, but even so shows no evidence for more than two or three expanded segments. Restudy of the specimen suggests that this is to be explained by the rather indifferent preservation. Walcott himself was not entirely consistent, for although the orientation of his diagramatic outline of a trunk limb (1931, Fig. 4) is not entirely clear, the outline shows no expansion of any of the segments – all joints are of the hinge type, with two setae present at each. As has been shown above the present study clearly indicates that the inner joints are almost certainly of pivot type. No trace has been found for any dorsally positioned setae and ventrally placed ones have only been seen at the joints between the third and fourth, fourth and fifth, and fifth and sixth segments (Pl. 11: 1, 3). Simonetta's reconstruction of the walking-leg (1970: 29) is considerably different. As already mentioned he introduced a pre-coxa, but he also reduced the number of distal segments by one. Further he showed the coxa and first segment (his throcanter) to have multiple rows of strong spines along their inner surface. No evidence for such spines has been found; on the contrary Pl. 5: 2 clearly shows there are no spines. Simonetta also reconstructed the joint between segments two and three (his femur and patella) as a 'knee-joint'. By analogy with modern arthropods it is believed that if this were the case then the cuticle would have been very much thickened at the joint, this would then appear in the fossil as the most prominent joint. Since this is not the case it is thought unlikely that a knee-joint was developed here or at any other point along the walking-leg, and that the attitude of the leg was more as shown in Fig. 3.

The outer, gill, branch of the trunk appendages is rarely well-preserved and is best seen in specimen USNM 83947n (Pl. 6: 6, 8). This specimen is exposed from the ventral side and it is the underside of the left gill-branches that is visible. These are oval in outline, and each one is overlapped (in dorsal aspect) by the next most anterior one. They are positioned dorsal to the walking branch (see below) and in this specimen the left walking-legs will be preserved within the matrix of the counterpart (which has not been recognised). As with the walking-legs there is gradual diminution in size to the posterior. No jointing or filamentous structure within the lobe has been detected, and contrary to Walcott's statement (1931: 18, and explanation Pl. 14: 4) no indication of any fringing setae have been seen. Traces of seven gill branches are seen (Pl. 6: 6) which supports the evidence for seven trunk walking-legs. Other specimens showing traces of the gill branches (Pl. 8: 4, Pl. 10: 1) show no indication of any being present in the cephalic region. Because the specimens in which the gill branches are clearly visible are preserved in such a way that the leg branches are not

seen, it is difficult to prove the relationships between the two branches. However, in USNM 83947f (Pl. 4: 2, 4) there is a structure which it is believed can only be part of a gill branch, lying dorsal to the walking-legs. Specimen USNM 114242 (Pl. 10: 1, 2), which is exposed from the dorsal side, also suggests that the gill branch is dorsal to the walking-legs. Walcott figured a specimen (1931, Pl. 16: 6) which he believed indicated that there was an anterior support to the gill branch (his exopodite) which extended beyond the lobe and terminated in two minute spines. Størmer (1944) commented on this specimen and believed Walcott's interpretation to be correct. This specimen (Pl. 5: 6, 7) is laterally compressed and seen from the left side. The proximal portion of the left walking-legs have broken away, revealing the proximal portions of the right-side appendages. The anterior edge of these right-side appendages appears prolonged and is clearly the structure interpreted by Walcott and Størmer as the anterior support for the gill branch. It is thought more likely, however, that this is part of the right walking-leg and that it continues into the sediment beneath the left walking-legs. Whether or not the broad basal portion exposed is a single structure is not certain. As shown in Fig. 21, the posterior part of the basal region is at a slightly higher level within the matrix than the anterior part, although as can be seen in Pl. 5: 7 this change in level is very small. Since the gill branch is believed to be dorsal to the walking-leg, in a laterally compressed specimen seen from the left side, the right gills should be at a lower level than the right walking-legs. It is thought that this specimen may be explained in one of two ways. Either the walking-legs were rotated on compaction and buckled so that the ventral portions were pressed upwards, or on compaction portions of the gill branches were pushed up between the dorsal portions of the walking-legs. Whichever is correct, it does not affect the interpretation of the supposed anterior supports to the gill branches of Walcott being part of the right walking-legs. The point of attachment of the gill branch is not seen in any specimen. Pl. 6: 6, however, clearly shows the proximal portion of the gill to be very close to the body, and even allowing for some lateral extension of the body on compaction, the gill must have been attached very near the proximal end of the appendages, presumably to the coxa.

The posterior trunk appendage appears to be little more than a short uniramous spike-like structure (Pl. 4: 1–4, Pl. 5: 2, 5, Pl. 7: 8, Pl. 8: 1, 5) which may represent a reduced walking-leg. Walcott (1931: 18) stated that one specimen showed a modified 'exopodite' consisting of a central axis with seven sharp spines projecting from the posterior side and a terminal spine at the posterior, although he considered that this structure might possibly be a walking-leg, the 'spines' being part of the expanded portions of the inner segments of the leg that he believed were developed. However, since he showed it as a modified appendage in his reconstruction he clearly favoured the first explanation. Oddly he made no reference to this structure on any of the plate explanations, though restudy of his collections indicates that he was referring to the structure seen in specimen USNM 83947e (Walcott 1931, Pl. 16: 1, herein Pl. 3: 4, 5, 7, 9). It is clear that some kind of apparently spinose structure is present (Pl. 3: 7) though its details are not well-preserved. As no other specimen shows any indication of a second spike-like branch to the posterior trunk appendage, it is thought unlikely that this structure represents any such second branch. Similarly Walcott's suggestion that the 'spines' are the expanded parts of the inner segments of the walking-legs can be discounted since it is now known that only the first two segments of the walking branch bear expansions on the ventral side. If the appendage on this eighth trunk somite does represent a reduced walking branch, then the six or seven spine-like extensions might be homologous to the setae known to occur at least at some of the joints of more anteriorly placed walking-legs. Alternatively it is possible that this structure does not belong to the specimen at all, for it could be argued that since all other trunk appendages of both left and right sides are preserved 'below' the body, it would be unlikely that the posterior appendage, whether left or right, should be preserved in such a different attitude. However, other specimens both of *Burgessia* and other genera show that such twisting of specimens is quite possible. Simonetta (1970) was unequivocal in considering this posterior-most appendage to be a specialised, reduced, walking-leg, lacking any outer branch, and he made no reference to Walcott's biramous interpretation.

Telson

The trunk terminates in a short segment with no lateral appendages, interpreted by Walcott (1931: 18) as the anal segment, and a long caudal spine. This terminal segment and spine are considered to form a telson. The one specimen that shows the terminal segment most clearly (Pl. 9: 2) shows neither the alimentary canal nor the posterior appendages, and so it is difficult to be certain of the relationships between these various structures. However, the evidence

afforded by USNM 204717 (Pl. 9: 2) as to the size of the segment, and by USNM 155680 (Pl. 7: 8, 10) as to the position of the last lateral appendage in relation to the point of flexure at the base of the caudal spine, strongly suggests that the last trunk appendage belongs to the somite immediately to the anterior and not to the terminal segment. Walcott described an anal plate on this segment (1931: 18, Figs. 3, 5, Pl. 17: 3), rather curiously showing it on both his ventral and dorsal reconstructions. Despite his assertion in the plate explanation that the anal plate was 'clearly indicated', his illustration does not support this. Restudy of the specimen, Pl. 5: 1, 3, 4, Pl. 6: 1, shows that the shield-shaped structure referred to by Walcott as the anal plate appears to be the faint impression of the rounded posterior of the alimentary canal within the terminal segment. If this interpretation is correct, this is the only specimen that shows the alimentary canal definitely within the terminal segment. Some specimens show a thread-like structure apparently extending posteriorly from the end of the alimentary canal, particularly well seen in USNM 83947d (Pl. 2: 8) and USNM 83947c (Pl. 2: 3). This could be a short anal passage, but other specimens e.g. USNM 155680 (Pl. 7: 8), USNM 83947h (Pl. 4: 5) also show a thread-like structure which continues back through the terminal segment and along the centre of the caudal spine. This is seen best when the specimen is viewed with high incident angle illumination, and is thought to represent some fluid-bearing vessel (Whittington 1971b: 15) that lies along the axis of the body either dorsal or ventral to the gut, and which only becomes visible in the flattened specimen behind the termination of the alimentary canal. Thus although Walcott's large anal plate cannot be substantiated, it is thought that the anus lies within the terminal segment.

Walcott believed the caudal spine (his telson) to be segmented with at least thirty segments (1912: 178, 1931: 15). This was not questioned by subsequent workers until Simonetta (1970: 41) considered it to be an unsegmented conical spine. The present study supports Simonetta's interpretation. The great majority of specimens show no sign of any segmentation of the spine. Although Walcott does not specifically identify the specimen showing at least thirty segments, it seems likely from his illustrations that the figure of thirty may have been based in part at least on specimens USNM 57677 and USNM 57680 (1912, Pl. 27: 2; Pl. 30: 3). However, both these photographs have been considerably retouched (Pl. 27: 2 even appears to show setae present at the joints), and it can be seen (Pl. 1: 1, 4–7) that neither of these specimens shows any sign of segmentation. A few specimens, notably USNM 83947a (Pl. 3: 1, 8) and USNM 83947d (Pl. 2: 1, 5, 8), show some changes in direction along the spine that might be interpreted as joints. However, since they show no definite joint structure nor any regularity in position, it is preferred to consider them as *post-mortem* fractures. One specimen USNM 204712 (Pl. 12: 1, 8, Fig. 31) does show what could possibly be joints, if there are, then there would appear to be of the order of twelve rather than thirty segments. However, as can be seen from the illustration, the indications of joints are extremely tenuous and I am not convinced that they represent original structures.

Digestive system

Walcott (1912: 179, Pl. 27: 1, 2, 1931: 18–19, Fig. 5, Pl. 16: 4) described the mouth as being ventral, presumably opening into a gullet and passing into a stomach apparently divided, with a straight intestine extending from the rear of the stomach along the axis of the animal terminating in the telson. He considered the large kidney-shaped caecal system present, branching off from the fifth somite, to be an hepatic organ. This interpretation was accepted by subsequent authors including Simonetta (1970), with only small modifications in terminology, and the present study has revealed only a few further minor modifications. Relatively recent work by Öpik (1961), Bergström (1973) and Shergold (this volume) on agnostids has indicated that they possess a digestive system not unlike that of *Burgessia*. As stated above (*Terminology*) the terms employed here are based on those of Öpik (1961).

It is difficult to imagine the mouth being anywhere but on the ventral side, but the positive evidence for its position is very little. Walcott and Simonetta both believed a relatively large labrum to be present and presumed the mouth was positioned immediately to the rear of this. However, as shown above (*Labrum*), this view is no longer considered correct. GSC 35455 (Pl. 10: 5), which is seen in ventral aspect, shows, in high angle illumination, a distinct lobe-like structure at the anterior end of the body which is interpreted as the outline of a downturned, rearward facing portion of the digestive tract, presumably with the mouth at the posterior. Other specimens (e.g. USNM 204702, Pl. 10: 1) show the outline of a similar lobe which has been compacted to be at a slight angle to the main portion of the alimentary canal. Further specimens GSC 35461 (Pl. 12: 9) and USNM 83947m (Pl. 5: 1) show the impres-

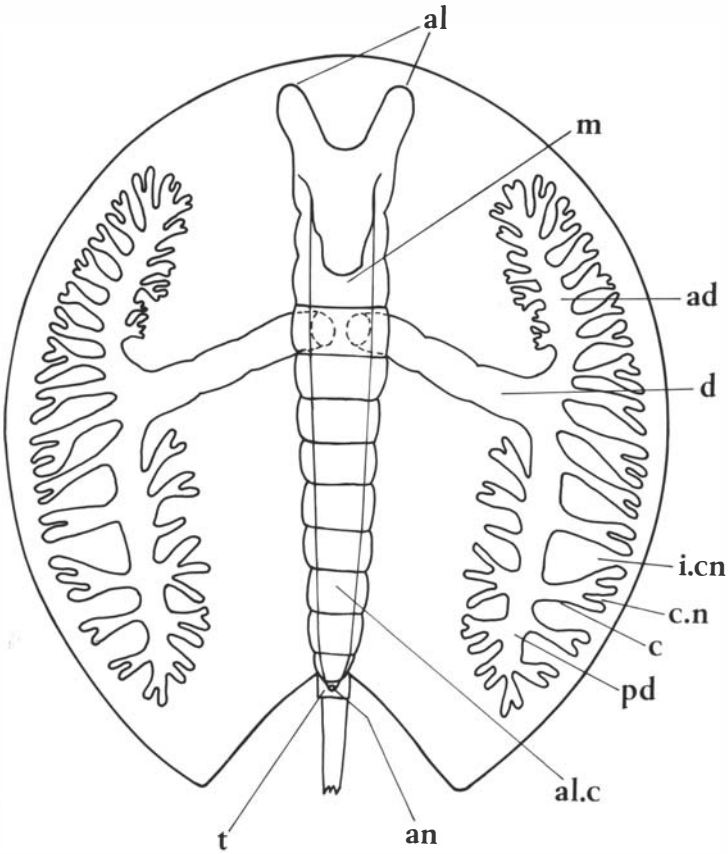

Fig. 4. Ventral reconstruction of digestive system of *Burgessia bella.*

sion of the ventral surface of the gut and also show indications of some lobe-like structure. In Walcott's reconstruction (1931, Fig. 5) a third 'anterior central lobe of stomach' is shown. This is thought to have been based on such specimens as USNM 57677 (Pl. 1: 1) where there is some indication of a third central lobe anteriorly (originally thought by Walcott (1912) to represent the labrum). However, this and similar specimens are believed to be explained by the rearward facing anterior portion of the gut having been pushed forwards by oblique compaction. It should be noted (Pl. 1: 1) that there are other signs that the carapace has been pushed posteriorly and slightly obliquely with respect to the remainder of the animal, in that no appendages are visible behind the carapace, and the right antenna, as far as can be seen, appears as if it joins the body far forward on the anterior gut lobe (cf. Pl. 9: 8). The frontal part of these anterior gut lobes is thought to have been the point of attachment for muscles from the fore end of the body to the carapace (see *Musculature*), and the lobes themselves may have housed some kind of digestive gland. The diverticulum leading to the lateral gut-caecal system arises from the gut at the posterior-most cephalic somite which also bears the fourth pair of lateral appendages. It is a moderately large tube and occasionally shows some signs of annulation (Pl. 1: 2). Distally it bifurcates, one branch directed anteriorly, the other posteriorly. Numerous short caecal tubes branch off these both internally and externally, commonly dividing once or even twice to give a bifid or trifid caecum (Pl. 4: 5). The caecae to the anterior of the diverticulum tend to be closer packed than those to the posterior, particularly on the inner side of the anterior diverticulum. Those on the posterior diverticulum tend to have much deeper caecal nodes and larger intercaecal nodes (Pl. 4: 5, 6, Fig. 4). Whether or not this organ served as a digestive organ or simply as a storage organ is not known, and for this reason it is preferred to consider it simply as a gut-caecal system rather than as an hepatic or hepatopancreatic organ as it has been termed in the past. In *Burgessia* this is a cephalic organ; hepatic or hepatopancreatic organs are more typically organs of the post-cephalic region in arthropods. The posterior portion of the gut, occupying the trunk region, tapers slightly posteriorly and appears to be bluntly rounded at its extremity on the telson. In many specimens the entire digestive system is not flattened to the same extent as the remainder of the animal due to it having been filled at the time of burial with sediment-rich fluid. In many specimens in which the gut is so preserved, it appears as if it entirely fills the body cavity. However, it is clear that other organs, such as the heart, circulatory system, muscles and nervous system must have been present, and it is thought that the

gut must have spread out on compaction so as to appear to more or less fill the body cavity. Nevertheless it is believed that the gut must originally have occupied a large proportion of the body cavity in both the cephalic and trunk regions.

