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THE ARTHROPOD *BRANCHIOCARIS* N. GEN., MIDDLE CAMBRIAN, BURGESS SHALE, BRITISH COLUMBIA

D. E. G. Briggs

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Preface

The world famous Burgess Shale of Yoho National Park, British Columbia, is unique because of its remarkable and diverse Cambrian fauna, including the primitive ancestors of nearly every class of arthropod as well as several other animal phyla.

The small quarry lying high above Emerald Lake, from which C.D. Walcott obtained the material on which he based his studies, was reopened by the Geological Survey in 1966 and 1967 and much additional material was obtained. The results of detailed studies of this material by paleontologists from within and outside the Geological Survey are being published in our Bulletin series.

In this report the author presents the results of a study of the bivalved arthropod *Protocaris pretiosa* Resser, 1929. On the basis of new information he has removed the species to a new genus, *Branchiocaris*. To facilitate his study Dr. Briggs also re-examined two other species and the results of these redescriptions are also published.

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

D.J. McLaren
Director General
Geological Survey of Canada

Ottawa, 18 November 1975

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Abstract

A study of new specimens of the bivalved arthropod *Protocaris pretiosa* Resser, 1929 from the Burgess Shale has added much information to the original description, and the species is removed to a new genus *Branchiocaris*. *Protocaris marshi* Walcott, 1884 and *Dioxycaris argenta* (Walcott, 1886) are also redescribed to facilitate comparison.

The cephalic region of *Branchiocaris pretiosa* bore a paired antenna anterior to a pair of stout appendages which may have been chelate. Suboval valves, the dorsal margin terminating anteriorly and posteriorly in a small pointed process, covered the anterior of the body. The trunk included about 46 divisions followed by a telson bearing a pair of short pointed processes. The lamellate trunk appendages may have been biramous, with a short, segmented proximal element. The animal probably swam near the seabed by metachronal movements of the lamellate appendages, which may also have functioned in respiration. *B. pretiosa* shows closest affinities to the branchiopod Crustacea among extant arthropods but is considered unlikely to represent a direct evolutionary predecessor of this group.

The trunk of *Protocaris marshi* included about 65 divisions; the telson processes were elongate and curved. The appendages are unknown. The carapace of *Dioxycaris argenta* is similar in outline and size to that of *Branchiocaris pretiosa* but the only known specimen is poorly preserved and lacks evidence of the soft-part morphology.

Résumé

Une étude de nouveaux spécimens de l'arthropode bivalve *Protocaris pretiosa* Resser 1929, trouvés dans le schiste de Burgess a permis d'ajouter de nouveaux éléments d'information à la description originale et de classer l'espèce dans un nouveau genre *Branchiocaris*. Ce document présente en outre une nouvelle description de *Protocaris marshi* Walcott, 1884, et de *Dioxycaris argenta* (Walcott, 1886), pour faciliter la comparaison.

La région céphalique de *Branchiocaris pretiosa* portait une paire d'antennes devant une paire de gros appendices, qui étaient peut-être des chélicères. Les valves qui couvraient la partie antérieure du corps avaient une forme presque ovale, le sillon dorsal se terminant à l'avant comme à l'arrière en une petite excroissance pointue. Le thorax se composait d'environ 46 segments antérieurs d'un telson qui portait à son extrémité une paire de courts prolongements en forme de pointe. Les appendices du thorax étaient lamellés; il est possible qu'ils aient été biramés et pourvus de parties proximales courtes et segmentées. L'animal nageait probablement près du lit de la mer par des mouvements de ses appendices lamellés qui servaient peut-être aussi d'organes de respiration. *B. pretiosa* présente les plus grandes affinités avec les crustacés phyllopodes (branchiopodes) de tous les arthropodes existants; cependant, il est peu probable qu'il constitue un prédécesseur direct de ce groupe.

Le thorax de *Protocaris marshi* était formé d'environ 65 segments; les prolongements du telson étaient allongés et courbés. On ne connaît rien sur les appendices. La carapace de *Dioxycaris argenta* ressemble à celle de *Branchiocaris pretiosa* par son profil et ses dimensions; toutefois le seul spécimen connu est mal conservé et il manque trop d'éléments pour qu'on puisse définir la morphologie de ses parties molles.

Introduction

Protocaris marshi was described by Walcott (1884) on the basis of a single specimen from the Lower Cambrian Parker Slate of Vermont. The original part and counterpart remain hitherto the only known material of this species; they have been re-examined, photographed, drawn and measured as a basis for a new description and reconstruction (Textfig. 1) presented in this report.

To this genus Resser (1929) referred a second species, *Protocaris pretiosa* from the Burgess Shale, basing his description on the part and counterpart of a single specimen in Walcott's collection in the United States National Museum. Rolfe (1962) listed a second specimen among some Burgess

Shale arthropods collected by the Museum of Comparative Zoology expedition of 1930, the counterpart of which was found by a Royal Ontario Museum party in 1975. The Geological Survey of Canada expeditions of 1966 and 1967 (Whittington, 1971a) yielded no further material of this species. The new description and reconstruction (Textfig. 2) are based on the two previously recorded specimens, together with an additional three that were subsequently discovered among Walcott's material in the United States National Museum. These five specimens have been studied, prepared where necessary, drawn and measured using techniques similar to those described by Whittington (1971b, 1974). The fossils are preserved orientated at various angles to the bedding planes and the morphological features lie in discrete layers—the carapace, for example, is separated by a layer of matrix from the trunk and appendages. Recognition of how a specimen is orientated (Whittington, 1971a) thus

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permits a differentiation between right and left, dorsal and ventral sides. Different levels are exposed by the splitting of the rock and by subsequent preparation. These differences are expressed by a minute 'scarp' on the specimen, which either casts a shadow or reflects light, depending on the angle of illumination. As far as possible, the plates illustrate the evidence on which the reconstruction (Textfig. 2) is based. An adjacent camera lucida drawing (Textfigs. 3–7) presents an interpretation of a specimen where necessary. The specimens were rotated in relation to a unidirectional light source during the preparation of the drawings; varying the direction of illumination revealed different aspects of the morphology.

New information that has come to light during this work has necessitated the removal of the species *Protocaris pretiosa* to a new genus, *Branchiocaris*. The family Protocarididae Miller, 1889 (name corrected by Rolfe, 1969) is retained, with a new diagnosis, to include both genera. *B. pretiosa* is one of the rarer arthropods in the Burgess Shale fauna: only five specimens are known, in contrast to over 400 of *Yohoia tenuis* (Whittington, 1974), and an estimated 12 thousand of *Marrella splendens* (Whittington, 1971b) in the United States National Museum alone. In addition to Walcott's collection, material held by the Geological Survey of Canada, the Royal Ontario Museum, the Peabody Museum of Yale University, the Museum of Comparative Zoology at Harvard and the American Museum of Natural History has been searched without success for further specimens. In 1886 Walcott described a single valve from the Middle Cambrian of Utah as *Leperditia argenta*, which Gürich in 1929 made the type species of a new genus, *Dioxycaris*. The carapace of *B. pretiosa* is similar in outline to that of *D. argenta*, which is figured and redescribed here as a basis for comparison, but they are not synonymized, as the latter is based on a single poorly preserved valve, whereas more of the morphology of *B. pretiosa* is known, including that of the trunk and appendages.

The morphological terms used in the descriptions are those of Moore and McCormick (1969) as far as possible; the telson is not considered to be a true somite. Sagittal (sag.) refers to the direction parallel to the long axis of the body and transverse to the direction normal to this. The symbols used in the textfigures are explained below. The U.S. National Museum is abbreviated to USNM, the Museum of Comparative Zoology to MCZ and the Royal Ontario Museum to ROM.

Explanation of symbols on textfigures

a	anus
al	alimentary canal
an	antenna
ap	lamellate appendage, numbered where possible ap1, ap2, etc., posteriorly from the principal appendage (the suffix 'post' indicates the posterior margin)
b	border of carapace
c	cephalic region
cd	oval depression in the cephalic region
h	hinge or fold of carapace
l	prefix indicating left side
m	mouth
ms	muscle scar
pa	'principal' appendage
pe	'proximal element' of lamellate appendage, numbered where possible pe1, pe2, etc., to correspond to the attached lamella
q	lateroventral ridge
r	prefix indicating right side
s	'striations'
t	telson
t-1, t-2, etc.	numbered trunk somites (t-1 is the somite immediately before the telson)
tl	tranverse lineations on the lateroventral ridge
tp	telson process
v	valve of carapace
vm	ventral margin of trunk

Dashed lines indicate the anterior margins of lamellate appendages (Textfig. 4), which are preserved as ridges on the overlying lamellae. Hachures represent breaks of slope, with the solid line at the upper edge of the break and the hachures directed downslope. 'Outcrops' of matrix within the outline of a specimen are stippled.

Systematic Descriptions ·

Class and Order uncertain
Family PROTOCARIDIDAE Miller, 1889

Name corrected by Rolfe, 1969, from Protocaridae
Protocaridae Raymond, 1935
Protocarioidea, Protocariidae, Novozhilov, 1960

Diagnosis. Carapace bivalved, extending posteriorly more than half the total sagittal length; trunk elongate, multi-segmented, with over 40 short, wide divisions; telson bearing a pair of pointed processes.

Genus *Protocaris* Walcott, 1884

Procaris Woodward, 1895
not *Protacaris* Jones, 1883
not *Protocaris* Jones, Etheridge and Woodward, 1884
not *Protocaris* Jones and Woodward, 1888
not *Protocaris* Vogdes, 1893 in part (p. 363)
the last four = *Proricaris* Baily, 1870

Type species. *Protocaris marshi* Walcott, 1884 (by original designation)

Diagnosis. Carapace valves subtrapezoidal; trunk with up to 65 divisions; telson processes elongate, curved.

Geological horizon. Lower Cambrian, Parker Slate Formation, *Olenellus* Zone, Vermont.

Protocaris marshi Walcott, 1884

Plate 1, figures 1–3; Textfigures 1, 3

1884 *Protocaris Marshi*, Walcott, p. 330, 331, Pl. 10, fig. 1
1886 *Protocaris Marshi*, Walcott, p. 47, 54, 147, 148, Pl. 15, fig. 1
1889 *Protocaris marshi*; Miller, p. 525, 563, Fig. 1049
1889 *Protocaris Marshi*; Vogdes, p. 2, 31
1890 *Protocaris Marshi*; Jones, Etheridge and Woodward, p. 64
1890 *Protocaris marshi*, Walcott, p. 569, 590, 594, 629, Pl. 81, fig. 6
1890 *Protocaris marshi*; Vogdes, p. 152, 174
1892 *Protocaris Marshii*; Whiteaves, p. 207, 208
1892 *Protocaris Marshi*; Jones, Wiltshire and Woodward, p. 515
1893 *Protocaris Marshi*; Jones, Wiltshire and Woodward, p. 300
1893 *Protocaris marshii*; Clarke, p. 799–801, Fig. 8
1893 *Protocaris marshi*; Vogdes, p. 364, 404, *not* p. 363
1894 *Protocaris Marshi*; Bernard, p. 413, Fig. 1
1897 *Protocaris marshii*; Schuchert, p. 673–676, Pl. 58, fig. 1
1897 *Protocaris marshi*; Bernard, p. 398–401, 403, Fig. 1
1900 *Protocaris marshi*; Zittel, p. 641, Fig. 1336
1902 *Protocaris Marshii*; Woodward, p. 543
1910 *Protocaris marshi*; Grabau and Shimer, p. 332, Fig. 1651
1922 *Protocaris marshi*; Ruedemann, p. 317
1929 *Protocaris Marshi*; Gürich, p. 34, 35, Fig. 1,1
1929 *Protocaris marshi*; Resser, p. 12, 13, Pl. 6, figs. 1, 2
1934 *Protocaris marshi*; Straelen and Schmitz, p. 189, 210, 229, 237
1937 *Protocaris marshi*; Schuchert, p. 1026
1938 *Protocaris marshi*; Resser and Howell, p. 203, 232, Pl. 13, fig. 8;
    not p. 205, 232 in part, Pl. 10, fig. 7
1944 *Protocaris marshi*; Shimer and Shrock, p. 655, Pl. 277, fig. 2
1953 *Protocaris marshi*; Dechaseaux, p. 261, 262, Fig. 13
1954 *Protocaris marshi*; Shaw, p. 1041
1955 *Protocaris marshi*; Shaw, p. 775, 777, 798
1958 *Protocaris marshi*; Shaw, p. 531
1960 *Protocaris marshi*; Jux, p. 1146
1960 *Protocaris marshi*; Novozhilov, p. 217, 218
1960 *Protocaris marshii*; Novozhilov, p. 217, Fig. 446
1965 *Protocaris marshii*; Woods, p. 2
1969 *Protocaris marshi*; Rolfe, p. 331

Holotype. USNM 15400, part and counterpart, Plate 1, figures 1, 2, respectively, original of Walcott, 1884, Plate 10, figure 1.

Other material. Unknown. USNM 90826, Plate 1, figure 4, 'plesiotype' of Resser and Howell, 1938, Plate 10, figure 7 rejected here.

Locality and stratigraphical horizon. Lower Cambrian, Lower Parker Slate, *Olenellus* Zone, Noah Parker quarry, 150 feet above the base of the Parker Slate Formation (Shaw, 1955), on Parker Cobble, west-northwest of Georgia Center, Milton quadrangle, Vermont (*see* Shaw 1954, 1958 for an account of the geology and stratigraphy of the formation).

Preservation. The only known specimen of *Protocaris marshi* is preserved in a dark fine-grained micaceous shale. Since the locality from which it was collected, the Noah Parker quarry, "has been entirely quarried away" (Shaw, 1954) there is apparently no prospect of collecting additional material from this site. Postdepositional compaction of the specimen has destroyed most of the original relief. The fossil appears to have split along the surface of the exoskeleton, allowing a distinction to be drawn between the 'part' (Pl. 1, fig. 1), which preserves the slightly convex carapace from beneath which the trunk extends posteriorly, and the 'counterpart' (Pl. 1, fig. 2), in which the carapace is concave and has no apparent thickness. The specimen apparently was intact on burial but the counterpart slab is incomplete and lacks the anterior margin of the carapace. The asymmetry of the carapace valves indicates that the orientation of the specimen is slightly oblique (*see* Whittington, 1971a); the

sagittal plane is almost normal to the bedding but tilted slightly to the left (in the part, Pl. 1, fig. 1).

Description

Cephalic region. A small semicircular feature (Pl. 1, figs. 1, 3), which projects from beneath the anterior margin of the carapace in the midline, is assumed to represent part of the cephalic region. Unfortunately it is poorly preserved and included on that area of the counterpart which is unknown. The feature bears two small, closely spaced circular prominences medially but although these invite interpretation in association with the cephalon they are more likely to be inorganic in origin. The anterior of the carapace (Pl. 1, figs. 1, 3) has been compressed, fractured and partly exfoliated. This accounts for the "two large nearly circular depressions" recorded by Schuchert (1897), who considered that they "may represent eyes" and listed several criteria based largely on a comparison with the notostracan branchiopod *Triops* to support the occurrence of eyes in this position. Only one depression is, in fact, well defined—that on the right valve (Pl. 1, figs. 1, 3). There is no evidence that eyes or any other feature of the cephalic region are represented by the carapace relief in this area.

Carapace. The bivalved carapace (Pl. 1, figs. 1, 2) covered the anterior of the body except for the small projection in the cephalic region, but where and how it was attached cannot be observed. The valves are probably preserved in a slightly unnatural attitude because the tissues that attached them to the body are partly decayed. They are considered to have flanked the trunk more closely than the specimen indicates and are reconstructed in this position (Textfig. 1). The slight obliquity of compression has distorted the left valve, which has been folded beneath itself; the right valve is preserved with an apparently complete outline (Pl. 1, figs. 1, 2). The concentric breaks of slope around the margin of the left valve may indicate the original convexity. The junction of the carapace valves was probably straight, the slight curvature preserved being the result of compression; inadequate preservation obscures its full extent both anteriorly and posteriorly. There is no evidence of whether the valves were actually hinged or the carapace simply folded. The valves were approximately trapezoid in outline, tapering slightly anteriorly. The anterior and posterior margins were almost straight and diverged from the hinge or fold at angles of about 110° and 120°, respectively, giving the valves a blunt appearance and creating a more pronounced embayment of the carapace posteriorly than anteriorly. There is no evidence of a rostrum. The carapace had a narrow, smooth border, which is preserved only on the right valve. No features that can be interpreted as evidence of the underlying morphology are preserved on the surface.

Trunk. The trunk is obscured anteriorly by the overlying carapace (Pl. 1, figs. 1, 2) from beneath which 30 somites, in addition to the telson, extend posteriorly. The somites are short (sagitally); the width, gradually increasing anteriorly along the trunk, exceeds length by a progressively larger factor. Somite length (sag.) appears to increase slightly anteriorly and, based on this, the number of somites included in the trunk is estimated to total more than 65. The length of the somites immediately preceding the telson
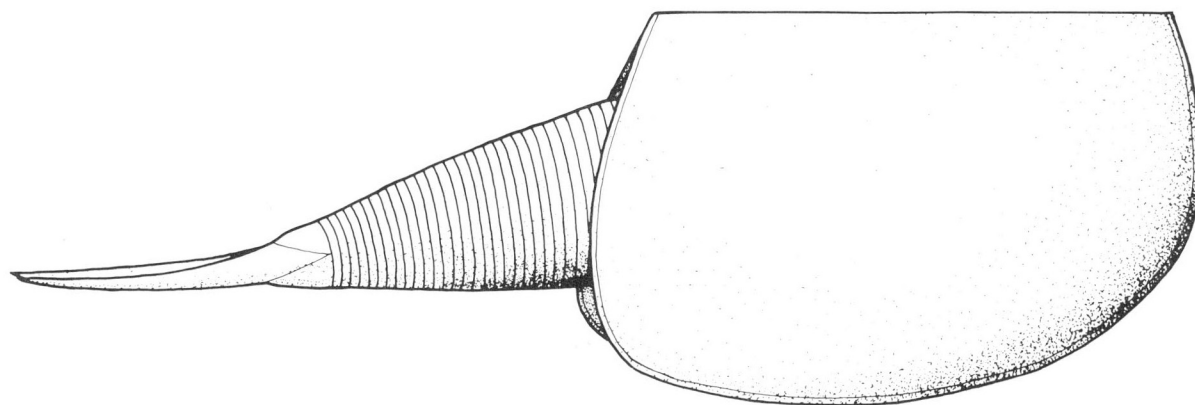
A   5 mm
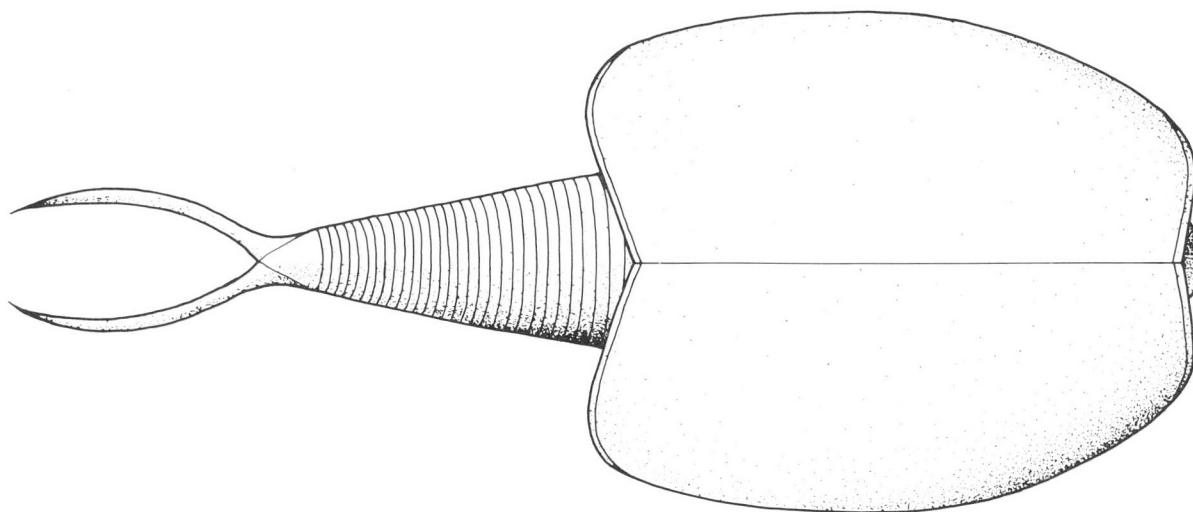
B   5 mm

Textfigure 1. *Protocaris marshi* Walcott, 1884. Reconstructions in right oblique lateral (*A*) and dorsal (*B*) views.

increases slightly from left to right (Pl. 1, fig. 1), suggesting that flexing of the trunk may have been possible by telescoping along intersomite boundaries. There is no evidence that the latter were spinose but they are nevertheless preserved in relief, possibly because overlap increased the effective thickness of the cuticle. In the absence of material preserved in lateral aspect, the trunk is assumed for the purpose of reconstruction to have been subcircular in cross-section (Textfig. 1).

The specimen is compressed in a slightly oblique orientation, which accounts for the asymmetry of the carapace valves, and appendages attached laterally or ventrally would tend to be exposed on the right side of the trunk (Pl. 1, fig. 1; Textfig. 3), where it emerges from beneath the carapace. The occurrence of appendages in this position is supported by a lack of traces of the somite boundaries in this area and the apparent asymmetry of the trunk outline. A linear feature (Pl. 1, fig. 1; Textfig. 3) that extends anteriorly from the telson along the right side of the trunk may represent a line of appendage attachment. Because the evidence is equivocal, however, appendages are not included in the reconstruction (Textfig. 1). The diameter of the trunk where it emerges from beneath the carapace is reconstructed (Textfig. 1) as intermediate between its apparent width at this point and the distance normal to the sagittal axis between the left-hand margin and the linear feature discussed above. The apparent width of the trunk suggests a very large diameter in relation to the size of the carapace; the reconstruction approximates the probable diameter assuming ventrolaterally attached appendages. There is no trace of the alimentary canal.

The most distal division of the trunk (Pl. 1, figs. 1, 2) is assumed to have borne the anus and is designated the telson. It was elongate and triangular in outline and bore a pair of long narrow curved processes, which diverged proximally, tapered to a point and converged distally. These processes appear to have been joined to the telson along its lateral margins; they may have articulated at this point but preservation is inadequate to confirm this. The more pronounced curvature of the right process may be due to the slightly oblique compression.

Size. The sagittal length of the only known specimen is 43 mm, measured from the anterior margin of the carapace in the midline to the distal extremity of the telson processes. The hinge or fold of the carapace is 20 mm long, just under 50 per cent of the total length. The undistorted right valve is 23.4 mm in length parallel to the hinge or fold, and 14.2 mm in height normal to it, but the latter value obviously fails to allow for any original convexity.

Discussion

Previous descriptions. Walcott, in his original description (1884) of *Protocaris marshi* stated that it possessed a "carapace without evidence of a dorsal suture." Schuchert (1897) published a stylized line drawing based on a re-examination of the type specimen, which included traces of a medial feature on the carapace and an outline of the trunk beneath it, although neither are discussed in his description. He considered that *P. marshi* had strong affinities with the notostracan branchiopod *Triops* (or *Apus* as it was then

known), so that he probably interpreted the carapace feature by analogy with the medial dorsal carina of *Triops*. The type specimen of *P. marshi* provides no evidence to support either Schuchert's outline of the trunk anteriorly, or Gürich's (1929) suggestion that the transverse divisions, interpreted above as intersomite boundaries, might be the result of compression. It was not until 1929 that Resser observed the true bivalved nature of the carapace. Schuchert (1897), unlike Walcott, postulated the presence of eyes anteriorly on the carapace (*see* description of the cephalic region, above) based on a comparison with *Triops* and, although the specimen preserves no satisfactory evidence for this, the idea was reiterated by Bernard (1897), who regarded the supposed eyes "as corresponding with the paired eyes of *Apus*."

'Plesiotype' of Resser and Howell, 1938. Resser and Howell (1938, p. 205, 232, Pl. 10, fig. 7) figured a specimen (Pl. 1, fig. 4) from the Lower Cambrian Kinzers Formation of Pennsylvania (USNM locality 22L, 1/2 mile south of East Petersburg) which they regarded as "apparently referable to the species" *Protocaris marshi*. The outline is superficially similar to that of the type specimen but is indistinct in parts and encloses no recognizable features. The fossil is preserved in fine pale grey mudstone and is smaller than *P. marshi*, having a length of 25 mm along the midline and a maximum width of 14 mm. It is not considered identifiable as an arthropod but may be a fragment of algal material.

Affinities and classification. Much of the early discussion of the affinities of *Protocaris marshi* was based on a comparison of its morphology with that of the notostracan branchiopod *Triops* (or *Apus*). Walcott (1886) noted "the striking resemblance between the recent *Apus* and ancient *Protocaris*," a comparison which was also made by Clarke (1893), Bernard (1894, 1897), Schuchert (1897), who assigned both to a new subfamily Apodinae of the Apodidae, and Ruedemann (1922). Vogdes (1889, 1890, 1893) and Whiteaves (1892) grouped it with the Phyllocarida. Resser (1929), however, observed that the carapace was bivalved and noted that although previous authors had tended to classify *P. marshi* with *Triops*, Walcott (1886) had in fact originally suggested that "it also appears to be connected with the Nebalidae through *Hymenocaris*, *Peltocaris*, *Ceratiocaris* &c." Resser complicated the discussion by referring the better preserved Burgess Shale species *P. pretiosa* to the genus *Protocaris*, and although this species is removed here to a new genus *Branchiocaris*, further discussion of the affinities of *P. marshi* is included with that of *Branchiocaris*, so that they may be considered together in the light of the new information on *Branchiocaris pretiosa* that the present study has made available.

Genus *Branchiocaris* n. gen.

Type species. *Protocaris pretiosa* Resser, 1929

Diagnosis. Carapace valves subovate, dorsal margin produced anteriorly and posteriorly into a short pointed process, border with unevenly spaced, elongate shallow pits normal to the margin. Cephalic region bearing a pair of uniramous antennae, anterior to a pair of large segmented appendages. Trunk with up to 47 divisions; appendages lamellate, with

segmented proximal element, attached the full length of the trunk anterior to the telson; telson processes short, pointed, bladelike.

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

Branchiocaris pretiosa (Resser, 1929)
Plate 1, figures 5, 6; Plates 2–5; Plate 6, figure 1;
Textfigures 2, 4–7

1929 *Protocaris pretiosa,* Resser, p. 6, 13, Pl. 4, figs. 1, 2
1934 *Protocaris pretiosa;* Straelen and Schmitz, p. 189, 210, 229, 237
1944 *Protocaris pretiosa;* Shimer and Shrock, p. 655, Pl. 277, figs. 3, 4
1953 *Protocaris speciosa;* Dechaseaux, p. 262
1962 *Protocaris* cf. *pretiosa;* Rolfe, p. 7
1969 *Protocaris pretiosa;* Rolfe, p. 331, Fig. 154,6

Holotype. USNM 80483, part and counterpart, Plate 2, figures 1, 2, respectively, Plate 6, figure 1, original of Resser, 1929, Plate 4, figures 1, 2.

Other material. USNM 189028, part and counterpart, Plate 3, figures 1–4; USNM 189029, Plate 4, figures 1–4; USNM 189030, part and counterpart, Plate 5, figures 1–3; MCZ 5985, Plate 1, figures 5, 6 and counterpart, ROM 34308. USNM 189020, part and counterpart, may be a poorly preserved isolated valve.

Locality and stratigraphical horizon. Middle Cambrian, Stephen Formation, Burgess Shale Section, *Pagetia bootes* faunule of the *Bathyuriscus-Elrathina* Zone, situated on the ridge between Wapta Mountain and Mount Field, at approximately 7500 feet, three miles north of Field, southern British Columbia (*see* Fritz, 1971, for the stratigraphy of the shale).

The USNM specimens bear the locality number 35k. The MCZ specimen is labelled 'Walcott Quarry'. No specimens were collected by the GSC expeditions (Whittington, 1971a) and no positively identified isolated carapaces are known. All the specimens are on small pieces of shale. The associated fauna is confined to *Marrella splendens* and unidentifiable fragments that do not serve to limit the level in the Phyllopod bed at which *Branchiocaris pretiosa* may occur.