Musculature

With one exception, there is no trace of the musculature system. As has been mentioned above (*Eyes*), Walcott interpreted as eyes the two small highly reflective spots present on each side of the dorsal median axis. The present study confirms the presence of these spots on many specimens (e.g. Pl. 2: 6; Pl. 4: 5; Pl. 9: 3, 7). In some other specimens (Pl. 9: 8; Pl. 10: 5) the spots appear to be superimposed on top of the anterior ends of the anterior gut lobes. Since the relative position of the carapace with reference to the remainder of the animal varies according to the direction of compaction, this evidence is not inconsistent with Walcott's interpretation of these as eyes, presumably set on the dorsal surface of the carapace. A unique specimen, believed to be of *Burgessia* (GSC 35459, Pl. 7: 1, 2) has the carapace torn almost entirely free from the remainder of the specimen. However, there are a number of strands of organic material joining the carapace to the anterior portion of the body where two highly reflective spots are present, thus the silvery spots appear to be located beneath rather than on the dorsal carapace and are therefore presumably not eyes. It is thought that these strands represent muscles originally attached to the underside of the carapace and the frontal end of the anterior gut lobes, and that the highly reflective spots mark the attachment areas and not eyes. A possible alternative explanation of this unique specimen is that the strands represent the torn remains of the diverticulae. There is no evidence, however, that they extend far enough back to this to be a reasonable possibility.

Dark stain

Whittington (1971a: 1180–1190, Figs. 6a, c, 7, 9, 16, 1971b: 16) showed that a dark organic stain was almost always associated with specimens of *Marrella.* A similar, though smaller stain is present associated with only a few specimens of *Burgessia* (Pl. 4: 4; Pl. 7: 5; Pl. 10: 3). No chemical analyses have been made of the stain associated with *Burgessia,* but it is assumed to be of the same nature as those associated with *Marrella* and is thought to represent squeezed out organic matter.

Completeness of specimens

The figured specimens show that the vast majority of specimens are demonstrably complete individuals with all the appendages preserved in their entirety and are not exuviae. Others (e.g. Pl. 2: 6, 9) presumably have the missing portions present on the counterpart specimen. A few specimens (Pl. 7: 9; Pl. 9: 1) appear only to have the carapace and digestive organs visible, although the appendages may well be present within the matrix. The absence of the caudal spine may well be real or a function of the difficulty of preparation of some specimens, particularly the very small ones. No specimens show any clear evidence of predation and few of decomposition. The preservation of some (Pl. 7: 1, 2; Pl. 10: 1, 2) suggests that some decay may have taken place before or immediately after entombment. However, a moulted carapace of *Burgessia,* with no trace of the digestive organs, would be very difficult to recognise.

Function of appendages

There is little doubt that the uniramous antenna were tactile organs. The three cephalic flagella show no trace of fringing setae that might suggest a natory function, and it is believed that they also were tactile appendages, as are the antennules in many malacostracans and the triramous appendage in *Triops.* The cephalic and trunk walking-legs are believed to have functioned both as locomotory organs and as food gatherers, all ten walking-legs being able to reach the ground (Fig. 9). Since the cross-section of the body is relatively small compared to the size of the limbs, there was apparently little space within the body for any efficient extrinsic limb musculature to be developed. However, the large size, especially of the proximal segments of the walking-leg

and of the coxa, would allow ample space for a well-developed intrinsic musculature to be present which could allow a relatively slow gait. Such a musculature would enable the leg to be used propulsively both on flexure and by extension, and in common with many modern arthropods (Manton 1952, 1954, 1958) it is thought likely that in the more anterior appendages the propulsive stage was during flexure and in the more posterior during extension. This gives rise to a certain amount of fanning out of the appendages which is suggested in some specimens (Pl. 5: 2, 6) and is depicted in the reconstruction (Figs. 6, 9). The form of the proximal segments of the walking-leg and that of the coxa, particularly the large endital processes on the coxa and first segment (Fig. 3), suggests a gripping or crushing function, since on curling the leg up these two endites provide the 'jaws' of a very effective pincer (Fig. 5). Not only do these segments form an effective gripping or crushing mechanism, but by allowing a certain amount of dorso-ventral movement at the coxa-body joint, known to be possible in some modern hexapods (Manton 1972), then the pincer can be brought more or less into the mid-line (Fig. 5). By a simple process of slight rotation of the limbs and a successive gripping and releasing by the pincer, captured food could be brought into the mid-line and passed forwards to the mouth. It is particularly unfortunate that no knowledge is available of any modifications of the basal joints in the mouth region.

The gill branches are thought to be simply oxygen exchange organs. Bergström (1969) threw doubt on the previous interpretations that the gill branches in trilobites were respiratory, considering that the bulk of oxygen exchange took place through the ventral cuticle. He made no specific reference, however, to the function of the gill branches in the non-trilobite arthropods of the Burgess Shale. Whittington (this volume) has rejected Bergström's view and reaffirms that respiration in the trilobites was effected by the outer, or gill, branch of the biramous appendages. The gill branches in *Burgessia* overlap each other slightly and are believed to be able to come in contact, or very nearly so, with the underside of the carapace. It is considered that metachronal beating of the appendages would produce sufficient water currents to ensure an adequate oxygen supply in much the same way as has been described by Cannon (1933) and Sanders (1963) for branchiopods and cephalocarids, respectively.

The function of the posterior-most, probably uniramous appendage is uncertain. If it represents a degenerate walking-leg then it might have little or no function.

Mode of life

Very little comment has been made in the past regarding the possible mode of life of *Burgessia.* Walcott (1931: 20) suggested that the functions of the limbs of *Burgessia* were similar to those of *Marrella,* and he concluded (:35) that *Marrella* was free-swimming. Little further comment appears to have been made until Størmer (*in* Moore 1959: 027) stated that *Burgessia* with its broad carapace was likely to be a planktonic form. The only other remark appears to have been by Bergström (1973: 6) and concerned the diet of *Burgessia:* he suggested that *Burgessia* ingested fluid food.

As has already been discussed, the preservation and relationship between the specimens of *Burgessia* and the sediment indicate that it must have lived on or near the bottom, and was thus able to become caught up in the entombing sediment cloud. The detailed morphology of the appendages suggests that it would be feasible for *Burgessia* to walk, albeit rather slowly, on the sea bottom using the antennae and cephalic flagella as tactile organs, sweeping across and through the soft sediment. Whether or not *Burgessia* could swim is more uncertain. As mentioned above it seems unlikely that the flagella could have been natory in function. Also it seems unlikely

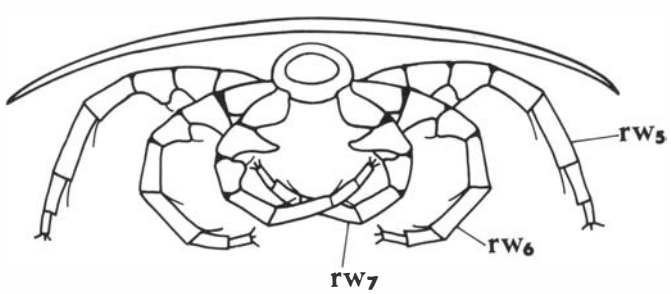

Fig. 5. Diagramatic cross-section of walking-legs 5 to 7 of *Burgessia bella* showing possible attitudes of legs to encircle food.

that it could use the walking-legs in swimming since it is improbable that they could be 'feathered' sufficiently on the return strokes. Whether or not metachronal beating of the gill branches would be sufficient to effect a swimming motion is debatable. As discussed above it is thought unlikely that any musculature was developed allowing swift motion of the appendages. Manton, in a series of papers (e.g. Manton 1952, 1954, 1958, 1972), has discussed the various gaits to be found in modern arthropods, and it would seem possible that *Burgessia* walked with left and right walking-legs in phase and with six pairs of legs on the ground at any given time. This would give a gait comprising two metachronal waves, each with five pairs of legs. Whittington (this volume) has described very fully the possible gait of *Olenoides* and the general style of gait in *Burgessia* is believed to be the same, i.e. each pair of legs moved in unison in a promotor-remotor swing about an approximately transverse axis at the coxa-body junction. One major difference in *Burgessia,* however, is caused by the progressive diminution of the length of leg posteriorly.

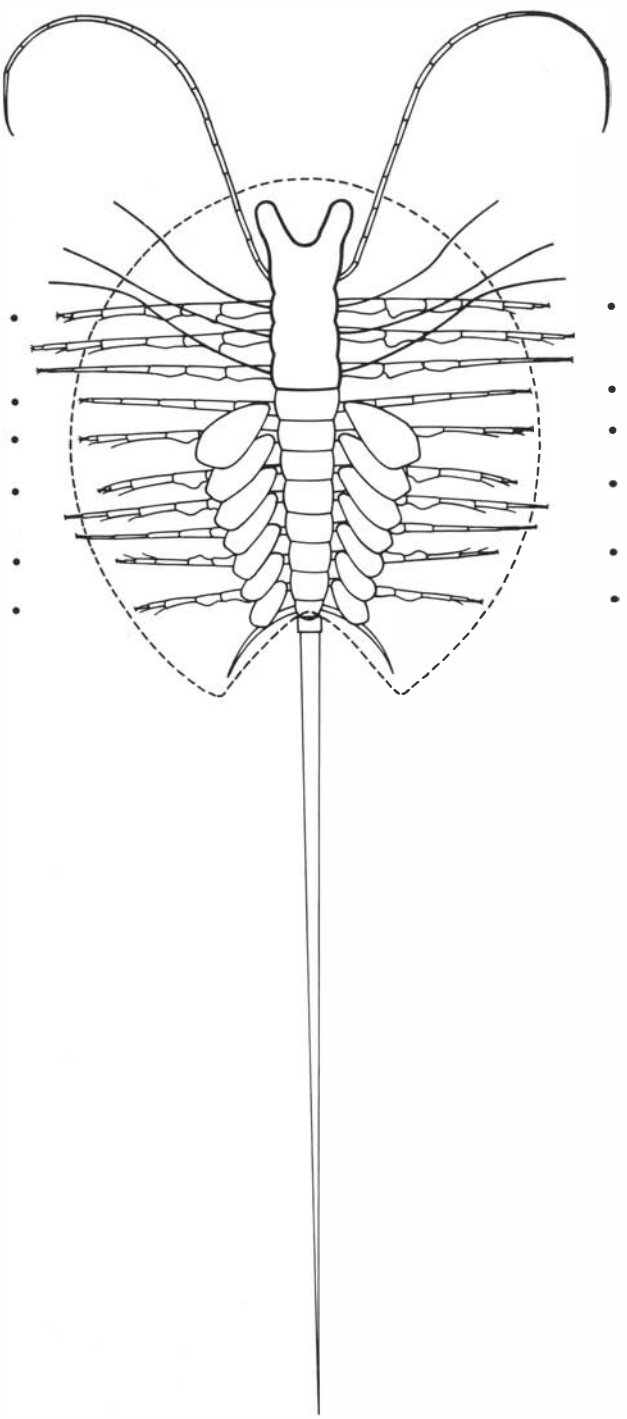

Fig. 6. Dorsal reconstruction of *Burgessia bella* with carapace and gut-caecal system removed to show appendages. Margin of carapace shown dotted. Gait assumed is with six pairs of legs on the ground (indicated by °) and four pairs off at any time (see text), giving two metachronal waves.

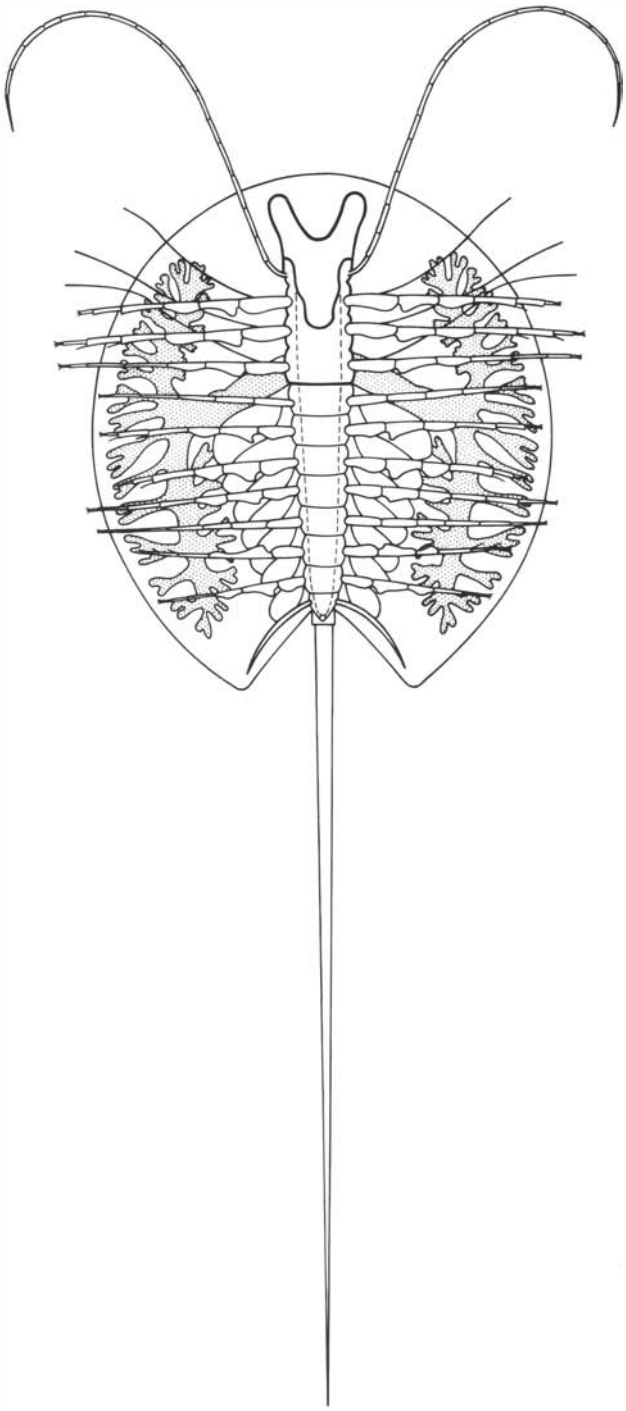

Fig. 7. Ventral reconstruction of *Burgessia bella.* Gait same as for Fig. 6, gut-caecal system stippled.

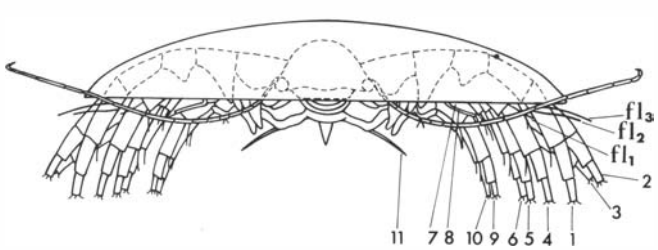

Fig. 8. Anterior reconstruction of *Burgessia bella.* Gait as for Fig. 6. Outline of first walking-leg and gut shown dotted.