Preservation. The five known specimens are exceptionally well preserved and appear to have been intact on burial, although two are incomplete because parts of the slabs on which they occur were lost. The carapace is partly preserved in all specimens. Traces of the antennae are preserved on three specimens, but the large segmented appendages borne behind them are complete on only one. Preservation appears to be essentially similar to that of *Marrella splendens* (Whittington, 1971a, b) and other subsequently described members of the Burgess Shale fauna. Two of the specimens are orientated approximately *parallel* (Pl. 3, figs. 1–4; Pl. 5, figs. 1–3), with the sagittal plane at right angles to the bedding and the valves symmetrical about the midline; one is *lateral* (Pl. 4, figs. 1–4), with the sagittal plane parallel to the bedding and the valves superimposed; and two are *oblique* (Pl. 1, fig. 5; Pl. 2, figs. 1, 2), with intermediate orientation, the outline of one valve nearly complete, the other folded beneath itself. The exoskeleton is preserved as a dark layer in all but one specimen (MCZ 5985, Pl. 1, fig. 5), which is lighter from weathering. The dark exoskeleton is reflective, some areas

more than others (for example the alimentary canal of USNM 189029, Pl. 4, fig. 2).

Whittington (1974) has emphasized the importance of establishing the plane through which the fossil has split. The holotype (USNM 80483, Pl. 2, figs. 1, 2), USNM 189029 (Pl. 4, fig. 1), and USNM 189030 (Pl. 5, figs. 1, 3) appear to have split along the surface of the exoskeleton and the 'part' preserves a concave carapace with a corresponding convex 'counterpart'. Resser (1929) removed some of the carapace of the holotype (Pl. 2, fig. 1) to expose the features beneath, and a similar technique has been used in USNM 189029 (Pl. 4, figs. 1, 3) and USNM 189030 (Pl. 5, figs. 1, 2). The specimen from the Raymond collection (MCZ 5985, Pl. 1, fig. 5) preserves the dorsal surface of the carapace but splitting has removed the central area, revealing the underlying appendages. The relationship of the part and counterpart of USNM 189028 (Pl. 3, figs. 1, 2) is more complex. The split follows the surface of the exoskeleton anteriorly, and this criterion is used to define the part and counterpart; the part preserves the convex surface of the carapace, which has been partly prepared (Pl. 3, figs. 3, 4) to expose the appendages. The division appears to traverse the specimen anteroposteriorly from the dorsal to the ventral surface, so that the counterpart (Pl. 3, fig. 2) preserves the posterior appendages in ventral aspect.

Description

Cephalic region. This region is compressed against the carapace of the holotype (Pl. 2, fig. 1) and was unknown to Resser (1929) in spite of his preparation of the specimen. The lateral specimen (USNM 189029, Pl. 4, figs. 1–4) is incomplete anteriorly, and although MCZ 5985 (Pl. 1, fig. 5) preserves traces of the antennae, the cephalic region is divided by a slight structural discontinuity. The description is largely based on the parallel specimens, USNM 189028 (Pl. 3, figs. 1–4) and USNM 189030 (Pl. 5, figs. 1–3).

The anterior margin of the cephalic region is preserved in only one specimen (USNM 189028, counterpart, Pl. 3, fig. 2) and appears to have been evenly convex. The region bore a pair of stout antennae anterodorsally (Pl. 3, fig. 4; Pl. 5, figs. 2, 3), which are assumed for the purpose of reconstruction and in the absence of a lateral specimen, to have been subcircular in cross-section (Textfig. 2). The antennae tapered gradually distally and were composed of at least 20 segments, nine or ten of which extended beyond the anterior margin of the carapace. The segments became progressively more elongate and slender towards the extremity of the antenna; individually they increased distally in crosssection, each segment inserting into the preceding one. The intersegmental boundaries thus formed, which were gently curved, concave distally, are preserved as ridges, probably from overlap. The antennae were apparently flexible and are curved through an angle of up to 180°. The segments at the points of flexure tend to be longer on the convex than on the concave side, indicating that the joints may have telescoped to allow movement in all directions.

The position of the boundary between the cephalon and the trunk is unknown but is assumed to have been posterior to a second large appendage, the 'principal' appendage (Pl. 3, fig. 4; Pl. 5, fig. 2), attached laterally behind both the
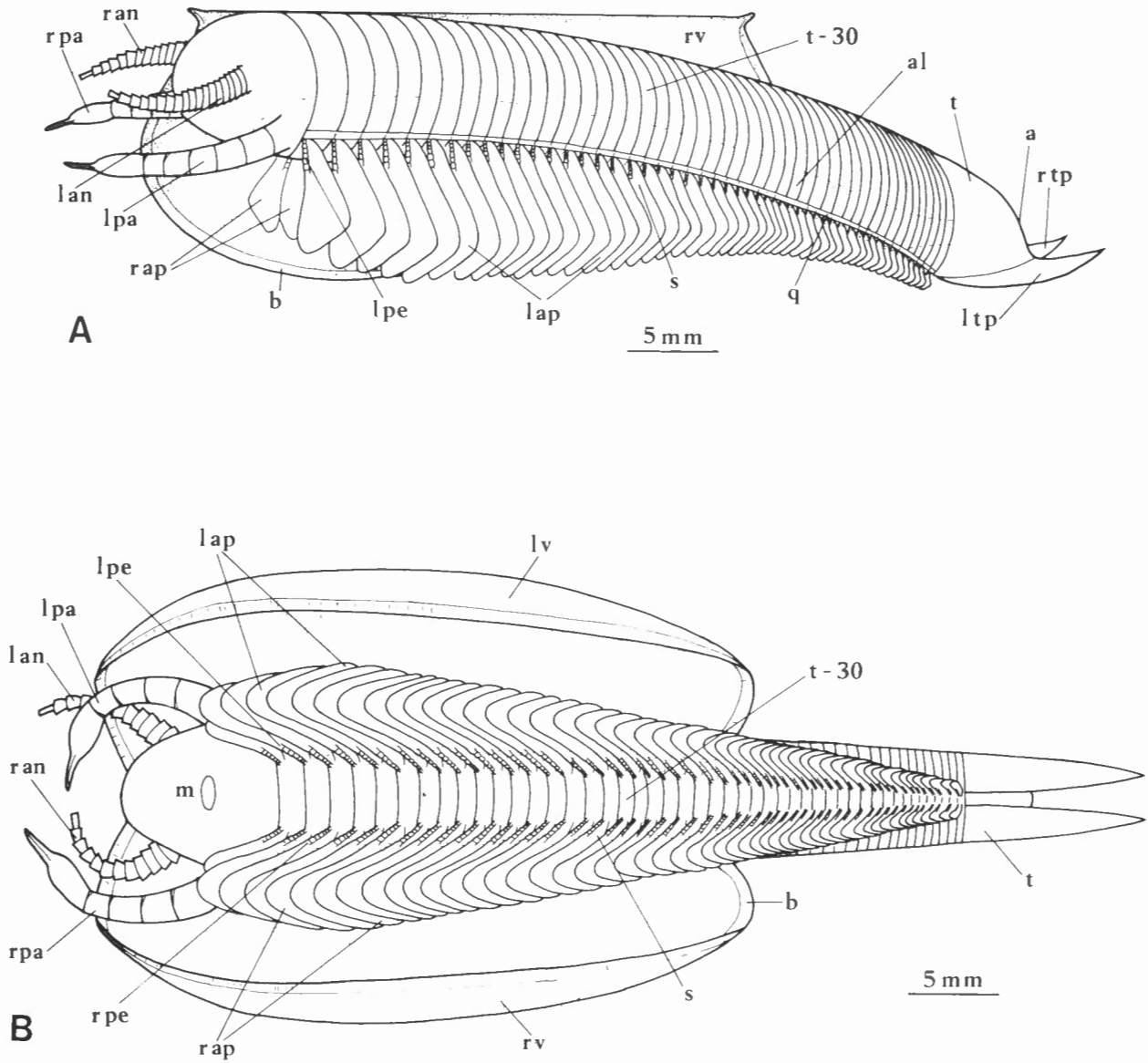
Textfigure 2. *Branchiocaris pretiosa* (Resser, 1929). Reconstructions in left oblique lateral (*A*) and ventral (*B*) views. Lateral view with left carapace removed. The attitude of the appendages is generalized. They may have moved in a metachronal fashion but the lack of evidence and large number of limbs make this impractical to reconstruct. The appendages of the lateral view are directed vertically downwards from the trunk, with the lamellae transverse to the sagittal plane and considerably foreshortened; those of the ventral view are directed anteriorly.

antenna and the maximum anterior extension of the alimentary canal. This appendage was composed of at least seven segments; the most distal extended beyond the anterior margin of the carapace ventral of the antenna (Pl. 3, fig. 4). It appears to have been flexible: in parallel aspect it is curved gently towards the sagittal axis of the trunk. The segments apparently were hinged on the outer convex margin; some of the boundaries are preserved as an elongate triangle, with the apex directed towards this side of the appendage, and these may represent areas of flexible cuticle permitting movement at the joint. The appendage tapered gradually to the proximal margin of the most distal segment; this segment is preserved only on USNM 189028, which shows it widening anteriorly to a point just beyond its midlength; there it narrowed abruptly, tapering distally into an elongate projection that is divided lengthwise along its midline by a break in slope. This invites interpretation as the two segments of a chela—a gently curved movable finger that tapers distally opposed by an elongate narrow projection of the distal margin of the enlarged preceding segment, the fixed finger, beyond which it appears to have extended slightly. The evidence for articulation, however, is slight; the 'fingers' of the 'chela' are juxtaposed and it is not evident which part of the divided projection might have been movable. In the absence of a specimen showing the fingers apart, which would substantiate their interpretation as a chela, the principal appendage must be regarded as terminating in a spine. The enlarged distal segment bearing the elongate projection is preserved at an angle of 60° to 70° to that immediately behind it. It is impossible to accurately reconstruct the outline of the principal appendage in cross-section without a lateral specimen but it is assumed to be subcircular (Textfig. 2).

Since the evidence for eyes in *Branchiocaris pretiosa* is equivocal they are not included in the reconstruction (Textfig. 2). USNM 189028 preserves a pair of large elongate depressions (Pl. 3, fig. 4) in the cephalic region between the points where the antennae were attached. These, however, are not highly reflective, a characteristic of eyes in some of the arthropod genera from the Burgess Shale (*Canadaspis*, *Waptia*, for example), nor are they situated at the anterior of the cephalic region but are concealed beneath the carapace. Their nature is problematical: they may be traces of a labrum. The alimentary canal is preserved extending forward beyond the attachment of the principal appendages (Pl. 3, fig. 4; Pl. 5, fig. 2) to a point near the base of the antennae, which may have been the position of the mouth.

Carapace. A bivalved carapace (Pl. 2, fig. 2) covered the anterior of the body, the proximal parts of the antennae and principal appendages and most of the trunk somites and appendages, but the attachment appears to have been confined to the cephalic region. Lateral (USNM 189029, Pl. 4, fig. 1) and oblique (USNM 80483, Pl. 2, fig. 1) specimens indicate that the valves loosely flanked the body; USNM 80483 preserves the outline of the left valve relatively undistorted but the right valve is folded beneath itself. Removal of the left valve of the lateral specimen, USNM 189029 (Pl. 4, fig. 3), reveals the dorsal margin of the trunk gradually converging anteriorly with the hinge or fold of the carapace. The front of this slab is unknown but 40 somites

are preserved, the most anterior of which is still some distance ventral to the hinge or fold. The carapace appears to have been attached axially in front of a point near the base of the principal appendages. The carapace is preserved impressed onto the underlying cephalic region in this area on parallel (Pl. 3, figs. 1, 4) and oblique (Pl. 2, fig. 1) specimens. Posteriorly and laterally it is separated from the body by a layer of matrix and has broken away during the splitting of the slabs, or it has proved possible to prepare it off to reveal the features beneath. The large smooth oval area preserved on the left valve of USNM 189028 (Pl. 3, figs. 1, 3, 4) near the base of the principal appendage is interpreted as a muscle scar and augments the evidence that the carapace was attached anteriorly, while indicating some possible movement of the valves about the hinge or fold.

The valves were suboval in outline (Pl. 2, fig. 2), expanding slightly anteroventrally, and appear to have been almost symmetrical about a line drawn normal to the hinge or fold at its midpoint (Pl. 2, fig. 2; Pl. 4, fig. 3). The dorsal margin was straight, its posterior extremity produced into a small oblique pointed projection which is preserved in lateral aspect on USNM 189029 (Pl. 4, figs. 1–3). The anterior extremity also extended into a projection but its outline and attitude to the dorsal margin are preserved only in oblique aspect (USNM 80483, Pl. 2, fig. 2) and although it presumably resembles the posterior projection (Textfig. 2), the evidence for this reconstruction is equivocal. There is no evidence for an articulated rostrum. Both the anterior and posterior margins of the valve were directed ventrally at an angle of about 120° to the hinge or fold (Pl. 2, fig. 2; Pl. 4, figs. 1–3), forming axial indentations. The hinge or fold is preserved in lateral aspect (Pl. 4, figs. 1–3) as a straight line, but is ill defined on the only specimen that shows it separating the valves (the counterpart of USNM 80483, Pl. 2, fig. 2). Its anterior extent is obscured on the parallel specimens, USNM 189028 (Pl. 3, figs. 1–3) and USNM 189030 (Pl. 5, figs. 1–3), by compression and exfoliation, and its nature remains problematical although the lack of recognizable hinge features suggests that it may have been a simple fold. In spite of flattening convexity is preserved on the carapace of some specimens (USNM 189028, Pl. 3, figs. 1–3; USNM 189030, Pl. 5, figs. 1–3) and further indicated by the concentric breaks of slope formed during compression, as on the right valve of USNM 189028 (Pl. 3, figs. 1, 3). The carapace had a narrow flat border (Pl. 2, figs. 1, 2; Pl. 3, figs. 1–4; Pl. 5, figs. 1–3) which apparently sloped outwards creating a shallow groove on the margin of the otherwise convex surface. On this border was a series of 150 to 200 unevenly spaced elongate pits orientated normal to the margin of the carapace.