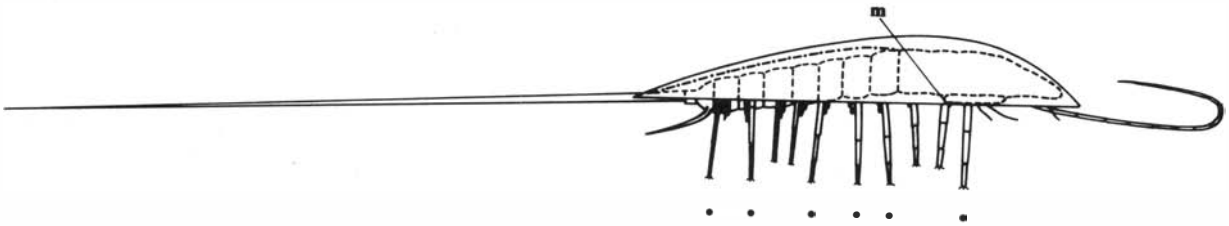

Fig. 9. Lateral reconstruction of *Burgessia bella.* Gait as for Fig. 6. Legs on ground indicated by ∘ , underside of carapace as seen in longitudinal section indicated by —·—. Cephalic region of body shown in heavy dashes, m — mouth.

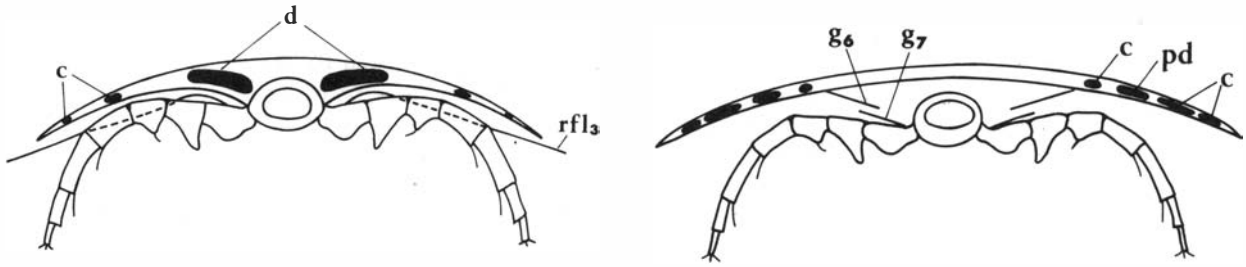

Fig. 10. Cross-sectional reconstructions of *Burgessia bella.* A — anterior of diverticulum, B — posterior of diverticulum (somite 7).

Symbols used on Figures are explained under *Terminology.*

In order to keep the stride length the same, the swing of legs must decrease anteriorly. An angle of swing of the posterior-most leg of 16° was taken, reducing to 12° for the anterior-most leg. As mentioned above it is believed the propulsive stage of the legs was mainly during flexure anteriorly and during extension posteriorly; accordingly the swing of the leg has been taken as 4° in front of the transverse plane and 12° behind for the posterior-most leg, changing progressively to 9° forwards and 3° back for the first walking-leg.

It is postulated that *Burgessia* walked slowly on the sea-bottom, walking on all ten pairs of legs. It is also possible that it could have moved with the leading edge of the carapace buried shallowly in the soft substrate. In this attitude only the anterior few pairs of legs could have been in contact with the ground, unless there was a large amount of flexing at the cephalon-trunk junction (Fig. 9). It is also possible that the long caudal spine dug into the substrate to help give a more positive forward motion, though its extreme length might argue against this.

Over-all shape might suggest some comparison with *Limulus,* indicating a possible inverted swimming attitude. However, the detailed morphology of the appendages of *Limulus* and its method of propulsion clearly show there to be no analogy with *Burgessia.* A more meaningful comparison is believed possible with many diplopods (Manton 1952, 1954). One feature of *Burgessia* is the wide carapace which virtually covers the long appendages, which is a feature commonly found in various diplopods as an adaption to a shallow burrowing habit, since the carapace gives protection to the propulsive appendages.

The detailed morphology of the appendages argues against *Burgessia* being a fluid feeder, although as Bergström (1973) correctly states the food must have been in a fluid state on reaching the gut-caecal system. Since nothing is known of any masticulatory apparatus, it is possible that whatever food *Burgessia* grasped with its walking-legs was simply held against the mouth and externally digested, being sucked into the alimentary canal by muscular contractions. If this is correct, then the anterior gut lobes may have functioned as digestive glands providing the necessary digestive fluids.

Affinities

Many of the authors who have considered the affinities of *Burgessia* have stressed the similarity with some notostracan branchiopods. Walcott (1912: 179—180) believed the best living branchiopods to compare with *Burgessia* were the Apodidae (= Triopsidae). He admitted, however, that the possession of eight pairs of thoracic (= trunk) appendages and the absence of abdominal segments with appendages in *Burgessia* distinguished it from apodids and were more characteristic of the Phyllocarida. Crampton (1919: 155) believed that *Burgessia*, with its resemblance to the recent notostracan *Lepidurus*, indicated what the first arthropods were like. Raymond

(1920) dissented in part, believing *Burgessia* to be both more primitive and more specialised than *Apus* (= *Triops*), pointing out that although the carapace and lack of limbs posteriorly were *Apus*-like, the form of the trunk appendages was more comparable with those of the trilobites. Raymond also believed that of the other Burgess Shale genera a closer comparison could be made with *Marrella.* However, he considered *Burgessia* a notostracan (1920: 109), but placed *Marrella* in the order Marrellina in a new subclass Haplopoda (1920: 148–149).

The present investigation has supported the interpretation of the trunk limbs as being trilobitan in *Burgessia,* i.e. having a six-segmented leg branch and a lobe-shaped outer branch from the coxa. Whittington (1971b) has shown that the walking-leg of *Marrella* may be different from that of *Burgessia* in having only five, and not six segments plus a coxa. Fedotov (1925: 385, 386), having rejected the two specimens figured by Walcott (1912, Pl. 30: 3, 4) as not belonging to *Burgessia,* unequivocally considered *Burgessia* to be a notostracan. He commented, however, that if the two rejected specimens were subsequently shown to belong to *Burgessia* (which they have), then, since these had segmented trunk appendages, it would be necessary to acknowledge that the appendages of the Cambrian notostracans were jointed, not unjointed as in recent genera. Henriksen (1928) followed the general concensus and considered *Burgessia* to have definite notostracan affinities, holding the opinion, contrary to Fedotov, that the early notostracan branchiopods had jointed appendages and that the unjointed condition in modern forms is a specialised condition. Walcott (1931) inferred that he still held that *Burgessia* was most closely related to the branchiopods. Raymond (1935) erected the order Pseudonotostraca in which he placed *Burgessia* together with *Waptia* and *Protocaris.* Størmer (1939: 236, 237), believing he had substantiated Walcott's suggestion that there was an anterior support to the gill branches, suggested there was a close resemblance between *Burgessia* and *Leanchoilia, Neolenus* (= *Olenoides*) and *Opabinia.* The present study, however, does not support this interpretation of the gill branch. Subsequently, Størmer (1944: 98, 99), having briefly reviewed the morphology and previous opinions as to the affinities of *Burgessia,* concluded that the large carapace and lack of trilobation pointed towards the Crustacea. On the other hand the trilobitan limb (here substantiated), the labrum (no longer believed to exist), the styliform caudal spine (thought by Størmer to be a segmented telson), and intestinal caecal system, strongly suggested to Størmer affinities with the Trilobita, merostome-like Cambrian arthropods, as well as to the Chelicerata. In his formal classification (1944: 133–136), he considered *Burgessia* to belong within the new Class Pseudocrustacea, which he placed in a new subphylum Trilobitomorpha. In 1959 (Størmer *in* Moore) he clearly still held much the same views on the affinities of *Burgessia,* although he made some modifications in the names of the higher taxonomic ranks, erecting a new class Trilobitoidea with Burgessida as an order within the subclass Pseudonotostraca. In a recent discussion of the phylogeny of the arthropods (Manton 1973) no attempt is made to place the Burgess Shale forms within what is, and must be, a framework based on extant forms. Simonetta (1973, pers. comm.) believes *Burgessia* to stand somewhat alone within the Burgess Shale fauna, possibly a 'proto-notostracan' and a possible ancestor to at least some crustaceans.

Various authors have commented on the similarities between *Burgessia* and *Naraoia,* especially the gut-caecal system and appendages (Walcott 1912, 1931, Størmer 1944). However, full assessment of these must await the redescription of *Naraoia.* Other occurrences of unusual fossil arthropods in the lower Palaeozoic rocks offer little help in deciding possible affinities of *Burgessia. Douglasocaris* Caster and Brooks, 1956 from the Ordovician of Tennessee, thought possibly to be a notostracan branchiopod (Rolfe *in* Moore 1969: R330), shows some superficial similarity; close comparison, however, reveals there to be little affinity between the two forms. The only other form exhibiting any similarity is *Cheloniellon* Broili, 1933 from the Devonian of Germany. Again detailed examination reveals no close similarity, any resemblance being thought to be most likely accounted for by convergent adaption to a similar mode of life. Sharov (1965, 1966) apparently accepted Walcott's ascertion that the appendages of *Burgessia* were trilobite-like, and considered *Burgessia* to be derived from the trilobite by the reduction in trunk pleurae accompanied by the backward growth of the head shield to cover the trunk segments.

Since the current restudy of all the Burgess Shale arthropods is revealing that the detailed morphology of these forms is not as previously thought, the present author considers further discussion of the affinities of *Burgessia* as premature; such discussion must await the completion of the redescription of all the arthropods within the fauna. What is apparent from this restudy is that *Burgessia* did possess a mixture of characters, e.g. carapace, trilobitan appendages (but no trilobitan labrum), an intestinal cephalic caecal system, antennae, styliform caudal spine, many of which are to be found in modern arthropods of various groups. Thus it is clearly possible that *Burgessia's* affinities are within an early arthropodan stock which gave rise, either directly or indirectly, to many of the major extant arthropod taxa.

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Plates 1 – 13

EXPLANATIONS OF PLATES 1–13 AND FIGURES 11–35

The photographs were taken on panchromatic film with ultraviolet radiation. The radiation was directed at 30° to the horizontal and the direction from which it was from is stated as west, north, etc., relative to the margins of the plate. Photographs referred to as reflected were taken with the incident radiation at 60° to the horizontal, and the specimen tilted slightly at about 10° so that the maximum reflective effect was directed into the camera. The orientation of the specimen relative to the bedding is given as dorsal, oblique, etc., the full explanation of the terms being given under *Preservation.*

Figures 11–35 are camera-lucida drawings showing parts of the animals present in a specimen and their relative levels within the rock. All or part of the specimen may be shown, and where counterparts are known some details from both may be incorporated in the drawing.

Symbols on the Plates and Figures are explained under *Terminology.* Depositories of specimens are USNM, United States National Museum, Washington, D.C., and GSC, Geological Survey of Canada, Ottawa.

The items explaining individual figures on the plates are arranged in the following order: depository and specimen number, orientation of specimen, direction of incident radiation, magnification, reference to previous illustration, comment and/or reference to Figure, locality and horizon in terms discussed in the text.

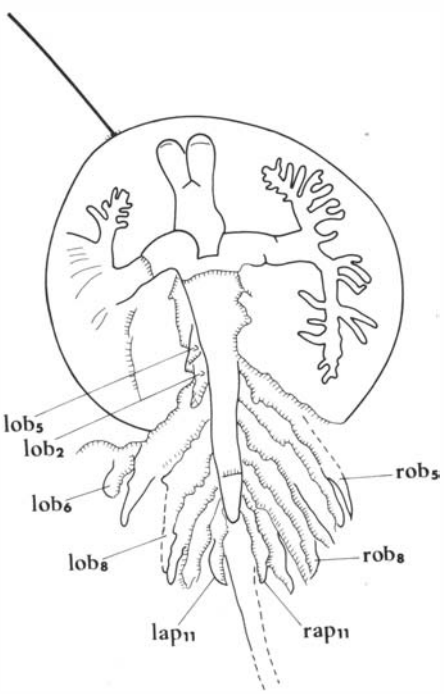


Fig. 11.

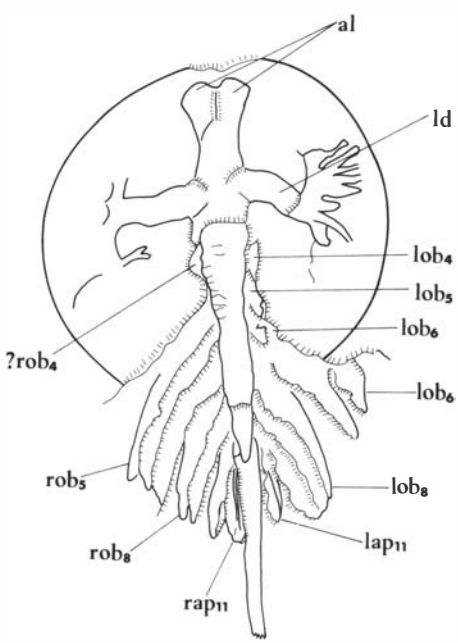
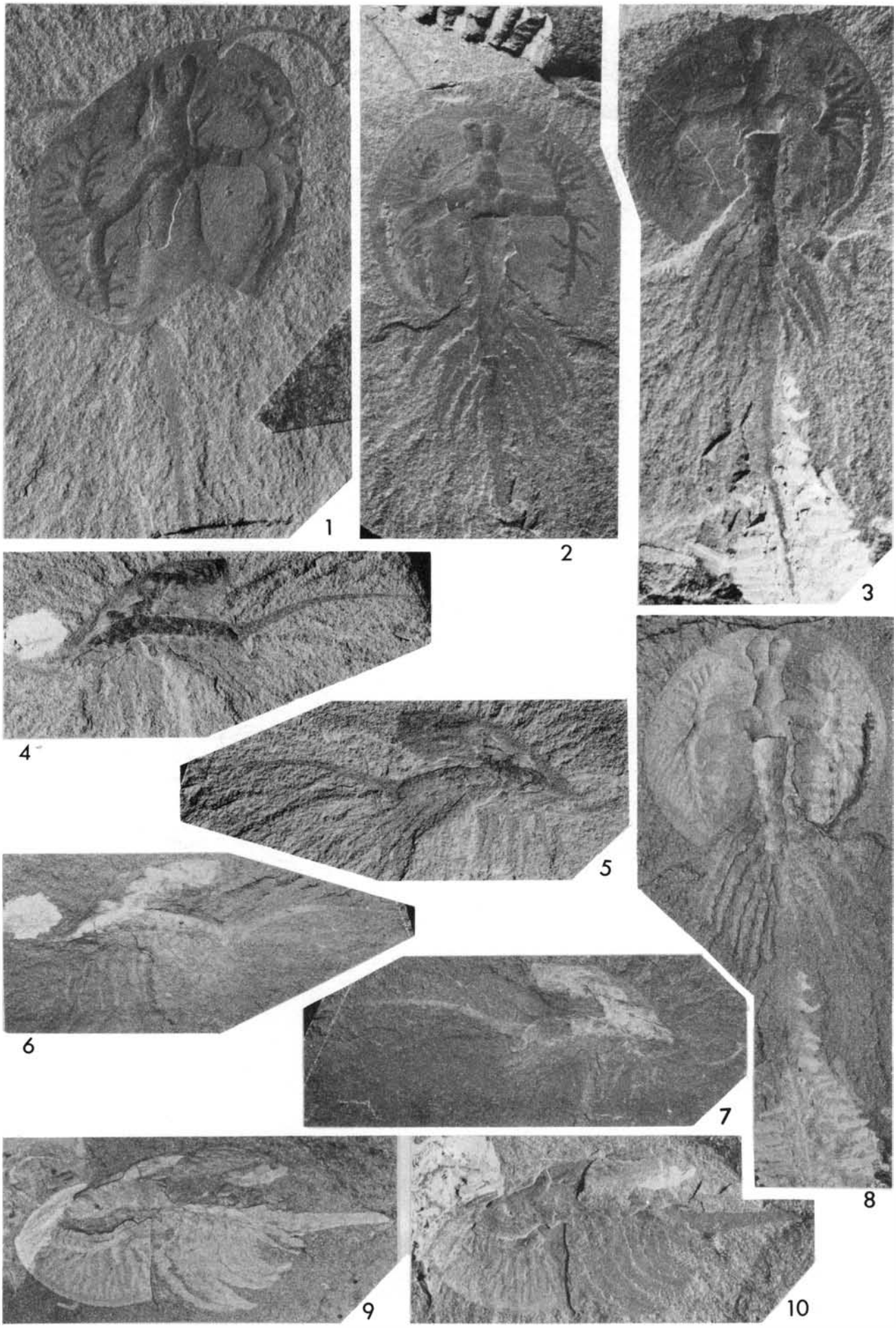


Fig. 12.

Plate 1

Burgessia bella Walcott, 1912. Phyllopod bed, Walcott quarry.

Fig. 1. USNM 57677, dorsal, west. X5, original of Walcott 1912, Pl. 27: 2; Simonetta 1970, Pl. 28: 2. *Figs. 2, 3, 8.* USNM 57676, part and counterpart 2. Dorsal, northwest, X5, see Fig. 11. 3. Ventral, northwest, X5, see Fig. 12, 8. Ventral, reflected, X5, original of Walcott 1912, Pl. 27: 1, Simonetta 1970, Pl. 28: 1a, b. *Figs. 4–7.* USNM 57680, part and counterpart. 4. Lateral, west, X3. 5. Lateral, west, X3. 6, 7. reflected, X3, original of Walcott 1912, Pl. 30: 3, Simonetta 1970, Pl. 28: 3a, b. *Figs. 9, 10.* USNM 155667, oblique. 9. Reflected, X5. 10. West, X5, original of Simonetta 1970, Pl. 32: 2.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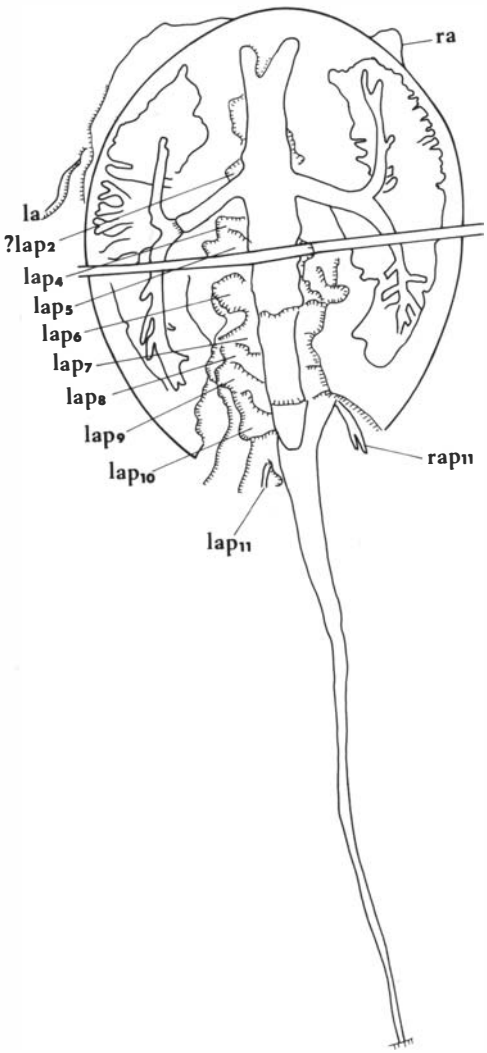


Fig. 13.

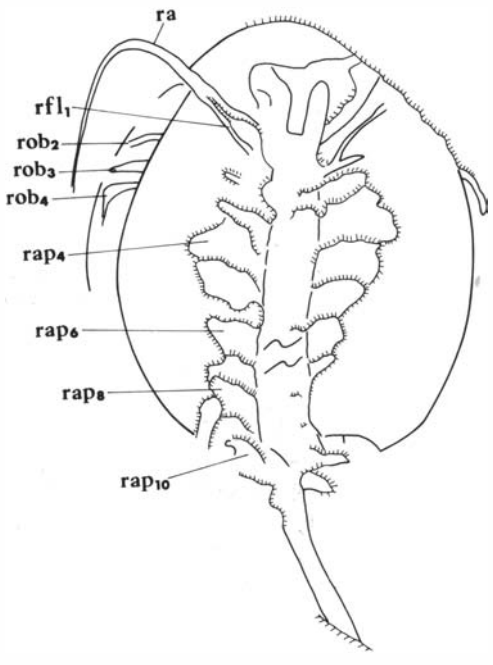


Fig. 14.

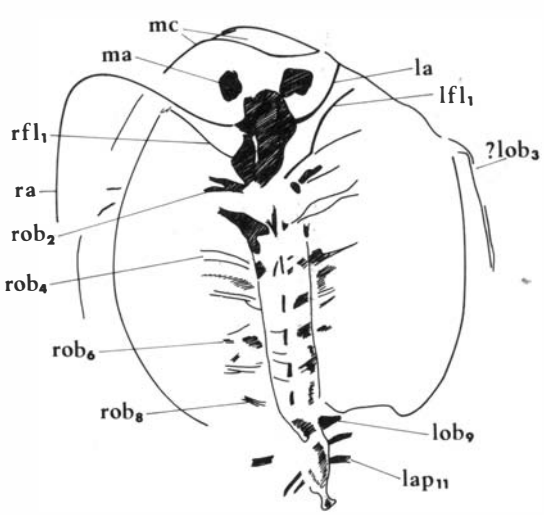
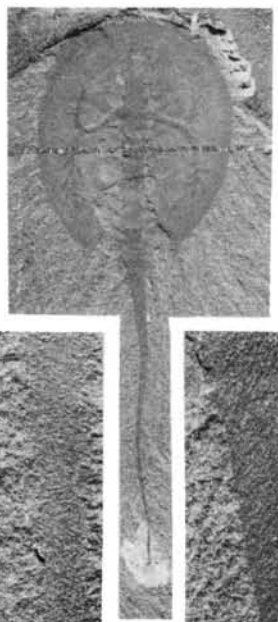


Fig. 15.

Plate 2

Burgessia bella Walcott, 1912. Phyllopod bed, Walcott quarry.

Figs. 1, 5, 8. USNM 83947d, dorsal. 1. North, X2½. 5. North, X10. 8. Reflected, X2½; original of Walcott 1931, Pl. 15: 7. Shows fractures in caudal spine, see Fig. 13. *Figs. 2, 4, 10.* USNM 83947b, dorsal. 2. Northwest, X2½. 4. North, X10. 10. Reflected, X2½; original of Walcott 1931, Pl. 15: 5. *Figs. 3, 7.* USNM 83947c, ventral. 3. Reflected, X5. 7. North, X5; original of Walcott 1931, Pl. 15: 6. See Fig. 15. *Figs. 6, 9.* USNM 57678, ventral. 6. Reflected, X5. 9. North, X5; original of Walcott 1912, Pl. 27: 3, Simonetta 1970, Pl. 28: 5. See Fig. 14.



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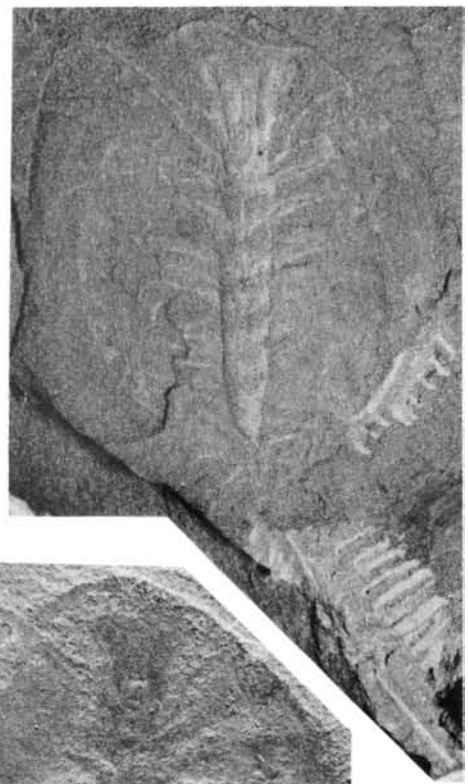

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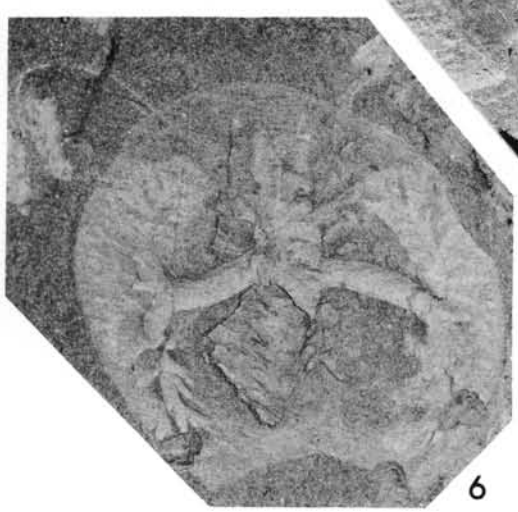

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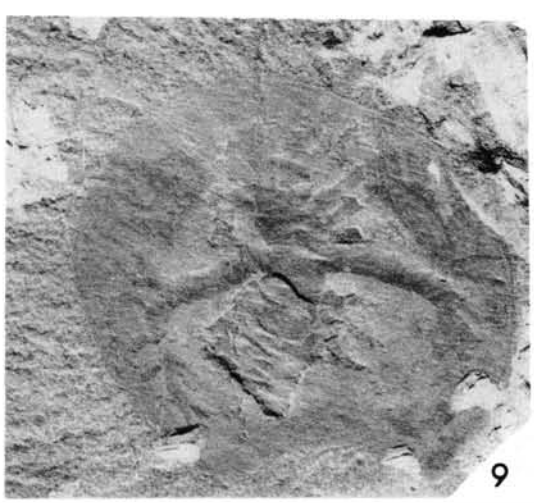

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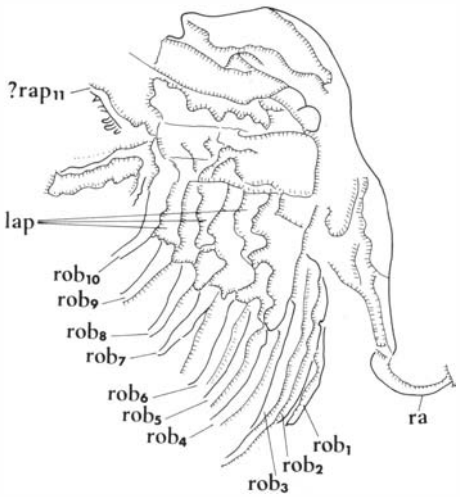

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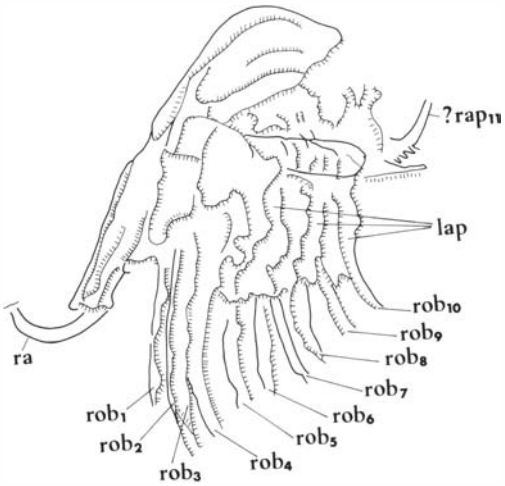


Fig. 17.

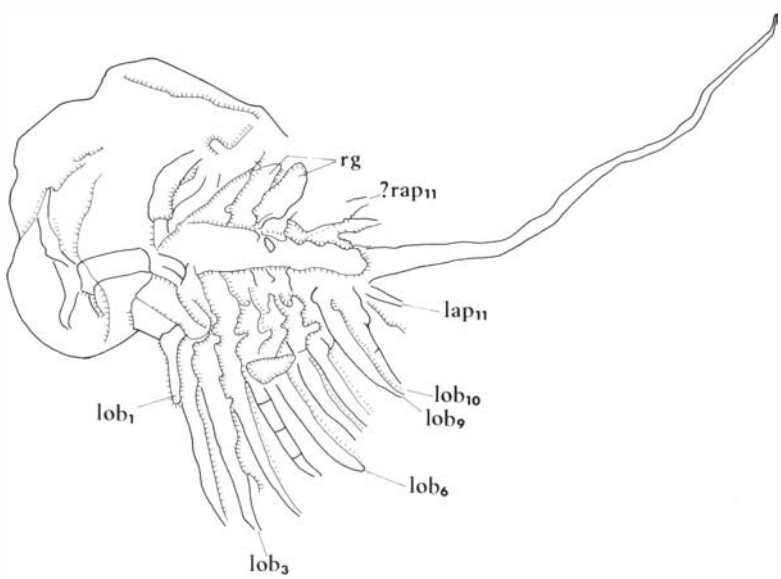
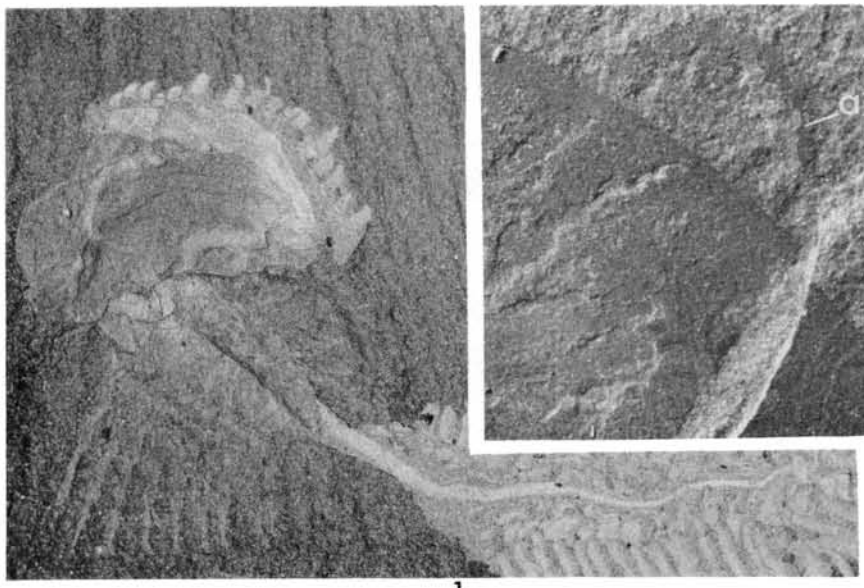


Fig. 18.

Plate 3

Burgessia bella Walcott, 1912. Phyllopod bed, Walcott quarry.

Figs. 1, 8. USNM 83947a, oblique. 1. Reflected, X5. 8. South, X5; original of Walcott 1931, Pl. 15: 4. See Fig. 18. *Fig. 2.* USNM 83947b, dorsal, northwest, X10. Shows one flagellum (fl). See Pl. 2: 2. *Figs. 3, 6.* USNM 155632, dorsal. 3. Reflected, X2½ 6. North, X2½, original of Simonetta 1970, Pl. 28: 8. *Figs. 4, 5, 7, 9.* USNM 83947e, part and counterpart, oblique. 4, 5. North X5, 7, 9. Reflected, X5, original of Walcott 1931, Pl. 16: 1. See Figs. 16, 17.