Trunk. The divisions of the trunk are referred to here as somites but they are so numerous that they may have been body annulations. The trunk is at least partly preserved in all five specimens but the somite boundaries are obscured where the carapace was attached. The holotype (Pl. 2, fig. 1) preserves traces of the boundaries of 44 somites in addition to the telson but the arrangement of the appendages indicates that there were at least 46 following that bearing the principal appendage. USNM 189028 (Pl. 3, figs. 1, 3) preserves traces of the boundaries of only 42 somites but

extrapolation anteriorly on the basis of length (sag.) indicates that this specimen has a similar number. Somites (excluding the telson) extending beyond the posterior border of the carapace vary from about 19 in the holotype (Pl. 2, fig. 2) and USNM 189028 (Pl. 3, figs. 1, 3) to 12 in USNM 189029 (Pl. 4, fig. 1), or even as few as one or two in MCZ 5985 (Pl. 1, figs. 5, 6) and although, particularly in the last case, the variation may be due to distortions during burial, it may indicate that the trunk was capable of telescoping.

All the known specimens are flattened in such a direction that the ventral or ventrolateral margin of the trunk is obscured by the appendages, which were apparently attached to a ventrolateral ridge (Pl. 2, fig. 1; Pl. 4, figs. 1–3) extending back to the anterior border of the telson. This margin may be indicated posteriorly, however, by a trace on the holotype (Pl. 2, fig. 1) in the area of the lamellate appendages attached to the trunk somites immediately in front of the telson. The exact anterior width of the trunk is unknown. The width of the somites in lateral aspect (Pl. 4, fig. 3), however, appears to diminish gradually posteriorly; a similar decrease occurs in parallel (Pl. 3, figs. 1–3) and oblique (Pl. 2, fig. 1) specimens. The width appears to be greater in lateral and oblique than in near-parallel aspect, indicating that the trunk was suboval in cross-section, with the longer axis parallel to the sagittal plane. The sagittal length of the somites (Pl. 2, fig. 1; Pl. 4, fig. 3) increased gradually anteriorly.

The posterodorsal margins of the four or five somites immediately preceding the telson of USNM 189029 (in lateral aspect) bear minute posteriorly directed spines (Pl. 4, fig. 4; Textfig. 6); this indicates that the somite boundaries may have been spinose throughout. They are not represented as such on the reconstruction (Textfig. 2), as there is no evidence for the distribution of spines elsewhere. Some of the boundaries preceding the telson of the holotype (Pl. 2, fig. 2) are preserved in relief, gradually widening ventrally where they appear to divide. This also occurs on USNM 189029 (Pl. 4, fig. 3); the boundaries diverge near the dorsal margin of the trunk and the gap increases ventrally, possibly indicating the overlap of successive somites. The specimens do not provide much evidence that the trunk was flexible. The gentle curvature of the trunk observed in the oblique (Pl. 2, figs. 1, 2) and lateral (Pl. 4, fig. 3) specimens may have been the natural attitude but the somites near the point of maximum flexure are longer on the dorsal margin and shorten ventrally, indicating that overlap of the somites in that direction may have facilitated movement.

The telson is preserved in four of the five known specimens. The dorsal margin (Pl. 4, fig. 3) is continuous with that of the preceding trunk somites in lateral aspect. The holotype (Pl. 2, figs. 1, 2) preserves a posterior trace that may represent the ventral margin of the trunk; this would indicate a slight increase in width ventrally between the telson and the somites immediately preceding it. The telson is wider in lateral (Pl. 4, figs. 1–3) than in parallel (Pl. 3, figs. 1–3) or oblique (Pl. 2, figs. 1, 2) aspect, indicating that the anterior cross-section was suboval, in continuity with the preceding somites. The dorsal margin curves ventrally through an angle of about 30° in lateral aspect (Pl. 4, figs. 2, 3) into the posterior margin, which was gently concave and

bore the anus. The outline of the telson in oblique (Pl. 2, figs. 1, 2) and parallel (Pl. 3, figs. 1, 2) aspects is slightly obscured by flattening onto the underlying processes. Its outline appears to have been trapezoidal, convex laterally and tapering to a blunt posterior margin bearing the anus. A flat elongate straight-sided, wedge-shaped feature is preserved on the dorsal surface of the telson of MCZ 5985 (Pl. 1, fig. 6) widening posteriorly from the anterior margin along the midline. The holotype (Pl. 2, fig. 1) also bears traces of this feature.

The telson extended ventrally into a pair of broad, lanceolate processes (Pl. 2, figs. 1, 2; Pl. 3, figs. 1–3), which appear to have been attached to its ventral surface. The preservation does not indicate whether or not the process articulated proximally. It extended back from the posterior margin of the telson, gently curved, concave upwards, narrowing gradually to a point, and apparently tapered forward beneath the telson towards its margin with the trunk somites (Pl. 4, figs. 2, 3). In parallel aspect (Pl. 3, figs. 1–3) the processes taper gradually to the distal point along gently convex margins. They appear to have been subcircular in posterior cross-section but flattened dorsoventrally where they are attached beneath the telson. The alimentary canal appears to narrow at the anterior margin of the telson in lateral aspect (Pl. 4, figs. 2, 3) but expands into the anus, which occupies most of the posterior margin of the telson over the processes and bears traces of annulations. The canal is not preserved in the telson in either the parallel or the oblique specimens but the anus is assumed to have been symmetrical about the midline and situated between the processes.

Traces of the alimentary canal occur in three of the five known specimens. USNM 189029 (Pl. 4, figs. 2, 3) preserves the outline in lateral aspect in the posterior part of the trunk and in the telson. The canal is not preserved in relief but as an area which appears relatively dark in low-angle (Pl. 4, fig. 3) but reflective in high-angle illumination (Pl. 4, fig. 2). A study of *Canadaspis perfecta*, in progress, indicates that this type of trace may not correspond to the actual width of the alimentary canal as interpreted on the basis of specimens that also preserve it in relief. The ventral margin cannot be traced anteriorly but the dorsal may be observed in about 15 somites preceding the telson. Anteriorly the margins of the canal are obscured but it may continue as a raised longitudinal band parallel to the dorsal margin of the trunk. This band is more highly reflective than the rest of the body (Pl. 4, fig. 2) and is marked by a series of longitudinal lines (Pl. 4, fig. 3). It may represent traces of longitudinal muscles. The band appears to deflect anteriorly the somite boundaries preceding the twentieth somite before the telson (Pl. 4, fig. 3), possibly as a result of compression, but this feature may indicate the original convexity. The anterior part of the alimentary canal is preserved in relief, possibly because of sediment fill, along the midline of USNM 189028 (Pl. 3, fig. 3) and USNM 189030 (Pl. 5, fig. 2) in parallel aspect. USNM 189030 preserves transverse annulations in this area, gently curved, concave anteriorly, but the curvature may result from the flattening of a subcircular cross-section. The canal narrowed anteriorly beyond the attachment of the principal appendages (Pl. 5, fig. 2; Pl. 3, fig. 3), presumably indicating the position of the mouth.

Appendages. As discussed above, two pairs of appendages have been observed in the cephalic region, a pair of antennae underlain by a pair of large segmented ('principal') appendages attached posterior to them. No further limbs appear to occur in front of these. Behind the principal appendage the trunk bore a series of wide thin, presumably flexible, lamellate appendages (Pl. 2, fig. 1), which extended to the anterior margin of the telson. Some of these are preserved in all five known specimens, without evidence for their structure; they may have included several discrete lobate areas. The evidence upon which the reconstructions of these appendages (Textfig. 2) are based is discussed below. Their arrangement is simplified; they probably moved in a metachronal cycle but evidence is insufficient to permit an assessment of their relative positions or phase difference during an oscillation. The lamellate appendages are considered to have been orientated approximately normal to the sagittal plane, the outer margins overlapping slightly posteriorly (Textfig. 2*A*). Their arrangement on the compacted specimens may reflect their relative attitude when the animal was overcome by sediment. Removal of the right valve of USNM 189030 (Pl. 5, fig. 2), preserved in parallel aspect, has revealed the anterior lamellate appendages compacted in a position that they might have occupied at the end of a forward stroke (as reconstructed in ventral view, Textfig. 2*B*). Hence the anterior, lateral and posterior margins of the lamellae as preserved on this specimen correspond to the inner, ventral and outer margins on the reconstruction. The specimen shows that the anteriormost lamellate appendage, referred to as the 'first', was attached immediately behind the principal appendage (Pl. 5, fig. 2). Its anterior margin is directed at an angle of about 50° to the axis of the trunk and curves gently to a sharply rounded apex. The lateral margin approximately parallels the axis. The second lamellate appendage was attached posterior and ventral to the first and extended forward a similar distance, but farther laterally. The third was attached behind the overlying second and extended beyond its lateral margin.

The holotype USNM 80483 shows successive appendages throughout the length of the trunk overlain by those immediately preceding them (Pl. 2, fig. 1); their lateral extension progressively diminishes (as opposed to the first few increasing) after the fourth or fifth lamellate appendage. This specimen is preserved in oblique aspect, which results in a relative arrangement of the margins of the lamellae similar to that found in USNM 189030, so that the inner, ventral and outer margins as depicted on the reconstruction (Textfig. 2*A*) are anterior, lateral and posterior on the compacted specimen. The anterior margins of the appendages exposed by Resser's (1929) preparation of the left valve of this specimen (Pl. 2, fig. 1) are preserved as ridges on those overlying them (Pl. 6, fig. 1; Textfig. 4) because the limbs were compressed during burial. The inclination of the anterior margin to the axis of the trunk appears to increase from about 50° at the first appendage (Pl. 5, fig. 2), to 90° at the fourth or fifth (Pl. 2, fig. 1) and up to 140° in those attached near and beyond the posterior margin of the carapace (Pl. 2, fig. 1). This variation may be a function of the relative position of the limbs during a metachronal oscillation (*compare* Cannon, 1933, p. 271, Fig. 1). The

anterior margin (Pl. 5, fig. 2; Pl. 2, fig. 1) was straight proximally and curved gently back into the lateral margin, which roughly paralleled the axis of the trunk.

None of the known specimens completely preserves the posterior (outer) margin of a lamellate appendage. Those of the lateral specimen (USNM 189029, Pl. 4, fig. 3) are so impressed together that the preparation of complete individual appendages is impossible but the specimen does indicate the posterior outline of some in lateral aspect. The ragged, broken posterior edges of the lamellate appendages exposed by Resser's (1929) preparation of the holotype (USNM 80483, Pl. 2, fig. 1; Pl. 6, fig. 1) may approximate, in direction at least, the original outlines. A similar direction is indicated by lineations to the left of the alimentary canal of the parallel specimen USNM 189030 (Pl. 5, fig. 2), which may represent posterior boundaries. The evidence thus suggests that the posterior margins of the appendages attached in the vicinity of somite t-40 on USNM 80483 are approximately straight and directed posteriorly at an angle of about 60°, this inclination increasing slightly in more posterior appendages.

The appendages were smaller (Pl. 2, fig. 1) after the fourth or fifth but evidently did not substantially alter in shape. The exact number cannot be determined because of their nature and poor preservation, particularly on the posterior somites, where they are very thin and compacted. It cannot be assumed that each somite bore a single pair; the evidence (discussed below) suggests that it did not.

The lamellate appendages evidently were attached to a raised lateroventral ridge (Pl. 2, fig. 1), which extended along the trunk parallel to the dorsal margin and terminated at the anteroventral margin of the telson. The margins of this ridge are poorly defined on the lateral specimen (USNM 189029, Pl. 4, fig. 3) but it appears to widen gradually towards the anterior. It becomes obscured beyond the twelfth or thirteenth somite before the telson. The lamellate appendages apparently were attached to the ventral margin of this ridge (Pl. 2, fig. 1; Pl. 4, fig. 3), extending ventrally over the margin of the trunk somites. A series of transverse lineations on the ridge may represent points of attachment; they appear to correspond to the somite boundaries anteriorly, but outnumber them towards the telson. The holotype (Pl. 2, fig. 1) shows the ridge in oblique aspect extending from the anteroventral margin of the telson through about 30 somites preceding it. The attachment of the posterior appendages is clearly shown by the counterpart of USNM 189028 (Pl. 3, fig. 2), which preserves what is effectively a ventral view of the posterior trunk somites in near parallel aspect. The lines along which the left and right appendages were attached diverged at the anteroventral margin of the telson and separated progressively farther anteriorly.

Two specimens indicate that the lamellate appendages may have been biramous, or strengthened by a short segmented 'proximal element'. USNM 189028 (Pl. 3, figs. 1–3) preserves a series of elongate features forming two rows next to the right and left lamellate appendages on each side of the axis, which become progressively shorter and closer together posteriorly and extend to the anterior margin of the telson. Apparently segmented, some preserve up to seven divisions, but no segmentation is evident on the smaller

elements attached to the posterior trunk somites. These proximal elements appear to narrow towards the sagittal axis of the trunk (their attachment?), extend posteriorly at an angle of about 45° to the axis and expand slightly distally. Because the few specimens are poorly preserved it is difficult to interpret these features and their relationship to the lamellate appendages. Those exposed by Resser (1929) beneath the left valve of the holotype (Pl. 6, fig. 1), however, appear to be continuous with the anterior (inner) margins of the adjacent lamellate appendages, which are preserved as ridges on the overlying lamellae. This cannot be confirmed because the appendages of USNM 189028 (Pl. 3, figs. 1–3) are badly preserved. Assuming that the proximal elements had a strengthening function or are proximal endites of the lamellate appendages this relationship can be used to calculate the number of trunk appendages, which cannot be assessed by counting the lamellae because of their state of preservation. USNM 189028 (Pl. 3, figs. 1–3) apparently had over 50 pairs of proximal elements, slightly more than the estimated number of trunk somites. The anterior 12 or 13 are significantly larger and more pronounced in relief than those behind them, a feature which may indicate a division of the trunk into anterior and posterior regions. The lamellate appendages of the holotype (Pl. 2, fig. 1) appear to be significantly larger and more evident in relief on the anterior than the posterior trunk somites, which led Resser (1929) to subdivide the body into thoracic and abdominal parts, but this difference is not evident on USNM 189028 (Pl. 3, figs. 1, 3) and may be due to the splitting and preservation of the original specimen. Anteriorly the paired proximal elements appear to correspond, one to one, to the trunk somites (Pl. 2, fig. 1; Pl. 6, fig. 1; Pl. 3, figs. 1, 3); posteriorly, however, they correspond to the transverse lineations on the raised latero-ventral ridge to which they apparently were attached, and the appendages definitely outnumber the trunk somites (Pl. 2, fig. 1; Pl. 3, figs. 1, 3).