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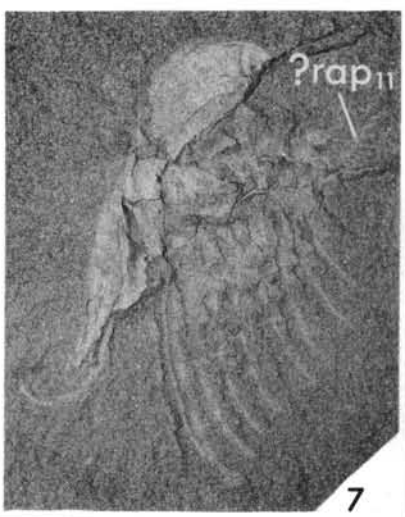

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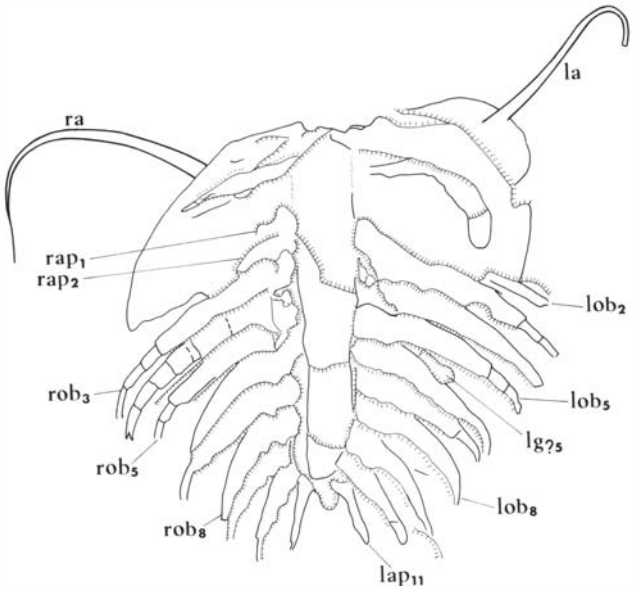

Fig. 19.

Plate 4

Burgessia bella Walcott, 1912. Phyllopod bed, Walcott quarry.

Figs. 1, 3. USNM 83947g, oblique lateral. 1. Reflected, X5. 3. West, X5; original of Walcott, 1931, Pl. 16: 3. *Figs. 2, 4.* USNM 83947f, ventral. 2. Reflected, X5. 4. North, X5; original of Walcott 1931, Pl. 16: 2. See Fig. 19. *Figs. 5, 6.* USNM 83947h, dorsal. 5. Reflected, X5. 6. Northwest, X5; original of Walcott 1931, Pl. 16: 4.

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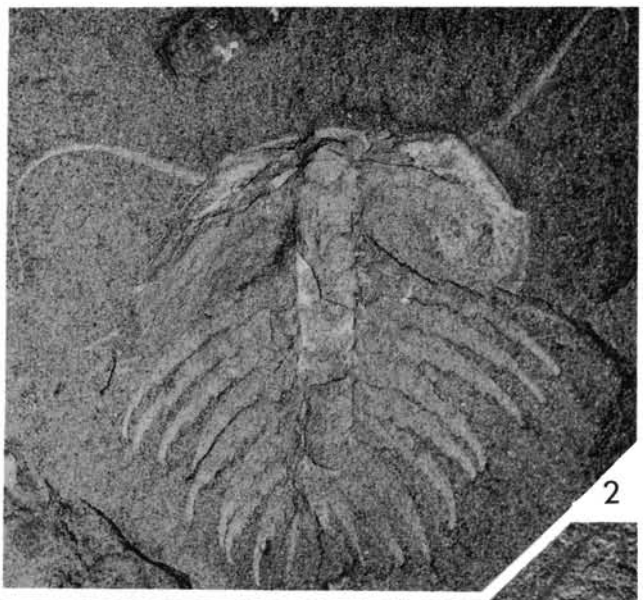

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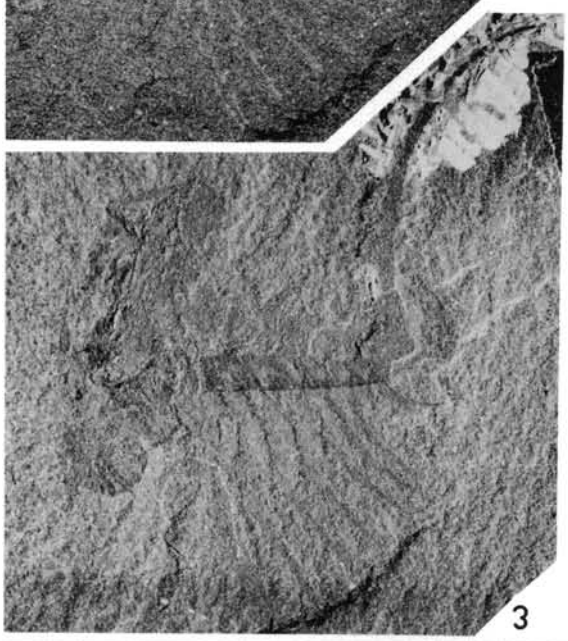

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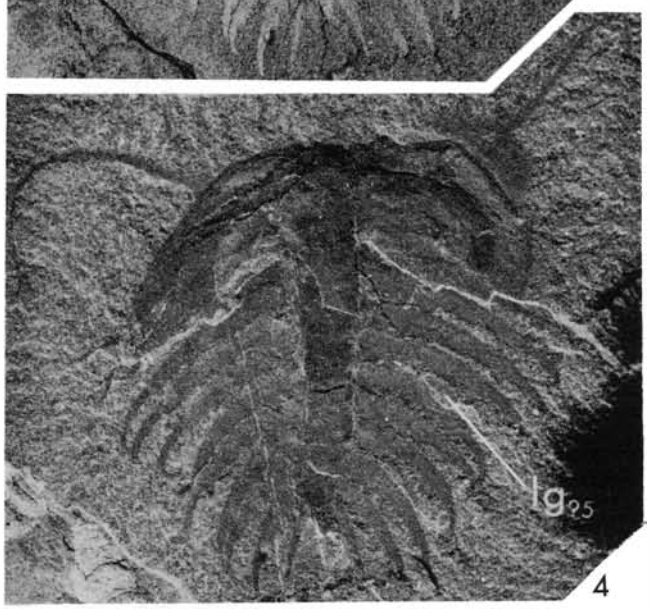

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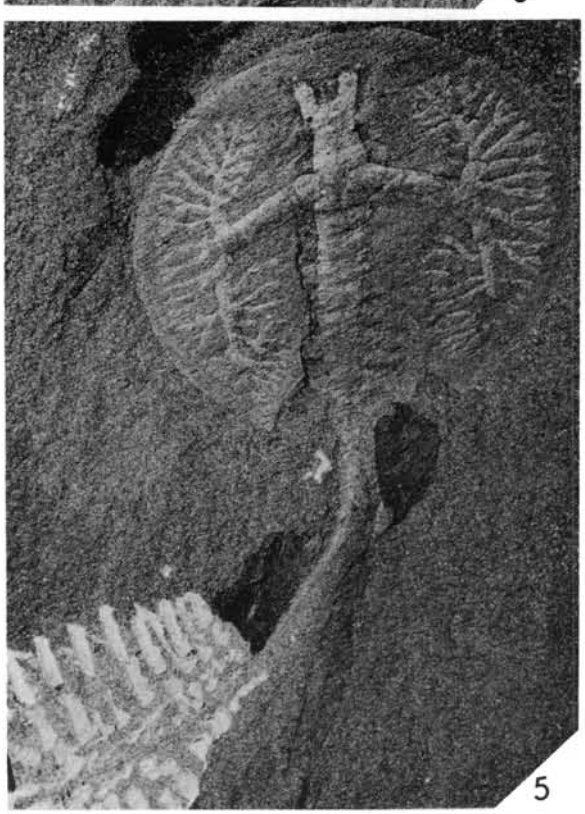

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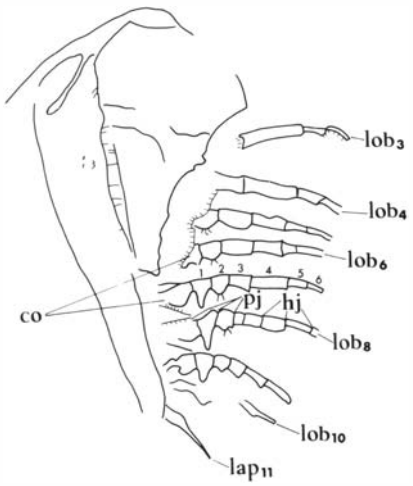

Fig. 20.

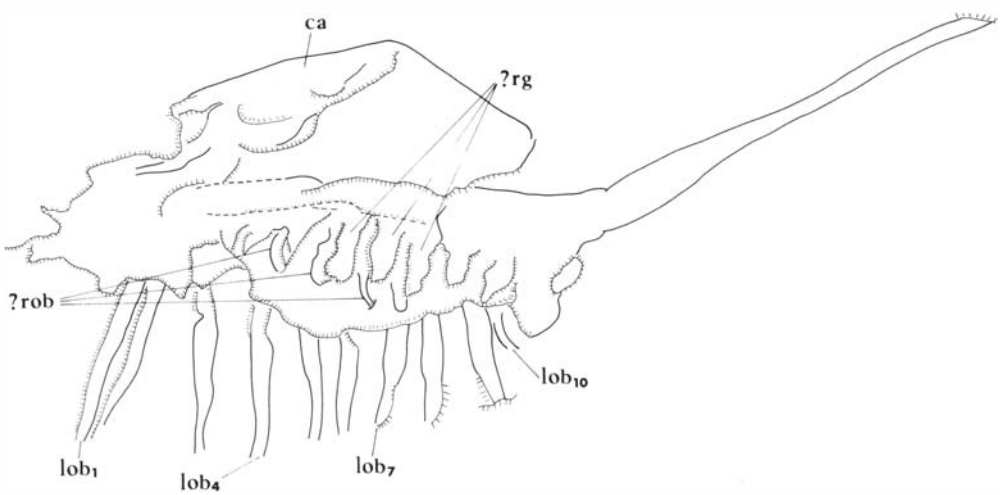

Fig. 21.

Plate 5

Burgessia bella Walcott, 1912. Phyllopod bed, Walcott quarry.

Figs. 1, 3, 4. USNM 83947m, part and counterpart. 1, 3. Ventral. 1. Northwest, X5. 3. Reflected, X5. 4. Dorsal, reflected, X5; original of Walcott 1931, Pl. 17: 3. See Pl. 6: 1. *Figs. 2, 5.* USNM 83947i, dorsal. 2. Reflected, X10. 5. South, X5; original of Walcott 1931, Pl. 16: 5. Shows details of walking-legs. See Fig. 20. *Figs. 6, 7.* USNM 83947j, lateral. 6. Reflected, X5. 7. North, X2½; original of Walcott 1931, Pl. 16: 6. See Fig. 21.

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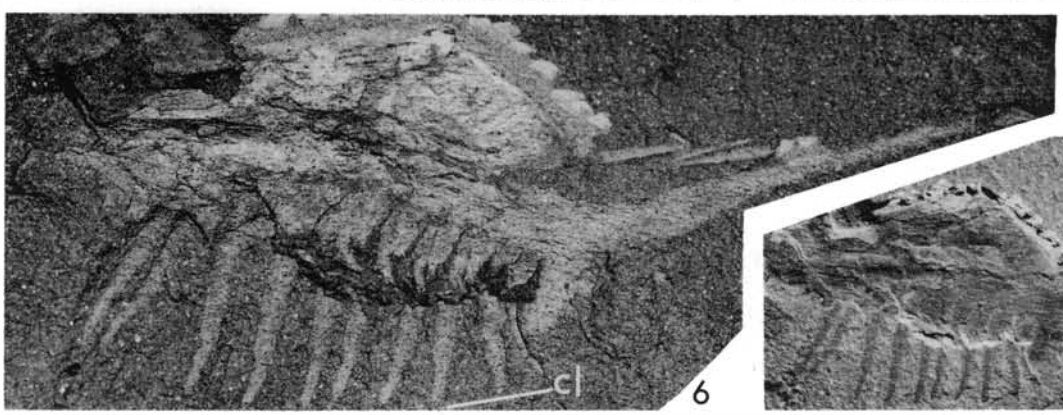

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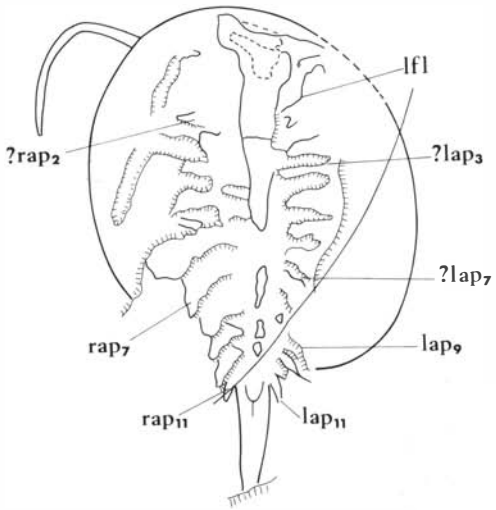
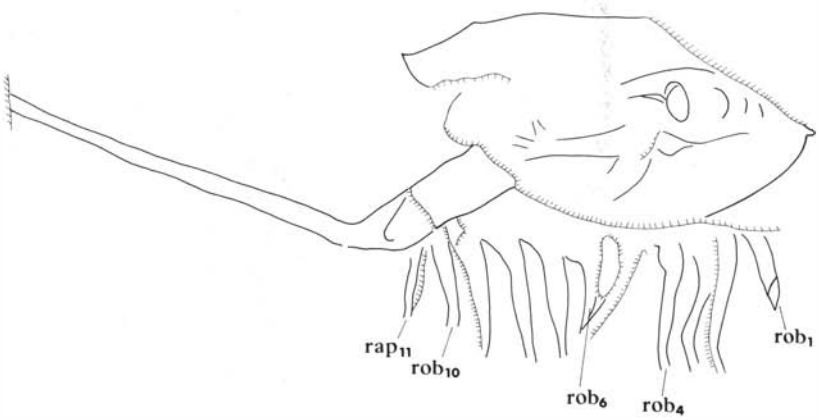


Fig. 22.



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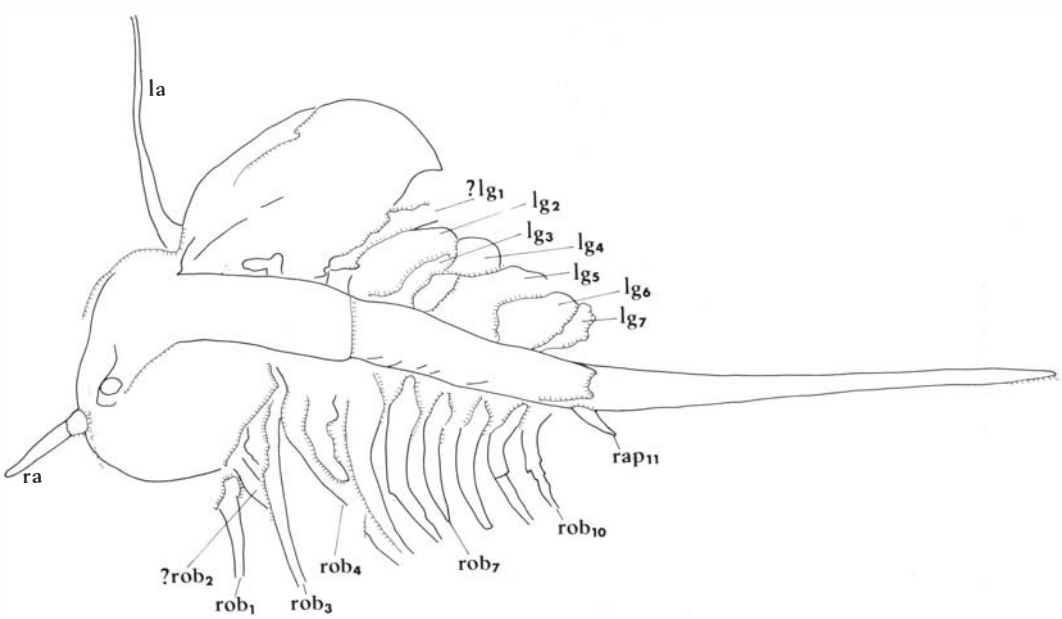

Fig. 24.

Plate 6

Burgessia bella Walcott, 1912. Phyllopod bed, Walcott quarry.

Fig. 1. USNM 83947m, ventral, north, X5; original of Walcott 1931, Pl. 17: 3. See Pl. 5: 1, 3, 4. and Fig. 22. *Fig. 2, 5.* USNM 83947k, lateral. 2. Reflected, X5. 5. West, X5; original of Walcott 1931, Pl. 17: 1. *Figs. 3, 4.* USNM 839471, lateral. 3. West, X2½. 4. Reflected, X2½; original of Walcott 1931, Pl. 17: 2. *Figs. 6, 8.* USNM 83947n, ventral, west. 6. X10. 8. X2½; original of Walcott 1931, Pl. 17: 4. Shows details of gill branches. See Fig. 24. *Figs. 7, 9.* USNM 83947o, lateral. 7. North, X5. 9. Reflected, X5; original of Walcott 1931, Pl. 18: 1. See Fig. 23.

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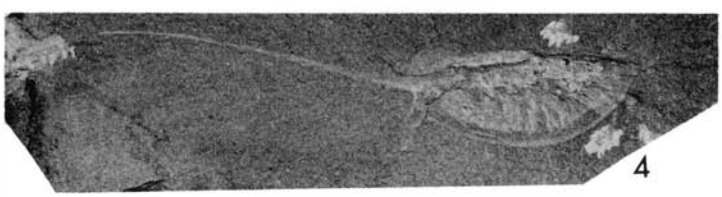

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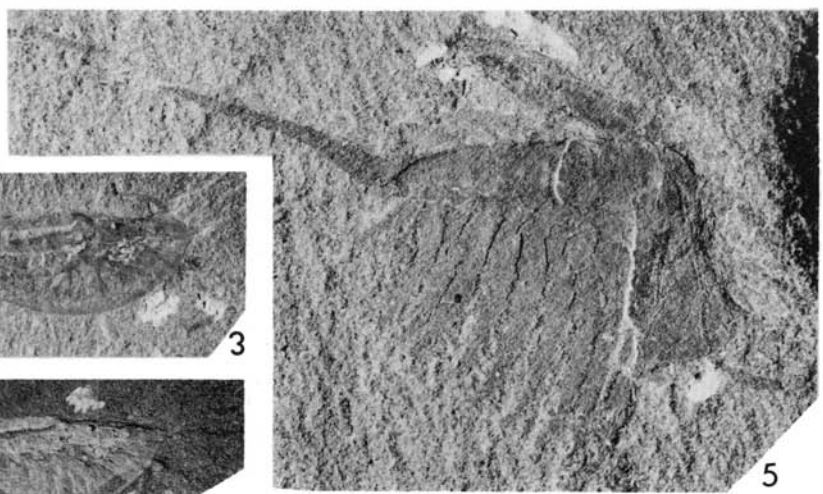

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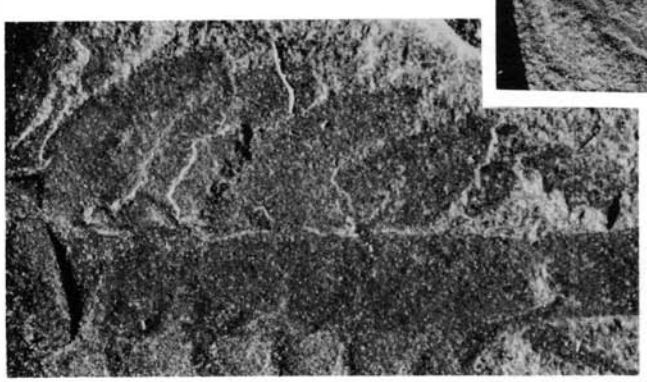

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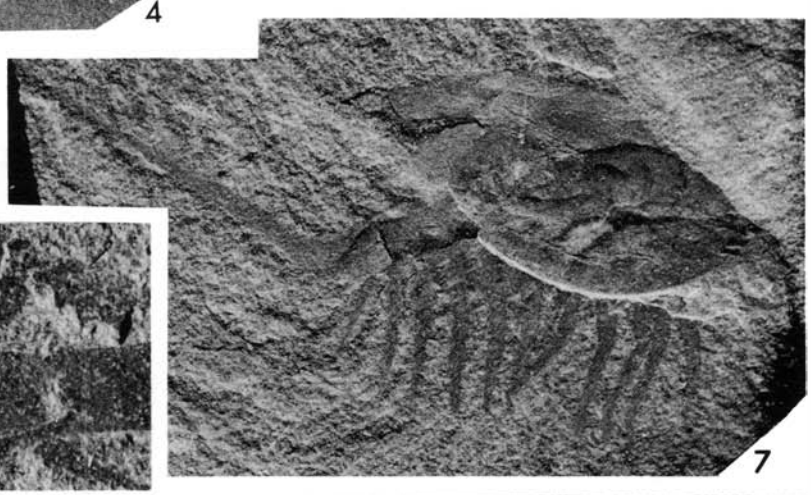

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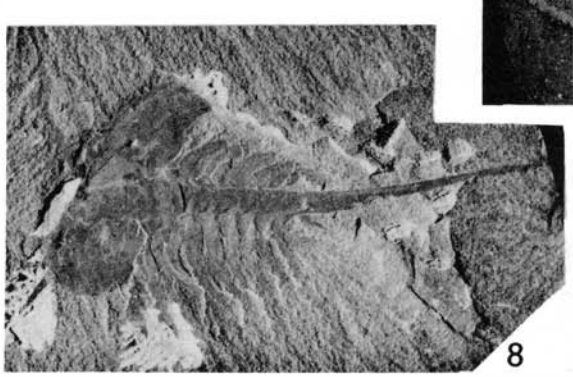

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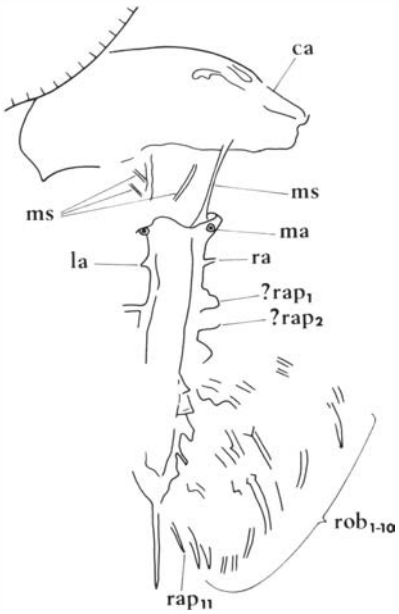

Fig. 25.

Plate 7

Burgessia bella Walcott, 1912.

Figs. 1, 2. GSC 35459, dorsal. 1. Northwest, X5. 2. Reflected, X5. See Fig. 25. Walcott quarry, level 6'7½" to 7'3½". *Figs. 3, 5.* USNM 155676, dorsal. 3. Reflected, X5. 5. Northwest, X5; original of Simonetta 1970, Pl. 32: 3. Phyllopod bed, Walcott quarry. *Figs. 4, 6, 7.* USNM 155624, ventral. 4. West, X10. 6. West, X2½. 7. Reflected, X2½; original of Simonetta 1970, Pl. 30: 3. Phyllopod bed, Walcott quarry. *Figs. 8, 10.* USNM 155680, oblique. 8. Northeast, X5. 10. Reflected, X5; original of Simonetta 1970, Pl. 28: 6. Phyllopod bed, Walcott quarry. *Fig. 9.* USNM 155630, dorsal, reflected, X5; original of Simonetta 1970, Pl. 32: 1. Phyllopod bed, Walcott quarry.

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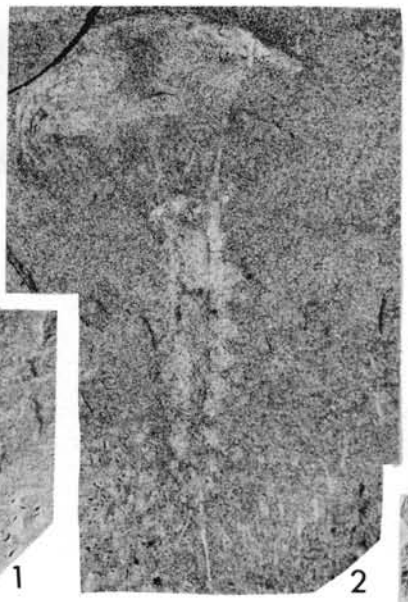

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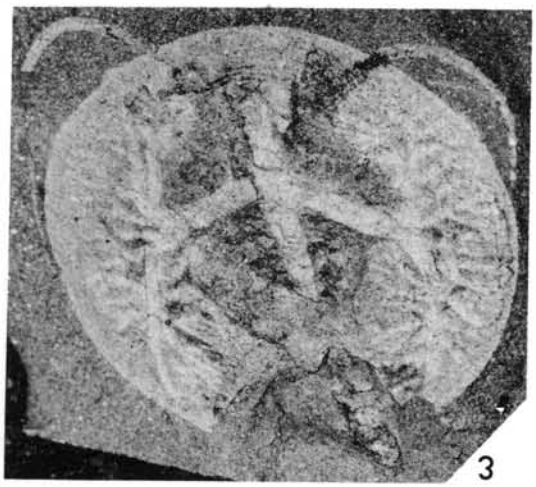

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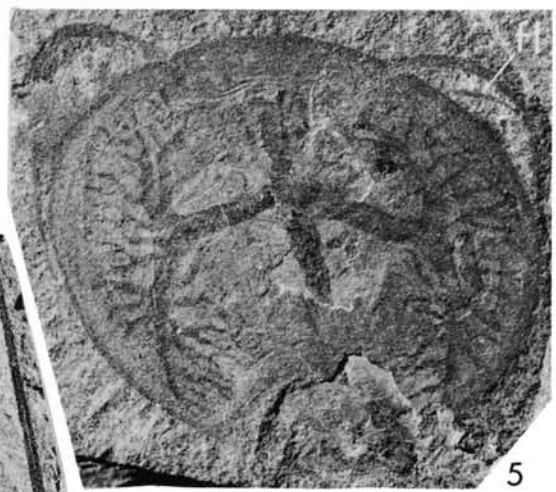

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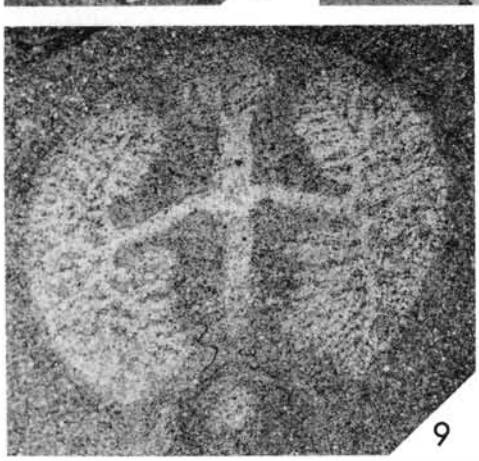

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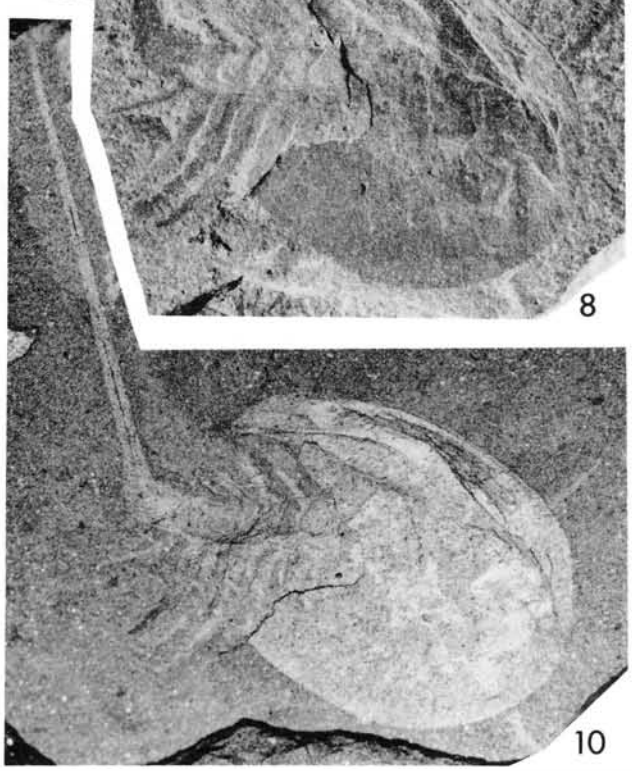

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Plate 8

Burgessia bella Walcott, 1912. Phyllopod bed, Walcott quarry.

Figs. 1, 5. USNM 155623, oblique lateral. 1. Northwest, X4. 5. Reflected, X4; original of Simonetta 1970, Pl. 30: 1. *Figs. 2, 7.* USNM 114243, part and counterpart. 2. Oblique lateral, north, X4. 6. Oblique lateral, west, X4; originals of Simonetta 1970, pl. 28: 10a, b. *Figs. 3, 4.* USNM 155626, oblique lateral. 3. Southwest, X4. 4. Reflected, X4; original of Simonetta 1970, Pl. 28: 9. *Fig. 6.* USNM 155665, ventral, north, X10; original of Simonetta 1970, Pl. 32: 4. *Fig. 8.* USNM 114240, lateral, northeast, X5; original of Simonetta 1970, Pl. 30: 2.

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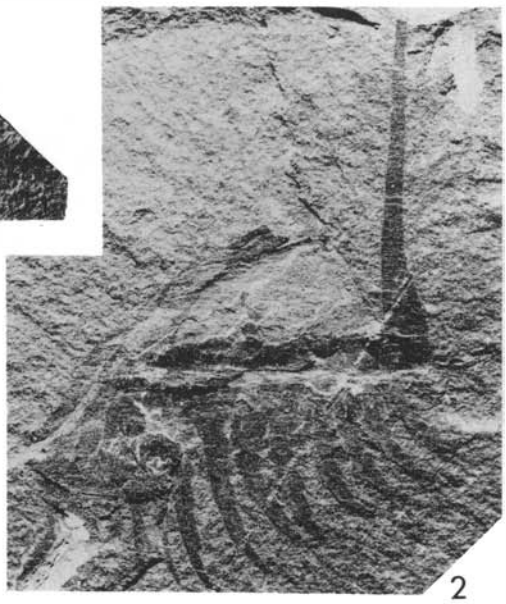

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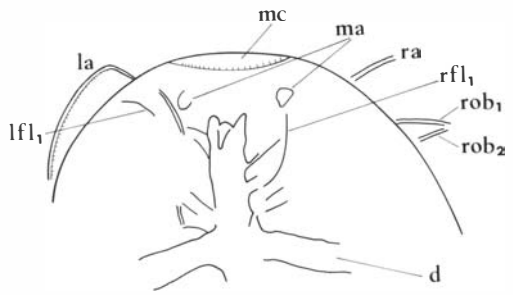

Fig. 26.

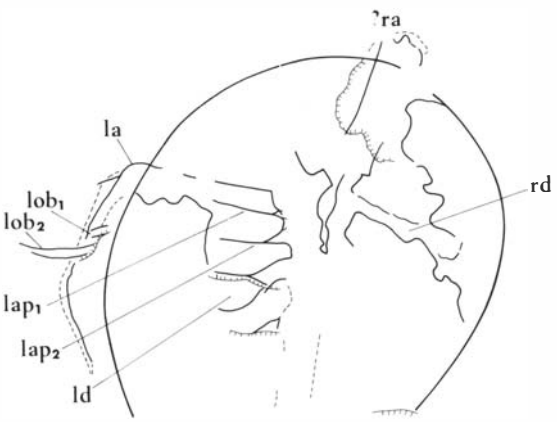

Fig. 27.