Attempts to interpret the structure of the trunk append-ages are complicated by a series of apparently discrete groups of striations preserved along the left side of the trunk of USNM 189028 (Pl. 3, figs. 1, 3) next to the lamellate appendages and occupying the same area as the proximal elements described above. These may represent setae attach-ed to the proximal elements although no conclusive spatial correspondence can be observed. They may, on the other hand, have been features associated with the lamellate appendages; striations appear to occur on the proximal part of the anterior lamellate appendages of USNM 189030 (Pl. 5, fig. 2).

Size. The few specimens, two of which are incomplete, the apparent ability of the trunk to vary its length by tele-scoping, and the flattening of the carapace in different directions make an accurate assessment of the size range impossible. The sagittal length from the anterior end of the hinge or fold (position estimated where necessary) to the distal extremity of the telson processes can be measured for three specimens. The holotype (USNM 80483, Pl. 2, figs. 1, 2), USNM 189028 (Pl. 3, figs. 1–3), and MCZ 5985 (Pl. 1, fig. 5) are 68 mm, 85 mm and 87 mm long, respectively. The trunk of the third appears to have been telescoped sagitally or distorted during burial, so that the maximum length of

the compressed carapace is 90 per cent of the sagittal length, compared with 64 per cent in USNM 189028, suggesting that MCZ 5985 may have been considerably larger than the other known specimens. Size can be further compared by measuring the length of the 30 trunk somites immediately preceding the telson; the holotype (Pl. 2, figs. 1, 2), USNM 189028 (Pl. 3, figs. 1–3) and USNM 189029 (Pl. 4, figs. 2, 3) give values of 24 mm, 30 mm and 28 mm, respectively. The incomplete USNM 189030 (Pl. · 5, figs. 1–3) cannot be measured for comparison, but appears to be similar to the other specimens. The holotype (USNM 80483) thus appears to be the smallest and MCZ 5985 the largest of the known specimens. The dimensions of the carapace can be satis-factorily measured only on the holotype (Pl. 2, fig. 2), the left valve of which is relatively undistorted by compression. The length of the hinge or fold of this valve is 42 mm, the maximum length of the carapace parallel to it 45 mm and the maximum height normal to it 31 mm (the third value clearly cannot allow for any of the original convexity). These figures represent 62, 66 and 46 per cent of the sagittal length, respectively.

Discussion

Habitat, mode of life, function of appendages. The preser-vation of *Branchiocaris pretiosa* and other previously described members of the Burgess Shale fauna (Whittington, 1971a, b, 1974) indicates that the specimens were part of a living population which was catastrophically buried. In the adult stage the species was presumably benthonic in habitat, swimming and feeding near the seabed (*see* Whit-tington, 1971b, p. 19–20, discussion of the habitat of *Marrella splendens*). A metachronal movement of the lamellate appendages probably served to propel the animal forward, simultaneously setting up a current or respiratory stream along the ventral surface of the trunk between the appendages and assisting the function of the lamellae as gills. The evidence for the detailed morphology of the trunk appendages of *B. pretiosa* is equivocal: any attempt to postulate the way in which they functioned must be based inevitably on a comparison with extant arthropods— particularly the notostracan branchiopods to which *B. pretiosa* bears certain similarities. The trunk appendages may have been similar to those of *Triops*, the proximal element and striations of *B. pretiosa* corresponding to the setiferous endites of *Triops*. However, the proximal elements of *B. pretiosa* did not likely serve to pass food particles forward to the mouth, as did the basal endite of the *Triops* trunk limbs— the opposing appendages appear to have been too far apart, although this may be partly the result of postdepositional compaction. The anterior 12 or 13 pairs of proximal elements are significantly larger than those following them, which may imply that the trunk was divided into thorax and abdomen as in the Branchiopoda. The principal appendages may have provided an adequate food-gathering mechanism, rendering any other superfluous, with the arthropod living on animal debris and plant material gathered on the seabed. They may have functioned together by grasping material between the distal extremities, or separately by pulling food towards the mouth or picking it up if they were, in fact, chelate. Since it apparently lacked eyes, *B. pretiosa* was not likely an active

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predator. The antennae presumably were sensory. The apparent absence of gnathobase-type structures probably rules out particle feeding (as found in the Notostraca), and even if the striations on the lamellae represent setae, filter feeding presumably was only of secondary importance. Cannon (1933, p. 333) argued that the ancestral Branchiopoda may have possessed a well developed maxilla which functioned as a feeding mechanism, that the development of a filtering system or structures to push food forward was only secondary to that of a respiratory stream and that the setae originally served to keep the lamellae clean, thus avoiding any impediment to the current of water over the gills. This viewpoint was disputed by Hessler and Newman (1975), who deduced that the original method of foodgathering in the Crustacea was postoral. The principal appendage of *B. pretiosa* thus presumably signifies a specialized condition that does not represent a stage in branchiopodan evolution. The apparent ability of the trunk somites to permit flexing of the trunk by telescoping may have aided in propulsion and steering; if the telson processes were articulated they probably also functioned in this respect.

Previous descriptions. The most significant new information on *Branchiocaris pretiosa* which the present study has brought to light concerns the morphology of the cephalic region. Resser's (1929) description of the species, based on the part and counterpart of a single specimen, stated that "none of the head parts are well known, since in flattening the original convexity the anterior portion was crowded together, thereby effacing the delicate structures." The discovery of paired antennae and the large segmented principal appendages in this region, however, has remedied this deficiency. In addition the trunk has been shown to bear lamellate appendages along its entire length preceding the telson. The only known specimen of *Protocaris marshi* preserves no positively identified appendages. Resser's (1929) preparation of the holotype of *B. pretiosa*, from which he removed much of the carapace to expose the underlying appendages, demonstrated an approach to the study of the Burgess Shale arthropods which has been profitably applied in the redescription of this and other genera (Whittington, 1971b, 1974). To him the "abdominal portion" of the trunk of this specimen appeared to have "much shorter or no appendages" and the erroneous idea that the species only bore appendages anteriorly was perpetuated by Størmer (1944, p. 101) and Rolfe (1969, p. 331). The appendages are not "trilobitan" as supposed by Raymond (1935) and Størmer (1939, p. 237; 1944, p. 101). The evidence that they were biramous is equivocal; the lamellae may have been filamentous but the proximal element bears no resemblance to the segmented walking leg of a trilobite.

Affinities and classifications. Remarks on the classification and affinities of *Protocaris* published after Resser's (1929) description of the species *Branchiocaris pretiosa* naturally took the morphology of the latter into consideration, as it was originally referred to this genus. Resser maintained that there are "but few important differences" between *B. pretiosa* and *Protocaris marshi*. The former, however, has well preserved appendages, and differs from the single poorly preserved specimen of *Protocaris marshi* in the outline of the carapace and telson morphology; this is considered to warrant its removal to a new genus. Both Raymond (1935) and Størmer (1939, p. 237; 1944, p. 101) considered that *Protocaris* (i.e., *B. pretiosa*) has trilobitan limbs, but the evidence for the morphology of the appendages does not support this view. Størmer (1944, p. 101) noted that he had examined in the United States National Museum in Washington "a specimen of the genus *Portalia* (similar to *Protocaris*) which had indications of gill blades on the appendages." He was referring to a specimen (probably USNM 189232) of *Odaraia* (Walcott, 1912a), presently under study, which was never described by Walcott, but bears the label '*Portalia alata*' in the collections. This specimen bears no relation to the species *Portalia mira* that Walcott figured (1918) and that he considered to be a holothurian. Rolfe (1969, p. 331) was of the opinion that Størmer was comparing *Protocaris* (i.e., *B. pretiosa*) with the only published material of *Portalia*, the holotype of *P. mira*; his remarks concerning Størmer's supposed interpretation of this holotype are based on this misapprehension.

Resser (1929), noting that *Protocaris marshi* possessed a bivalved carapace like that of *Branchiocaris pretiosa*, apparently considered that this feature precludes it from the notostracan branchiopods, and he suggested that both species had affinities with the Phyllocarida. Raymond (1935), however, deemed that what he supposed were the "trilobitan" limbs of *B. pretiosa* were a more important diagnostic feature than the gross morphology and he included *Protocaris* (i.e., both *P. marshi* and *B. pretiosa*) in a new order, Pseudonotostraca, which he considered was "leading to the Notostraca." Størmer (1944) also favoured an approach based on apparent appendage morphology and assigned *Protocaris* to a new class, Pseudocrustacea, of the subphylum Trilobitomorpha. He did not, however, retain the genus in the class Trilobitoidea (1959) when he subsequently reclassified many of the Burgess Shale arthropods, rejecting the bivalved forms from this subphylum. The present study of the Burgess Shale fauna (Whittington, 1971a) has produced new evidence that suggests that the 'trilobite limb' is not as constant a feature among these arthropods as was previously thought. A more cautious approach to the classification of early arthropods was suggested by Woods (1965), who noted that "formerly *Protocaris marshi* . . . has been considered to be a notostracan and the earliest branchiopod . . . . Without details of the structure of the appendages in these fossils, it is, however, impossible to place them even in the Crustacea generally."

Branchiocaris pretiosa cannot be assigned with certainty to any extant group of arthropods. Størmer (1944, p. 126, 127) compared the "great appendage" of *Leanchoilia* from the Burgess Shale with the chelicera of the Xiphosura and suggested that it might be a developmental stage of the latter. The contemporaneous *B. pretiosa* bore an anterior appendage, the principal appendage, which may have been much closer in morphology to a chelicera. The chelate appendages of chelicerates, however, are invariably preoral, whereas the principal appendage of *B. pretiosa* appears to have been postoral, and the former usually comprise no more than four segments, compared with eight in the latter. *B. pretiosa* shows closest affinities with the branchiopod Crustacea among extant arthropods, in spite of the anomalous princi-

pal appendage. The antennae and antennules of these arthropods may be reduced or absent and this may account for the apparent lack of a second pair of preoral antennae. The species is similar to the Notostraca in the large number of body somites and apparently simple, uniform morphology of the lamellate appendages. The bivalved carapace, however, suggests analogies with the Conchostraca. *Protocaris marshi* also possessed a bivalved carapace and many trunk somites. Unfortunately the preservation is inadequate to permit a study of the appendages but the evidence does not rule out a similar arrangement to that in *B. pretiosa*.

Information on the cephalic segmentation and the structure of the appendages of these arthropods is so limited that they cannot be classified satisfactorily nor can their evolutionary significance be accurately assessed. Clearly, however, *Branchiocaris pretiosa*, like many of the Burgess Shale arthropods, is a unique form which, although morphologically similar to some recent Notostraca, is unlikely to represent a direct evolutionary predecessor of this group. It apparently defies classification within any group of Recent arthropods. Størmer's (1959) class Trilobitoidea is not considered an acceptable solution to this problem, based as it is on the subjective criterion "appendages of typical or modified trilobite type." Discussion of an alternative classification would be premature until the completion of studies now in progress on *Canadaspis perfecta* and other bivalved arthropods in the Burgess Shale fauna.

Family uncertain
Genus *Dioxycaris* Gürich, 1929

Dyoxycaris Krestovnikov, 1961

Type species. *Leperditia argenta* Walcott, 1886

Diagnosis. Carapace bivalved; valves subovate, dorsal margin produced anteriorly and posteriorly into an oblique pointed process, narrow border defined by a shallow groove.

Geological horizon. Middle Cambrian, Ophir Shale, ?*Glossopleura* Zone (R. A. Robison, *pers. comm.*), Utah.

Dioxycaris argenta (Walcott, 1886)
Plate 6, figures 3, 4

1886 *Leperditia Argenta*, Walcott, p. 39, 47, 54, Pl. 8, fig. 5
1886 *Leperditia ? Argenta*, Walcott, p. 146, 147
1889 *Leperditia argenta*; Miller, p. 552
1889 *Leperditia argenta*; Vogdes, p. 25
1890 *Leperditia argenta*; Vogdes, p. 170
1890 *Leperditia ? argenta*, Walcott, p. 625
1891 *Leperditia argenta*, Walcott, p. 170, 319
1893 *Leperditia argenta*; Vogdes, p. 393
1912a *Hymenocaris argentea*, Walcott, p. 183
1912b *Isoxys argentea*, Walcott, p. 158, 189
1929 *Leperditia argenta*; Gürich, p. 34, 36
1929 *Leperditia ? argenta*; Gürich, p. 36
1929 *Hymenocaris argentea*; Gürich, p. 36
1929 *Dioxycaris argenta*; Gürich, p. 35–37, Fig. 1,3
1934 *Dioxycaris argentensis*; Straelen and Schmitz, p. 79, 80, 202, 217, 233
1953 *Dioxycaris argenta*; Roger, p. 311, 312, Pl. 1, fig. 4a
1956 *Leperditia (?) argenta*; Brooks and Caster, p. 9
1956 *Dioxycaris argenta*; Brooks and Caster, p. 11, Fig. 1,6, p. 13
1968 *Dioxycaris argenta*; Öpik, p. 10
1968 *Leperditia ? argenta*; Öpik, p. 10
1968 *Isoxys argenta*; Öpik, p. 10
1969 *Dioxycaris argenta*; Rolfe, p. 325, Fig. 150,4

Holotype. USNM 15401, part and incomplete counterpart, Plate 6, figures 2, 3, respectively, original of Walcott, 1886, Plate 8, figure 5 (line drawing).

Other material. R.A. Robison (*pers. comm.*) has spent considerable time and effort in an unsuccessful attempt to collect additional specimens from Walcott's type locality.

Walcott (1908, 1912b) recorded the occurrence of *Isoxys argentea* and *Isoxys* cf. *argentea* on the basis of some poorly preserved specimens which are similar in outline and size to the holotype, and may also belong to *Dioxycaris*. These are as follows: USNM 56513—part and counterpart of a valve and some additional fragmentary material from USNM locality 54a (*see* Walcott, 1908, p. 196; 1912b, p. 151, 202), Middle Cambrian, Ute Limestone, Blacksmith Fork section (15 miles east of Hyrum, Bear River Range, according to the specimen label), Utah; USNM 56514, 56518—six specimens from USNM locality 35g (*see* Walcott, 1908, p. 209; 1912b, p. 126, 198), Middle Cambrian, Eldon Limestone, at the north end of the amphitheatre northwest of the main ridge of Mount Bosworth, north of the Canadian Pacific Railway between Hector and Stephen, British Columbia.

The U.S. National Museum also holds five isolated valves (USNM 56512) and a complete carapace (USNM 56515) which may be *Dioxycaris*, from USNM locality 32x (*see* Walcott, 1908, p. 8; 1912b, p. 150, 195), Middle Cambrian, about 1700 feet above the Brigham Quartzite, Wasatch Canyon, east of Lakeview Ranch, 5 miles north of Brigham City, Boxelder County, Utah.

Locality and stratigraphical horizon. Middle Cambrian, Ophir Shale, ?*Glossopleura* Zone, Big Cottonwood Canyon, one mile from Argenta, Wasatch Range, Utah (USNM locality 30a, *see* Walcott, 1886, p. 147; 1912b, p. 158, 189).

Gürich (1929) discussed *Dioxycaris argenta* under the heading 'Lower Cambrian' and this error was perpetuated by Straelen and Schmitz (1934), Roger (1953) and Rolfe (1969). Brooks and Caster (1956, p. 9) indicated that the genus is from the Middle Cambrian Wheeler Shale. R.A. Robison (*pers. comm.*) confirms the locality and stratigraphical horizon given above and considers it "likely that the type locality is now covered by a paved highway to the Brighton Ski Resort."

Preservation. The only known specimen of *Dioxycaris argenta*, a single valve, is preserved in a dark fine-grained micaceous shale. The fossil appears to have split along the surface of the carapace and this allows a distinction to be drawn between the part (Pl. 6, fig. 2), which preserves an indication of the original convex relief, and the incomplete counterpart (Pl. 6, fig. 3), in which the valve is concave, has no apparent thickness and lacks the dorsal area. Compaction has destroyed most of the relief, which is reflected in a series of ridges and folds traversing the valve. The margin, however, appears to be intact, which suggests that the valve was orientated approximately parallel to the bedding. Several nodular features occurring within the area covered by the valve are preserved as pits on the part (Pl. 6, fig. 2). These

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may be the result of nucleation caused by decaying organic matter but examples also occur on the surrounding slab. Brooks and Caster (1956) described the carapace as "chitinous" but this designation is misleading without the corroboration of a chemical analysis.

Description. On the basis of considerations outlined below, the specimen is assumed to be the right valve of a pair. The valves were suboval in outline, expanding anteroventrally. The dorsal margin, the hinge or fold, is assumed to have been straight, although it is slightly deformed on the specimen probably because of compaction in a flexible state. It is produced anteriorly into a clearly defined small oblique pointed process. The posterior end of the hinge or fold is poorly preserved and partly destroyed as a result of some earlier worker's misguided preparation. A similar process appears to be present, however, as figured by Walcott (1886) and subsequent authors. The processes do not appear to have been articulated. The curved anterior and posterior margins of the valve were directed ventrally at an angle of about 110° to the hinge or fold. The carapace had a poorly defined narrow border bounded on the inner margin by a shallow groove (preserved on the counterpart in positive relief). This border appears to be smooth, although this cannot be confirmed because the specimen is inadequately preserved. There is no unequivocal evidence of a muscle scar. None of the other surface features appear to be original.

Size. The outline of the valve is considered to have been little altered by postdepositional compaction. The length parallel to the hinge or fold is 56 mm and the height normal to it 30.4 mm.

Discussion

Previous descriptions. In his original description of the specimen, Walcott (1886) interpreted the more tapered end of the valve as anterior and this orientation has not been subsequently queried except by Rolfe (1969, p. 325), who referred to it as "? left valve." The specimen is interpreted as a right valve here but this designation must be considered equivocal without a preserved muscle scar or traces of the soft parts. It is based on a comparison with *Branchiocaris pretiosa*, the carapace of which is similar in outline with the valves expanding slightly anteriorly. Photographs of *Dioxycaris argenta* (Pl. 6, figs. 2, 3) have not previously been published; all illustrations to date have been drawings of the complete part.

Affinities and classification. Walcott (1886) originally referred *Dioxycaris argenta* to the ostracod genus *Leperditia*. In 1912, however, he assigned the species to *Hymenocaris* and

consequently to the phyllocarid family Hymenocarididae in one paper (1912a), and to *Isoxys* in another (1912b). *D. argenta* has continued to be considered a phyllocarid although Straelen and Schmitz (1934), and subsequently Roger (1953) and Krestovnikov (1960) classified it in the family Ceratiocarididae. Brooks and Caster (1956) considered that "the similarity of the anterior and posterior processes of the carapace of *Isoxys*, *Dioxycaris* and *Tuzoia* is suggestive of a common relationship and sets them apart from the other phyllocarid types." They erected a new family, Isoxysidae, to include the three genera; the name was corrected to Isoxyidae by Rolfe (1969, p. 326) who pointed out that it is a junior synonym of Tuzoiidae Raymond, 1935, to which Öpik (1968) considered *Dioxycaris* probably belonged. Both family names are, in fact, junior synonyms of Isoxysidae Vogdes, 1893, which was originally erected to include *Isoxys* alone.

The valves of *Branchiocaris pretiosa* are similar in outline (assuming the orientation suggested above) and size to that of *Dioxycaris argenta*—both the anterior and posterior extremities of the hinge or fold are apparently produced into oblique spines or processes. However, the carapace of the only known specimen of *D. argenta* is inadequately preserved to indicate the presence or absence of the peripheral pits that are a distinguishing feature of *Branchiocaris*. The Utah species is known only from a single poorly preserved valve lacking traces of soft parts; evidence is inadequate to demonstrate whether or not *Dioxycaris* and *Branchiocaris* are congeneric and the latter is not synonymized with the earlier described form.

One may argue that *Branchiocaris* should be removed from the family Protocarididae Miller, 1889 and placed in the Isoxyidae Vogdes, 1893. This would imply that the morphological similarity between *Protocaris marshi* and *Branchiocaris pretiosa* was less diagnostic than the presence of dorsal processes on the valves of the latter. The significance of these processes is problematical—the anterior pair may have fulfilled the same function as the nonarticulating rostrum of some Crustacea. Alternatively they may have had a strengthening effect or facilitated movement about the hinge or fold of the carapace, thus explaining their presence posteriorly as well as anteriorly. The validity of using the presence or absence of these processes as the main basis for a familial division is thus questioned and *Dioxycaris* is not referred here to any family, without further evidence of its morphology. The preservation of the holotype of *Protocaris marshi*, after all, does not rule out the possibility that the carapace of this genus may also have borne processes on each valve at the extremities of the hinge or fold.

References

Baily, W. H.
  1870: On fossils obtained at Kiltorkan Quarry, Co. Kilkenny; Br. Assoc. Advan. Sci., Rep. (1869), p. 73–75.

Bernard, H.M.
  1894: The systematic position of the trilobites; Quart. J. Geol. Soc. London, v. 50, p. 411–434.
  1897: Fossil Apodidae; Nat. Sci., London, v. 11, no. 70, p. 397–403.

Brooks, H. K. and Caster, K. E.
  1956: *Pseudoarctolepis sharpi*, n. gen., n. sp. (Phyllocarida) from the Wheeler Shale (Middle Cambrian) of Utah; J. Paleontol., v. 30, no. 1, p. 9–14.

Cannon, H. G.
  1933: On the feeding mechanism of the Branchiopoda; R. Soc. Lond., Philos. Trans., Ser. B, v. 222, p. 267–352.

Clarke, J. M.
  1893: On the structure of the carapace in the Devonian crustacean *Rhinocaris*; and the relation of the genus to *Mesothyra* and the Phyllocarida; Am. Natur., v. 27, p. 793–801.

Dechaseaux, C.
  1953: Sous-classe des Branchiopodes; *in* Traité de paléontologie, J. Piveteau, ed.; Paris, v. 3, p. 257–268.

Fritz, W. H.
  1971: Geological setting of the Burgess Shale; Proc. North Am. Paleontol. Conv. 1969, Lawrence, Kansas, pt. 1, p. 1155–1170.

Grabau, A. W. and Shimer, H. W.
  1910: North American index fossils – invertebrates; New York, A. G. Seiler & Company, v. 2, 909 p.

Gürich, G.
  1929: *Silesicaris* von Leipe und die Phyllokariden überhaupt; Mitt. Mineral.-Geol. Staatsinst. Hamburg, v. 11, p. 21–90.

Hessler, R. R. and Newman, W. A.
  1975: A trilobitomorph origin for the Crustacea; Fossils and strata, no. 4, p. 437–459.

Jones, T. R.
  1883: Palaeozoic Phyllopoda; *as reported on to* the British Association, Southport, 1883, Sec. C: Geology; Geol. Mag., decade 2, v. 10, p. 461–464.

Jones, T. R., Etheridge, R. and Woodward, H.
  1884: The fossil Phyllopoda of the Palaeozoic rocks (first report); Br. Assoc. Advan. Sci., Rep. (1883), p. 215–223.
  1890: The fossil Phyllopoda of the Palaeozoic rocks (seventh report); Br. Assoc. Advan. Sci., Rep. (1889), p. 63–68.

Jones, T. R., Wiltshire, T. and Woodward, H.
  1892: The fossil Phyllopoda of the Palaeozoic rocks (ninth report); Geol. Mag., decade 3, v. 9, p. 513–515.
  1893: The fossil Phyllopoda of the Palaeozoic rocks (ninth report); Br. Assoc. Advan. Sci., Rep. (1892), p. 298–300.

Jones, T. R. and Woodward, H.
  1888: A monograph of the British Palaeozoic Phyllopoda (Phyllocarida, Packard); Palaeontogr. Soc., pt. 1, 72 p.

Jux, U.
  1960: *Montecaris lehmanni*, a new crustacean from the Rhenish Devonian and the problem of its systematic position; J. Paleontol., v. 34, no. 6, p. 1129–1152.

Krestovnikov, V. N.
  1960: Nadotryad Phyllocarida; *in* Trilobitoobraznye i rakoobraznye, N. E. Chernysheva, ed.; *in* Osn. Paleontol., Yu. A. Orlov, ed.; Moscow, p. 425–429.
  1961: Novyye rakoobraznye fillokaridy Paleozoya Russkoi platformy, Urala, Timana i Donbassa; Akad. Nauk SSSR, Geol. Inst., Tr., no. 52, p. 1–67.

Miller, S. A.
  1889: North American geology and palaeontology for the use of amateurs, students and scientists; Cincinnati, Western Methodist Book Concern, 664 p.

Moore, R. C. and McCormick, L.
  1969: General features of Crustacea; *in* Treatise on invertebrate paleontology, Pt. R: Arthropoda, R. C. Moore, ed.; Geol. Soc. Am. and Univ. Kansas Press, v. 4, no. 1, p. 57–120.

Novozhilov, N. I.
  1960: Podklass Gnathostraca; *in* Trilobitoobraznye i rakoobraznye, N. E. Chernysheva, ed.; *in* Osn. Paleontol., Yu. A. Orlov, ed.; Moscow, p. 216–253.

Öpik, A. A.
  1968: Ordian (Cambrian) Crustacea Bradoriida of Australia; Aust. Bur. Miner. Resour., Geol. Geophys., Bull., no. 103, 44 p.

Raymond, P. E.
  1935: *Leanchoilia* and other Mid-Cambrian Arthropoda; Harv. Univ. Mus. Comp. Zool., Bull., v. 76, no. 6, p. 205–230.

Resser, C. E.
  1929: New Lower and Middle Cambrian Crustacea; Proc. U.S. Natl. Mus., v. 76, art. 9, p. 1–18.

Resser, C. E. and Howell, B. F.
  1938: Lower Cambrian *Olenellus* Zone of the Appalachians; Geol. Soc. Am., Bull., v. 49, p. 195–248.

Roger, J.
  1953: Sous-classe des Malacostracés; *in* Traité de paléontologie, J. Piveteau, ed.; Paris, v. 3, p. 309–378.

Rolfe, W. D. I.
  1962: Two new arthropod carapaces from the Burgess Shale (Middle Cambrian) of Canada; Breviora, no. 160, 9 p.
  1969: Phyllocarida; *in* Treatise on invertebrate paleontology, Pt. R: Arthropoda, R. C. Moore, ed.; Geol. Soc. Am. and Univ. Kansas Press, v. 4, no. 1, p. 296–331.

Ruedemann, R.
  1922: On the occurrence of an *Apus* in the Permian of Oklahoma; J. Geol., v. 30, no. 4, p. 311–318.

Schuchert, C.
  1897: On the fossil phyllopod genera, *Dipeltis* and *Protocaris*, of the family Apodidae; Proc. U.S. Natl. Mus., v. 19, p. 671–676.
  1937: Cambrian and Ordovician of northwestern Vermont; Geol. Soc. Am., Bull., v. 48, p. 1001–1078.

Shaw, A. B.
  1954: Lower and Middle Cambrian faunal succession in northwestern Vermont; Geol. Soc. Am., Bull., v. 65, p. 1033–1046.
  1955: Paleontology of northwestern Vermont, 5: The Lower Cambrian Fauna; J. Paleontol., v. 29, no. 5, p. 775–805.
  1958: Stratigraphy and structure of the St. Albans area, northwestern Vermont; Geol. Soc. Am., Bull., v. 69, p. 519–568.

Shimer, H. W. and Shrock, R. R.
  1944: Index fossils of North America; New York and London, Wiley, 837 p.

Størmer, L.
  1939: Studies on trilobite morphology, Pt. 1: The thoracic appendages and their phylogenetic significance; Nor. Geol. Tidsskr., v. 19, p. 143–273.
  1944: On the relationships and phylogeny of fossil and Recent Arachnomorpha; Skr. Nor. Vidensk-Akad., I. Mat.-Naturv. Klasse., no. 5, 158 p.
  1959: Trilobitoidea; *in* Treatise on invertebrate paleontology, Pt. O: Arthropoda, R. C. Moore, ed.; Geol. Soc. Am. and Univ. Kansas Press, v. 1, p. 23–37.

Straelen, V. van and Schmitz, G.
  1934: Crustacea Phyllocarida (=Archaeostraca); *in* Fossilium Catalogus, I: Animalia, W. Quenstedt, ed.; Berlin, W. Junk, 's-Gravenhage, pt. 64, 246 p.

Vogdes, A. W.
  1889: A catalogue of North American Palaeozoic Crustacea, confined to the non-trilobitic genera and species; Ann. N.Y. Acad. Sci., v. 5, pt. 1, p. 1–38.
  1890: A bibliography of Palaeozoic Crustacea from 1698–1889, including a list of North American species and a systematic arrangement of genera; U.S. Geol. Surv., Bull., no. 63, 177 p.
  1893: A classed and annotated bibliography of the Palaeozoic Crustacea (1698–1892), to which is added a catalogue of North American species; Calif. Acad. Sci., Occas. pap., no. 4, 413 p.