Plate 9

Burgessia bella Walcott, 1912

Fig. 1. USNM 204711, dorsal, south, X10. Smallest identified specimen. Phyllopod bed, Walcott quarry. *Fig. 2.* USNM 204717, dorsal, reflected, X5. Phyllopod bed, Walcott quarry. *Fig. 3.* USNM 204709, dorsal, reflected, X5. Phyllopod bed, Walcott quarry. See Fig. 26. *Figs. 4, 6.*-USNM 204703, ventral. 4. Reflected, X5. 6. North, X5. Phyllopod bed, Walcott quarry. *Fig. 5.* GSC 35457, dorsal, reflected, X5. Walcott quarry, level 8'7". See Fig. 27. *Fig. 7.* USNM 204707, dorsal, reflected, X5. Phyllopod bed, Walcott quarry. *Fig. 8.* USNM 204716, dorsal, reflected, X5. Phyllopod bed, Walcott quarry.

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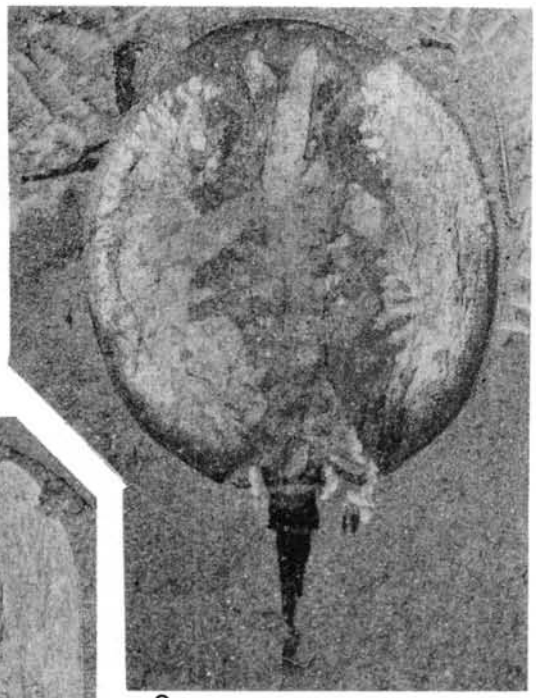

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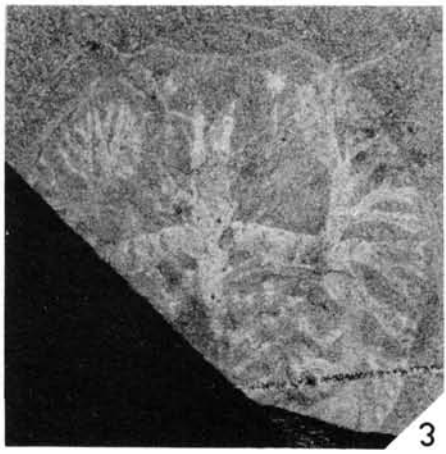

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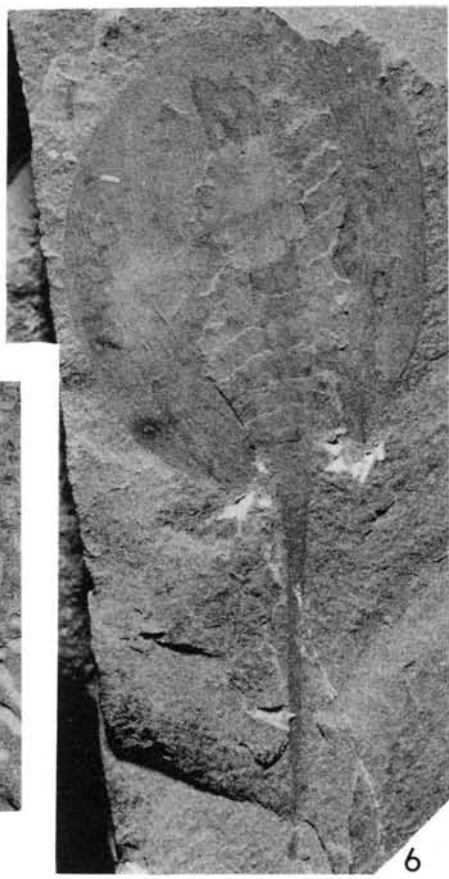

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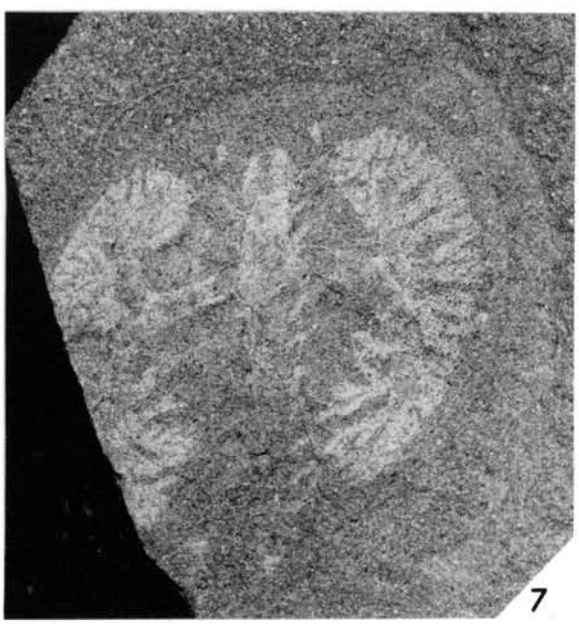

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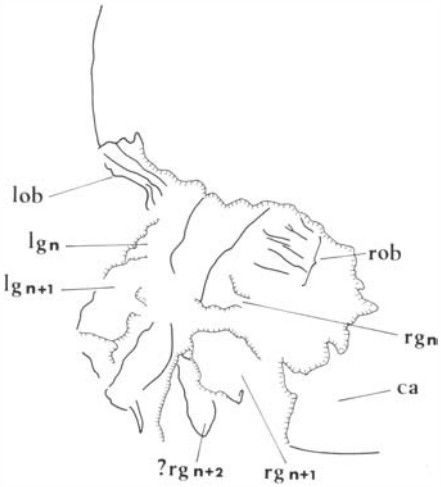
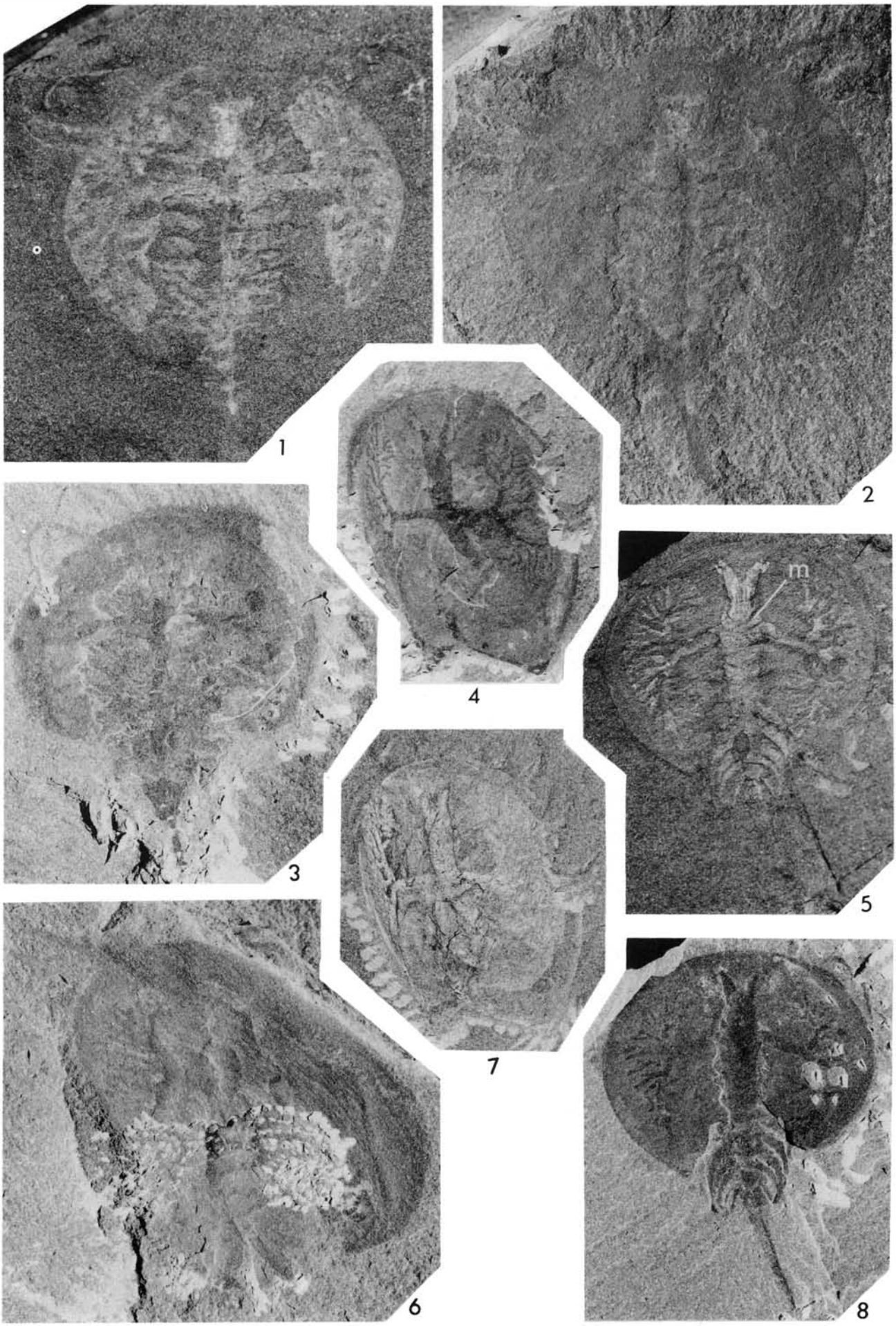


Fig. 28.

Plate 10

Burgessia bella Walcott, 1912

Figs. 1, 2. USNM 114242, dorsal. 1. Reflected, X5. 2. West. X5. Shows gill branches. Phyllopod bed, Walcott quarry. *Fig. 3.* GSC 35454, dorsal, west, X5. Walcott quarry, level 7'0". *Figs. 4, 7.* USNM 204710, dorsal. 4. North, X5. 7. Reflected, X5. Shows unsclerotized cuticle pulled away from margin posteriorly and right laterally. Phyllopod bed, Walcott quarry. *Figs. 5, 8.* GSC 35455, ventral. 5. Reflected, X5. 8. Northwest, X5. Shows position of mouth. Walcott quarry, level 6'11" to 7'4". *Fig. 6.* USNM 204713, dorsal, west, X5. Phyllopod bed, Walcott quarry. See Fig. 28.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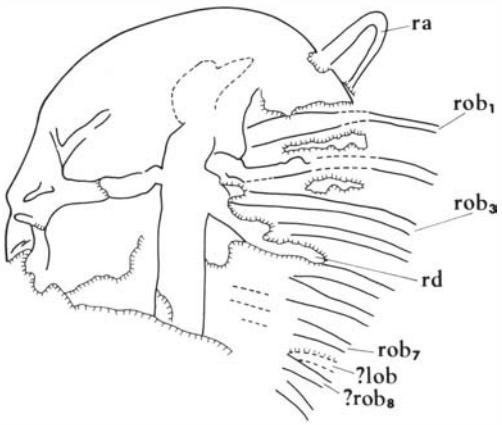

Fig. 29.

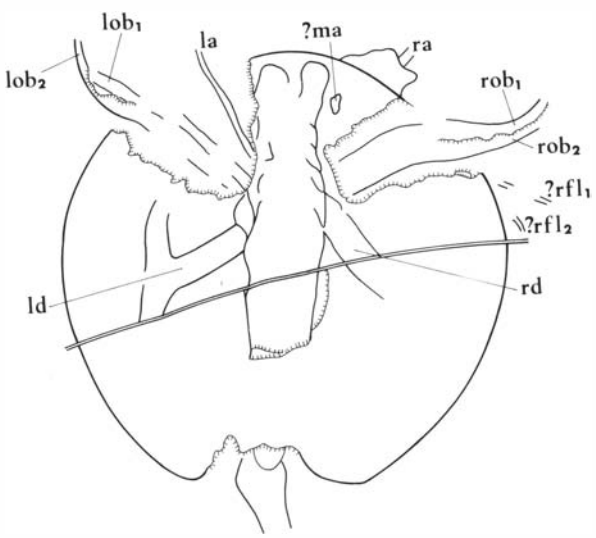

Fig. 30.

Plate 11

Burgessia bella Walcott, 1912

Figs. 1, 3. USNM 204719, oblique. 1. North, X10. 3. Northwest, X5. Shows detail of walking-legs. Phyllopod bed, Walcott quarry. *Figs. 2, 7.* GSC 35458, dorsal. 2. Reflected, X5. 7. Northwest, X5. Shows position of walking-legs beneath carapace. See Fig. 29. Walcott quarry, level 5'1" to 5'6". *Fig. 4.* GSC 35460, ventral, north, X5. Walcott quarry level 6'7" to 7'3½". *Figs. 5.* GSC 35463, dorsal, north, X5. Shows two walking-legs anterior to the diverticulum. Walcott quarry, level 6'11" to 7'0". See Fig. 30. *Fig. 6.* USNM 204706, dorsal, west, X5. Phyllopod bed, Walcott quarry. *Fig. 8.* USNM 204705, dorsal, west, X5. Shows gill branches posteriorly. Phyllopod bed, Walcott quarry.