Walcott, C. D.
  1884: On a new genus and species of Phyllopoda from the Middle Cambrian; *in* On the Cambrian faunas of North America, preliminary studies; U.S. Geol. Surv., Bull., no. 10, p. 330–331.
  1886: Second contribution to the studies on the Cambrian faunas of North America; U.S. Geol. Surv., Bull., no. 30, 369 p.
  1890: The fauna of the Lower Cambrian or *Olenellus* Zone; U.S. Geol. Surv., Rep., no. 10, p. 511–774.
  1891: Correlation papers – Cambrian; U.S. Geol. Surv., Bull., no. 81, 447 p.
  1908: Cambrian sections of the Cordilleran area; *in* Cambrian geology and paleontology, 2; Smithson. Misc. Collect., v. 53, no. 5, p. 167–230.
  1912a: Middle Cambrian Branchiopoda, Malacostraca, Trilobita, and Merostomata; *in* Cambrian geology and paleontology, 2; Smithson., Misc. Collect., v. 57, no. 6, p. 145–228.
  1912b: Cambrian Brachiopoda; U.S. Geol. Surv., Monogr., v. 51, pt. 1 – Text, 872 p.
  1918: Geological explorations in the Canadian Rockies; *in* Explorations and fieldwork of the Smithsonian Institution in 1917; Smithson. Misc. Collect., v. 68, p. 4–20.

Whiteaves, J. F.
  1892: Description of a new genus and species of phyllocarid crustacean from the Middle Cambrian of Mount Stephen, British Columbia; Can. Rec. Sci., v. 5, no. 4, p. 205–208.

Whittington, H. B.
  1971a: The Burgess Shale: history of research and preservation of fossils; Proc. North Am. Paleontol. Conv. 1969, Lawrence, Kansas, pt. 1, p. 1170–1201.
  1971b: Redescription of *Marrella splendens* (Trilobitoidea) from the Burgess Shale, Middle Cambrian, British Columbia; Geol. Surv. Can., Bull., no. 209, 24 p.
  1974: *Yohoia* Walcott and *Plenocaris* n. gen. arthropods from the Burgess Shale, Middle Cambrian, British Columbia; Geol. Surv. Can., Bull., no. 231, 27 p.

Woods, J. T.
  1965: The geological history of the Crustacea, with some remarks on their phylogeny; R. Soc. Queensl., Proc., v. 76, p. 1–14.

Woodward, H.
  1895: Some points in the life-history of the Crustacea in early Palaeozoic times; *in* Address delivered at the anniversary meeting of the Geological Society of London; Geol. Soc. Lond., Proc. (Session 1894–1895), v. 51, p. 70–88.
  1902: The Canadian Rockies. Part 1: On a collection of Middle Cambrian fossils obtained by Edward Whymper, Esq., F.R.G.S., from Mount Stephen, British Columbia; Geol. Mag., decade 4, v. 9, p. 502–505, 529–544.

Zittel, K. A. von
  1900: Textbook of Palaeontology; C. R. Eastman, trans. and ed.; London and New York, Macmillan, v. 1, 706 p.

Addendum

(June 8, 1967)

Since the manuscript was completed a reconstruction and brief description of *Protocaris pretiosa* by Simonetta and Delle Cave (1975) has become available. In addition to the holotype, they assigned (p. 13) 7 specimens to *P. pretiosa*. I have examined these specimens and, in my opinion, only three are correctly identified: USNM 189028 (Pl. 54, figs. 2a, 2b), USNM 189029 (Pl. 53, figs. 9a, 9b) and USNM 189030 (Pl. 53, figs. 7a, 7b), cited by Simonetta and Delle Cave as USNM 189302, 189300 and 189298, respectively. The others are as follows: USNM 189228 (Pl. 53, fig. 4), *Odaraia* Walcott, 1912a; USNM 189240 and 114255 (Pl. 53, figs. 5, 6), n. gen., n. sp., Briggs, *in press*; USNM 189022 (Pl. 53, fig. 8), cited as USNM 189299, *Canadaspis* Novozhilov, 1960. One further specimen, USNM 189199 (Pl. 54, fig. 5), was identified as *P. pretiosa*, apparently in error, in the plate explanation; it appears to be *Isoxys acutangulus* Walcott, 1908.

No discussion of the evidence upon which their reconstruction (Pl. 4, figs. 3a–c) is based was given by Simonetta and Delle Cave. They failed to note the large principal appendage in the cephalic region, and their contention that "compound eyes are present" was apparently based on the mis-identified USNM 114255. Their observation of "at least 55 short body segments" is an exaggeration (*see* Pl. 2, fig. 1; Pl. 3, figs. 1, 3 herein), and they considered that "it is impossible to make out any detail of the structure" of the trunk appendages. There is no evidence that the telson processes extend anteroventrally beneath 7 or 8 trunk somites to give a "dorsally annulated caudal structure" (*see* Pl. 2, figs. 1, 2; Pl. 3, figs. 1, 3; Pl. 4, fig. 3, herein).

References

Briggs, D. E. G.
  in press: New bivalved arthropods from the Middle Cambrian Burgess Shale of British Columbia.

Simonetta, A. M. and Delle Cave, L.
  1975: The Cambrian non trilobite arthropods from the Burgess Shale of British Columbia. A study of their comparative morphology, taxonomy and evolutionary significance; Palaeontogr. Ital., v. 69 (n.s. 39), p. 1–37.

Walcott, C. D.
  1908: Mount Stephen rocks and fossils; Can. alp. J., v. 1, no. 2, p. 232–248.

Plates 1–6 and Textfigures 3–7

The photographs were taken on fine-grained panchromatic film in ultraviolet radiation except for Plate 1, figures 1, 2, 4, 5, and Plate 6, figures 2, 3, which were taken in ordinary light. The orientation of the specimen relative to the bedding planes is given as parallel, lateral or oblique (*see* sections on preservation). The radiation was directed at 30° to the horizontal except where reflection was desirable, when the angle was increased to about 65°. The direction from which the fossil was illuminated is given relative to the margins of the plate. Textfigures 3–7 are camera lucida drawings giving an interpretation of the part or counterpart of a specimen illustrated on the adjacent plate. The drawings are labelled to indicate features referred to in the text; the symbols used are explained in the introduction. No attempt has been made to combine the features of both part and counterpart on the same drawing except in Textfigure 3, where the distal extremities of the telson processes were added from the counterpart. The specimens are held in the United States National Museum, Washington, D.C. (USNM) and the Museum of Comparative Zoology, Harvard, Cambridge, Massachusetts (MCZ).

The data referring to individual figures on the plates are arranged in the following order: depository and specimen number; orientation; direction of illumination; magnification; reference to previous illustration; comment; reference to textfigure.

Textfigure 3

Plate 1

Protocaris marshi Walcott, 1884

Figures 1–3. USNM 15400, part and counterpart, oblique; figure 1, part, north, ×3, original of Resser, 1929, Pl. 6, figs. 1, 2, Resser and Howell, 1938, Pl. 13, fig. 8; figure 2, counterpart, south, ×3; figure 3, part, northeast, ×6, showing cephalic region; *see* Text-figure 3.

Unidentifiable specimen referred to
Protocaris marshi by Resser and Howell, 1938

Figure 4. USNM 90826, east, ×3, original of Resser and Howell, 1938, Pl. 10, fig. 7.

Branchiocaris pretiosa (Resser, 1929)

Figures 5, 6. MCZ 5985, oblique; figure 5, north, ×1; figure 6, northeast, ×3, showing telson and posterior trunk.

Plate 1

Plate 2
Branchiocaris pretiosa (Resser, 1929)

Figures 1, 2. USNM 80483, part and counterpart, oblique; figure 1,
part, north, ×2.5, carapace removed from central area by Resser;
figure 2, counterpart, northwest, ×2.5, originals of Resser, 1929,
Pl. 4, figs. 1, 2; *see* Textfigure 4.
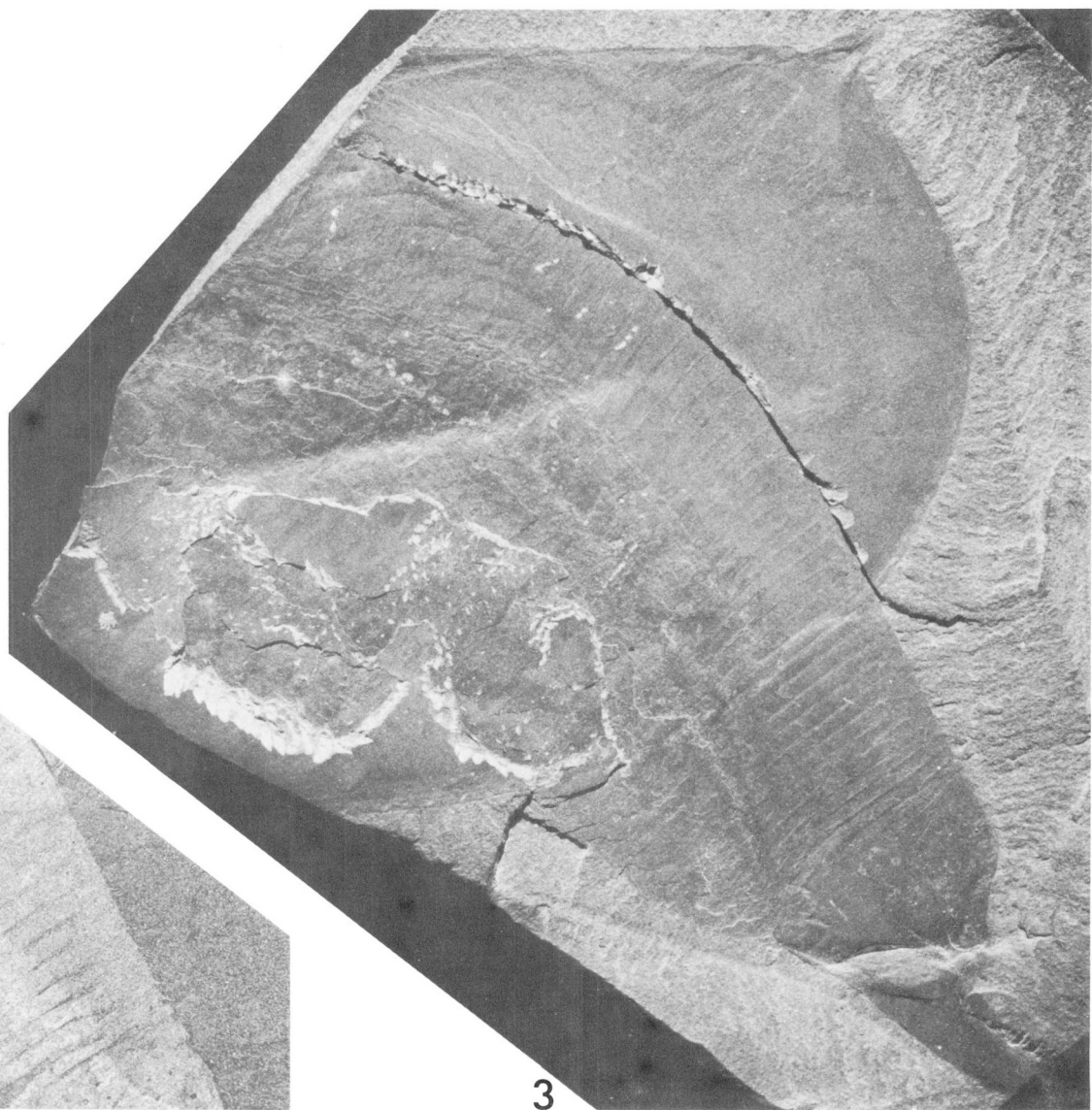