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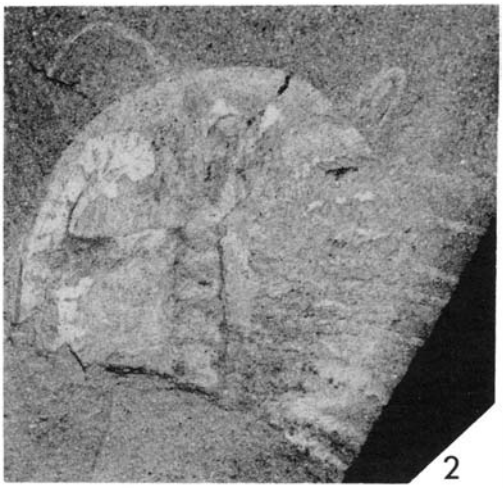

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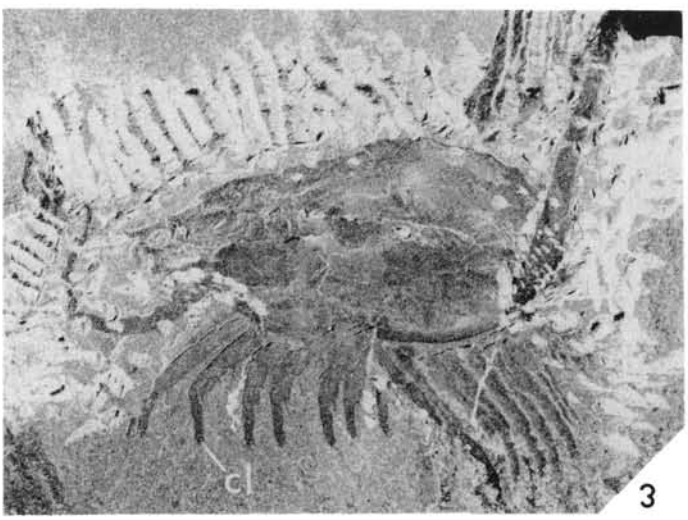

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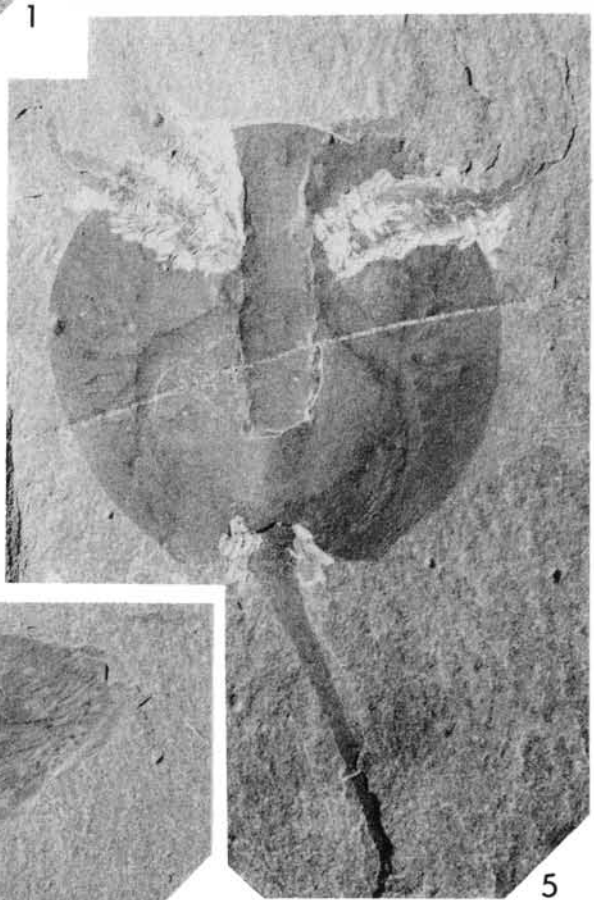

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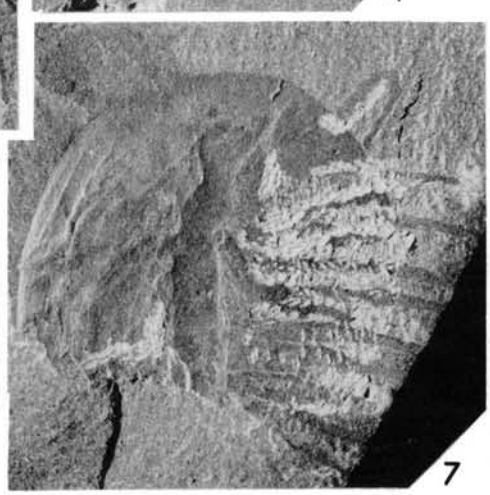

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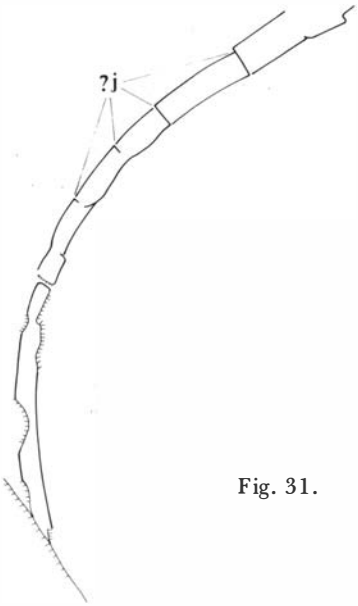


Fig. 31.

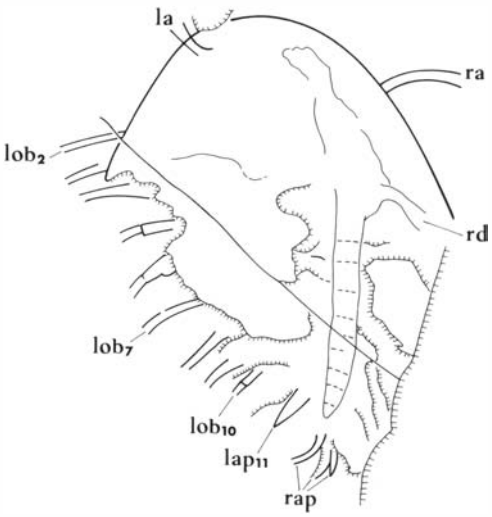


Fig. 32.

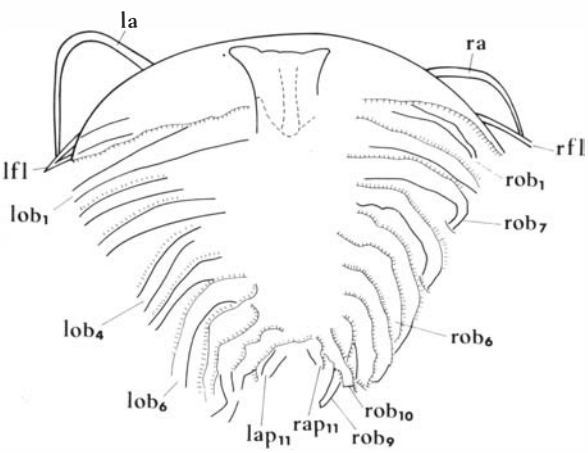
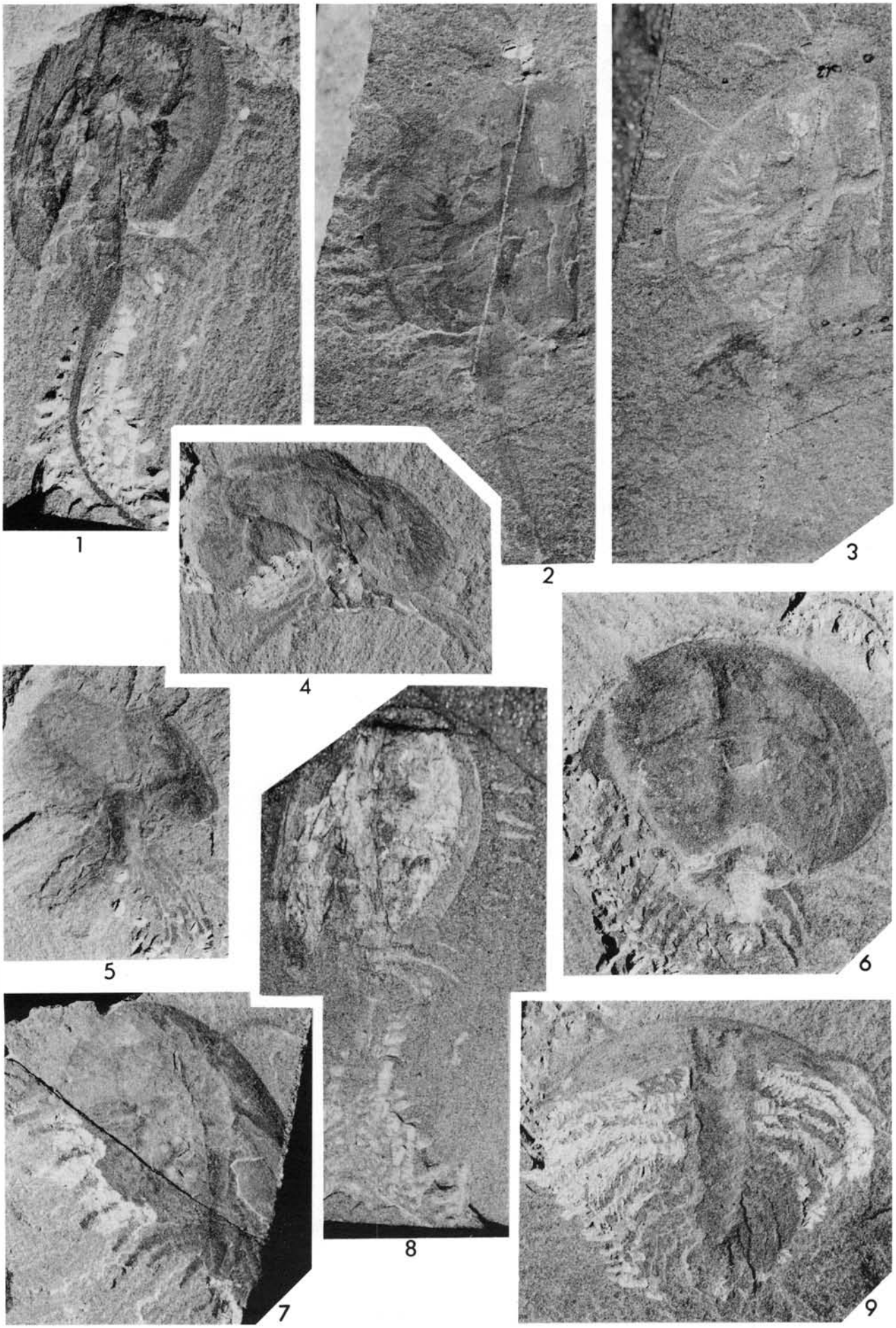


Fig. 33.

Plate 12

Burgessia bella Walcott, 1912

Figs. 1, 8. USNM 204712, ventral. 1. Northwest, X5. 8. Reflected, X5. Shows possible segmentation of caudal spine. See Fig. 31. Phyllopod bed, Walcott quarry. *Figs. 2, 3.* GSC 35456, ventral. 2. North, X5. 3. Reflected, X5. Walcott quarry, level 6'11" to 7'0". *Fig. 4.* USNM 204714, oblique, west, X5. Phyllopod bed, Walcott quarry. *Fig. 5.* USNM 204708, oblique, northwest, X5. Phyllopod bed, Walcott quarry. *Fig. 6.* GSC 35453, ventral, west, X5. Walcott quarry level 7'3". *Fig. 7.* GSC 35462, dorsal, northwest, X5. Walcott quarry, level 6'7" to 7'3½". See Fig. 32. *Fig. 9.* GSC 35461, dorsal, northwest, X5. See Fig. 33. Walcott quarry, level 6'7½" to 7'3½".



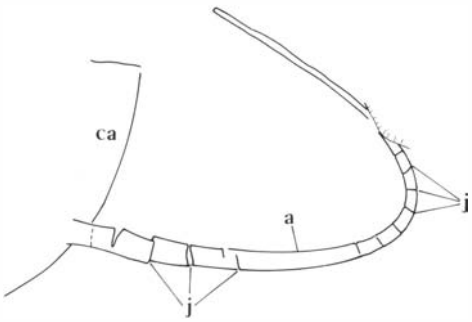


Fig. 34.

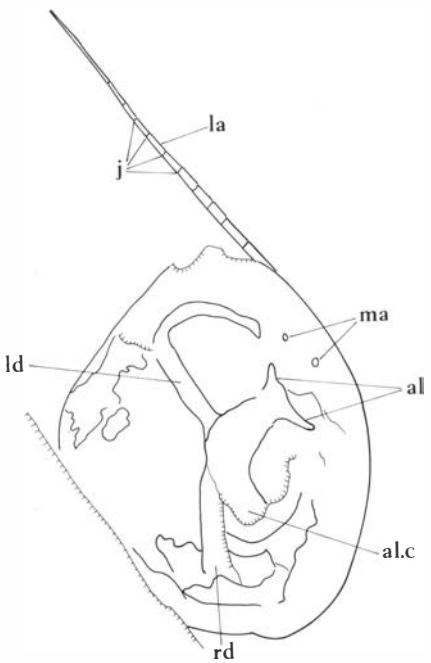


Fig. 35.

Plate 13

Burgessia bella Walcott, 1912. Phyllopod bed, Walcott quarry.

Figs. 1, 3. USNM 204704, oblique lateral. 1. West, X10. 3. Reflected, X5. *Figs. 2, 5.* USNM 204715, dorsal, 2. Northwest, X5. 5. Reflected, X5. Shows segmentation of antenna. See Fig. 34. *Fig. 4.* USNM 204718, oblique, reflected, X5. Shows segmentation of antenna. See Fig. 35. *Figs. 6, 7.* USNM 155669, ventral. 6. West, X5. 7. Reflected, X5; original of Simonetta 1970, Pl. 28: 7.

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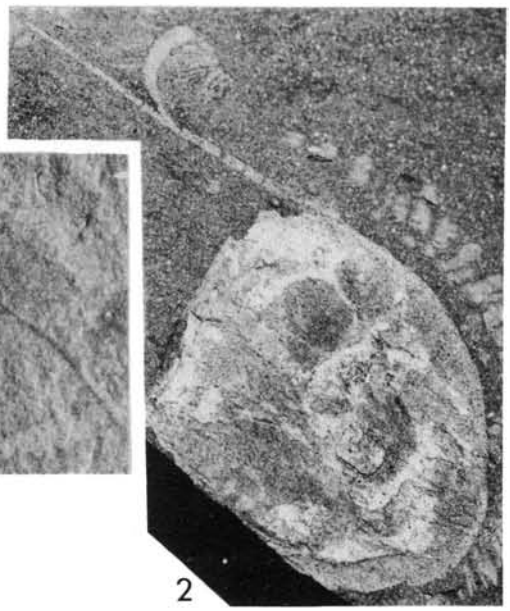

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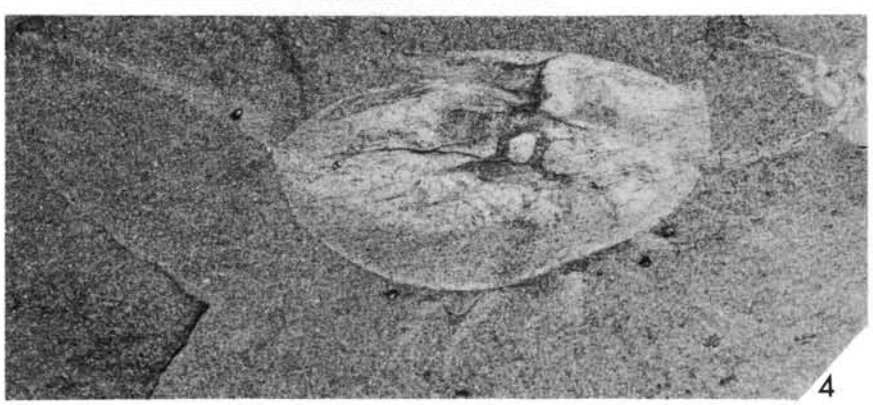

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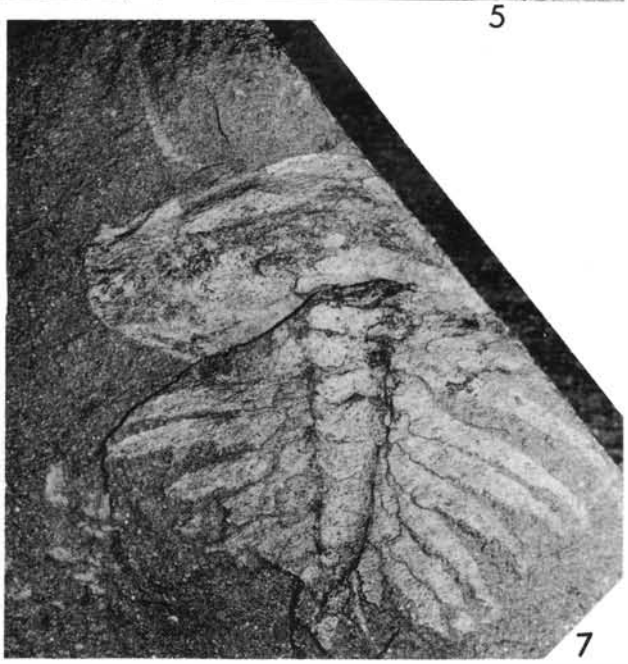

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