Textfigure 4
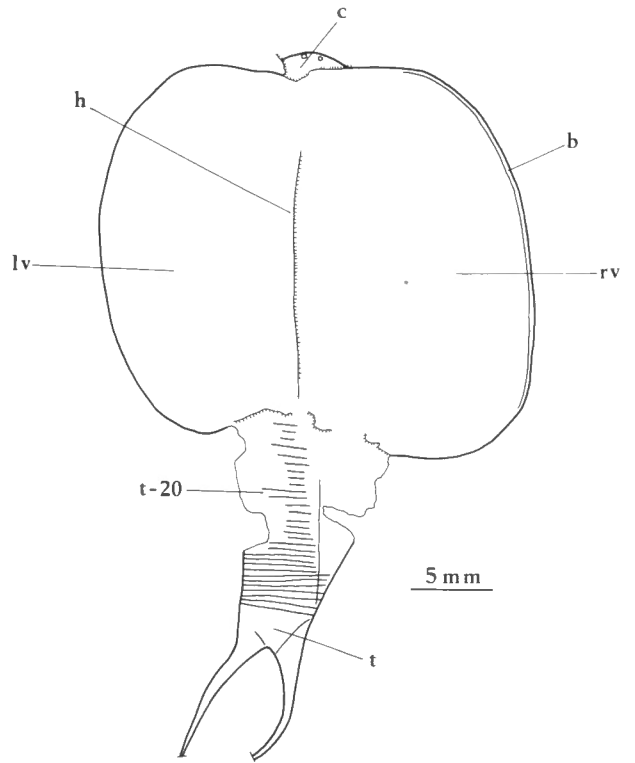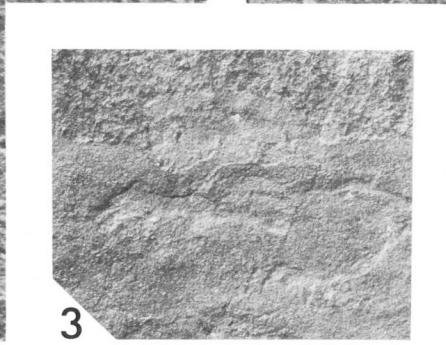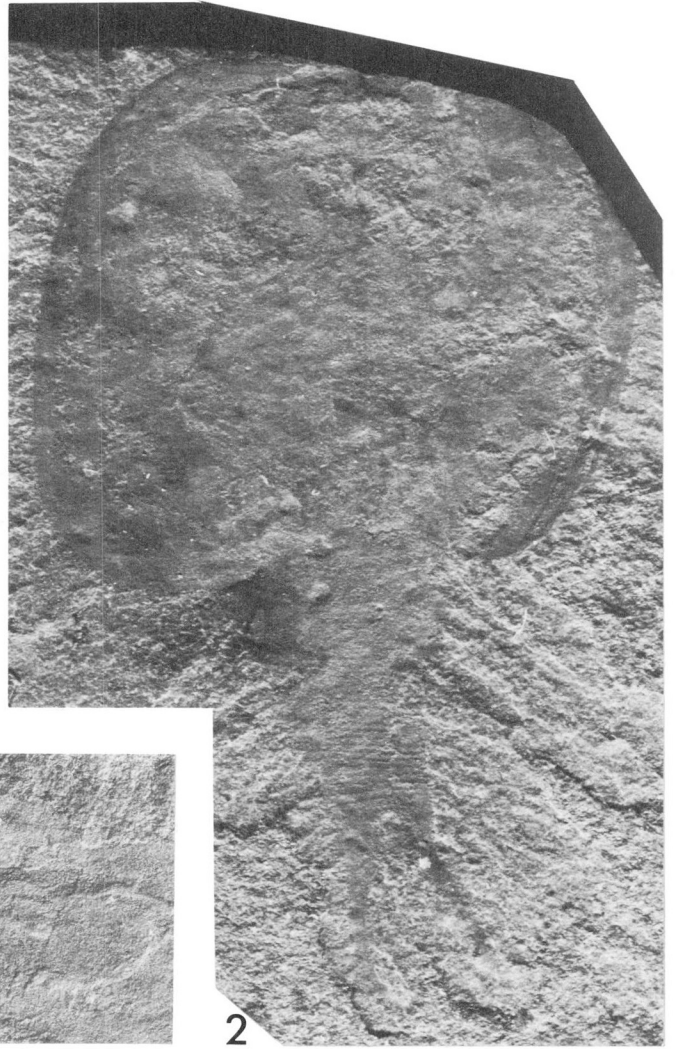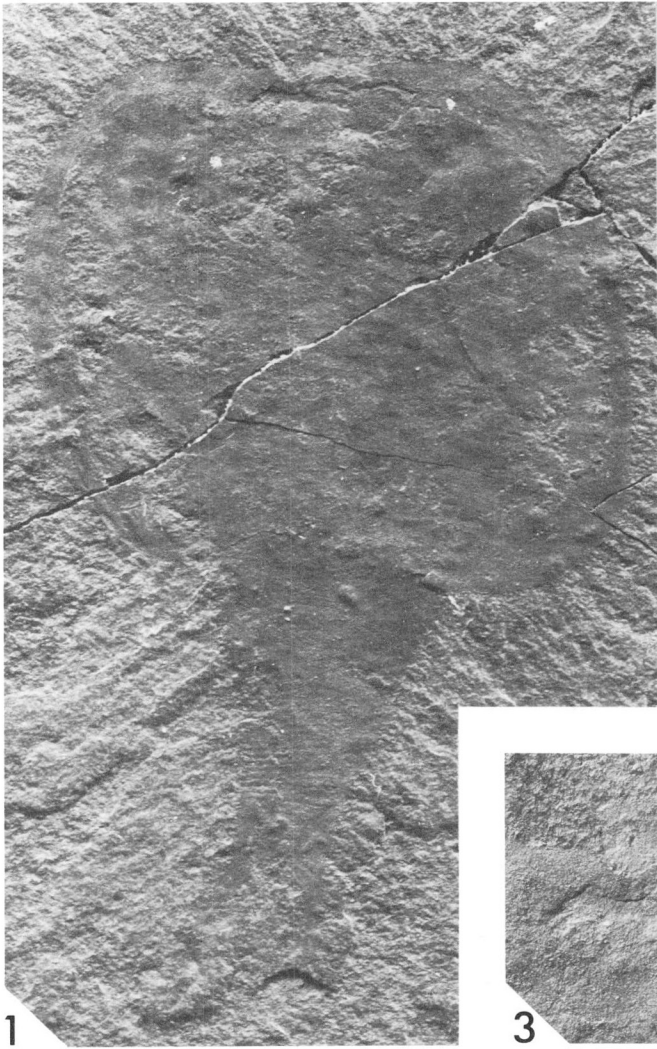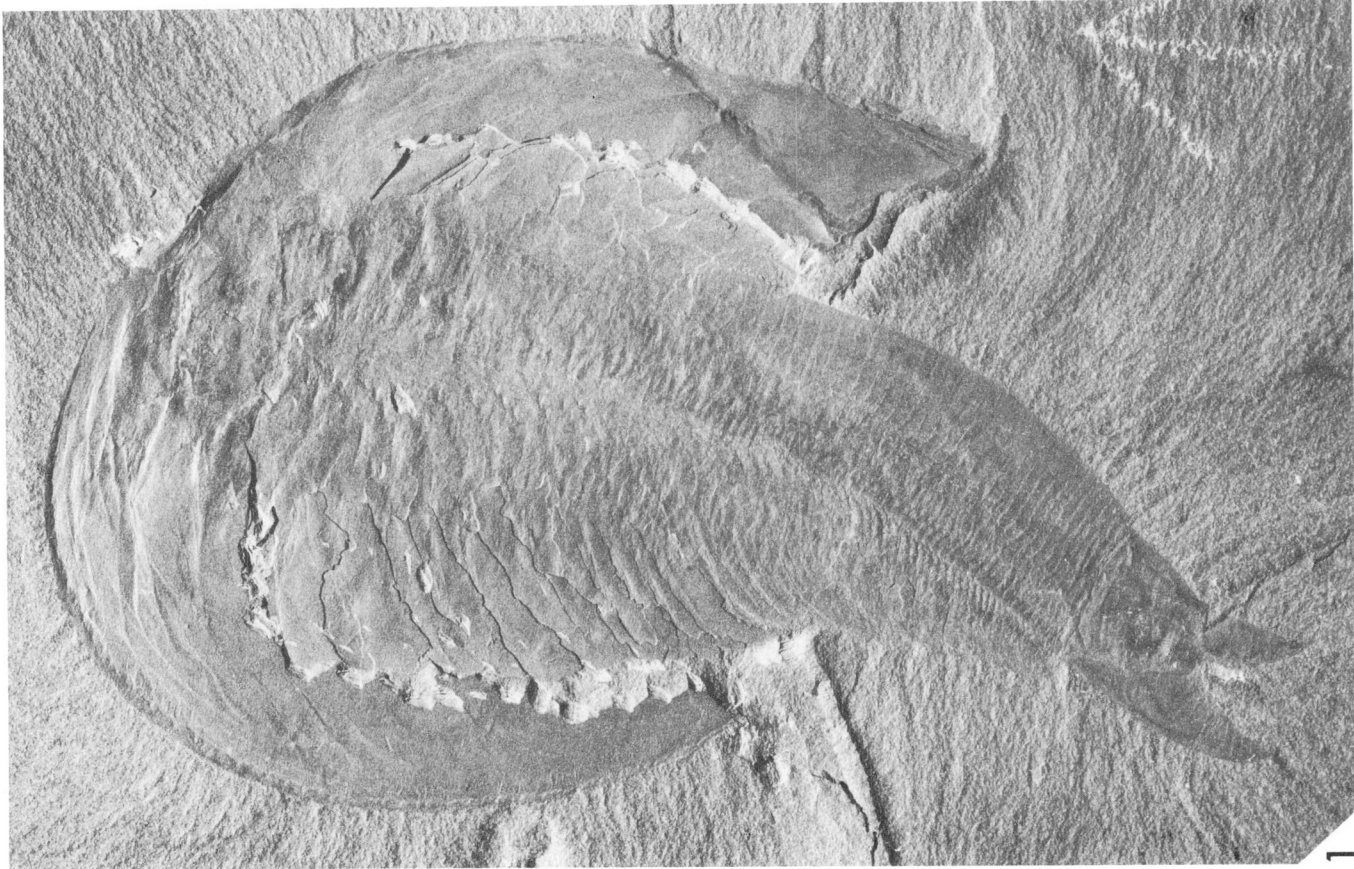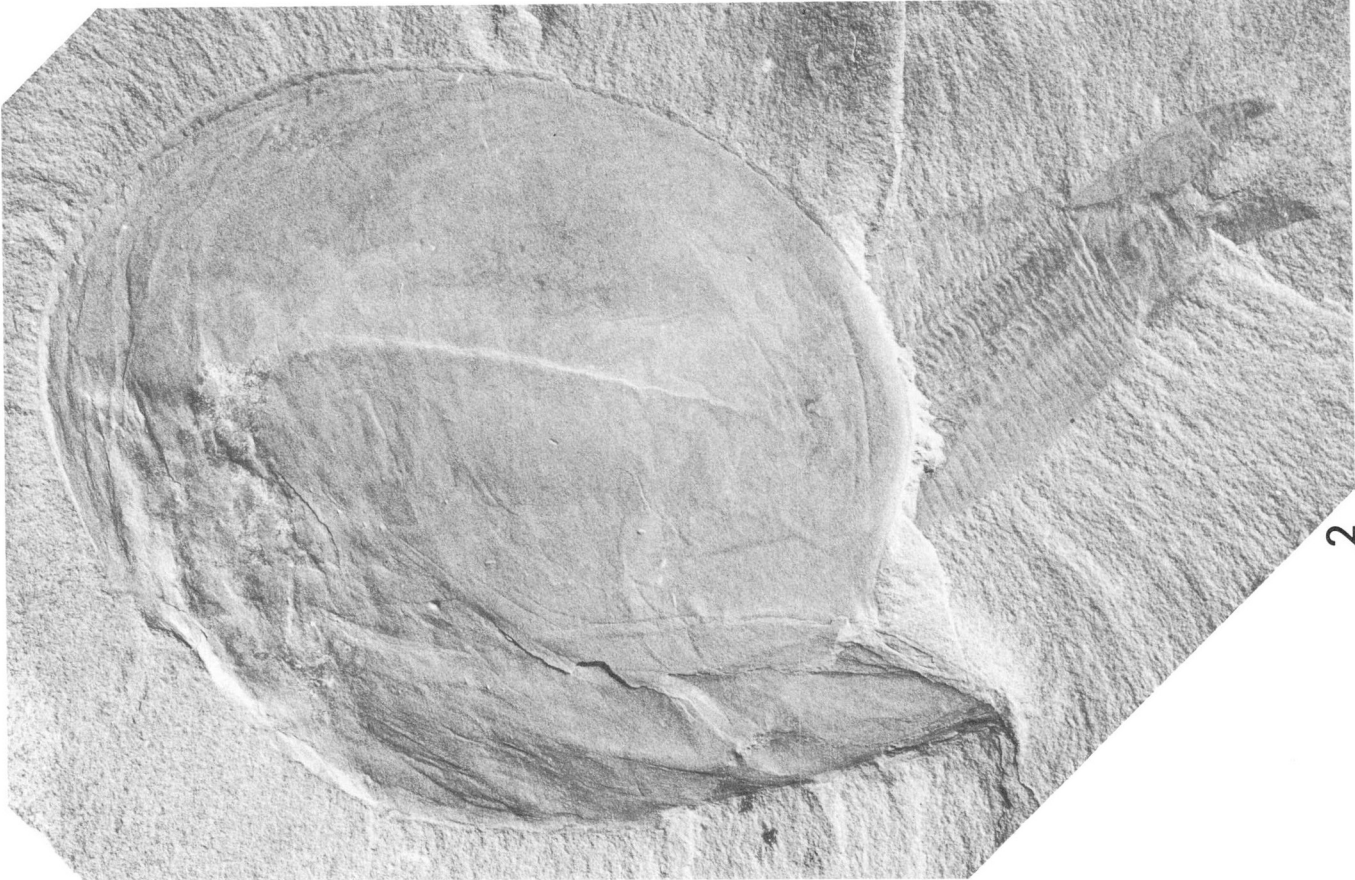
PLATE 2

Textfigure 5
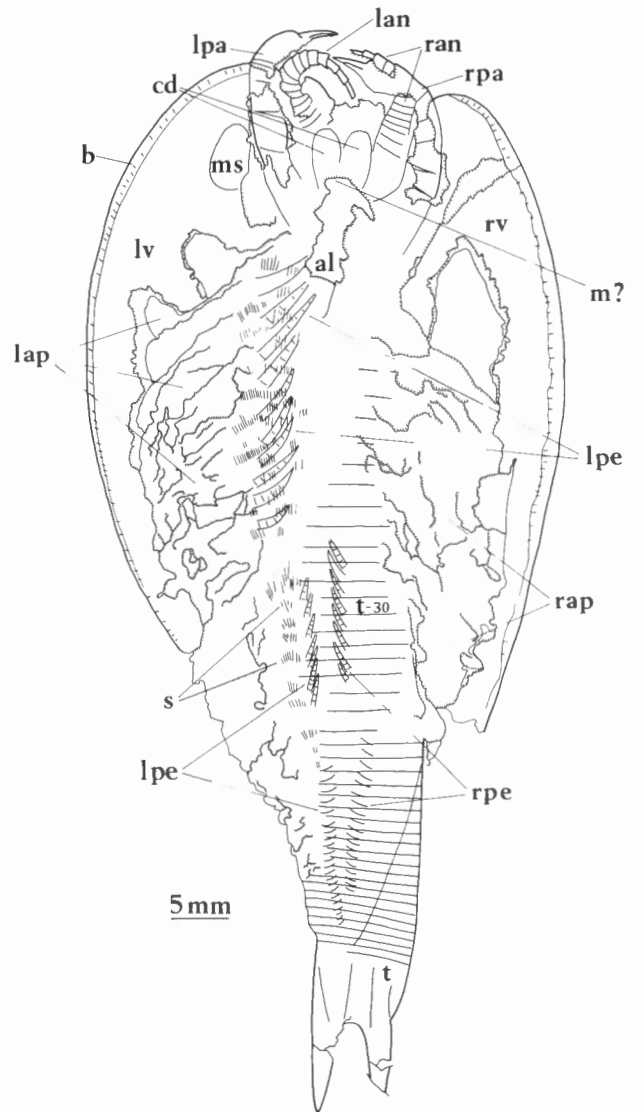
Plate 3
Branchiocaris pretiosa (Resser, 1929)

Figures 1–4. USNM 189028, part and counterpart, near-parallel; figure 1, part, reflected, west, ×1.5; figure 2, counterpart, north, ×1.5; figure 3, part, east, ×1.5; after removal of part of the carapace anteriorly; figure 4, part, north, ×4, showing anterior appendages after removal of part of the carapace; *see* Textfigure 5.

PLATE 3

Textfigure 6
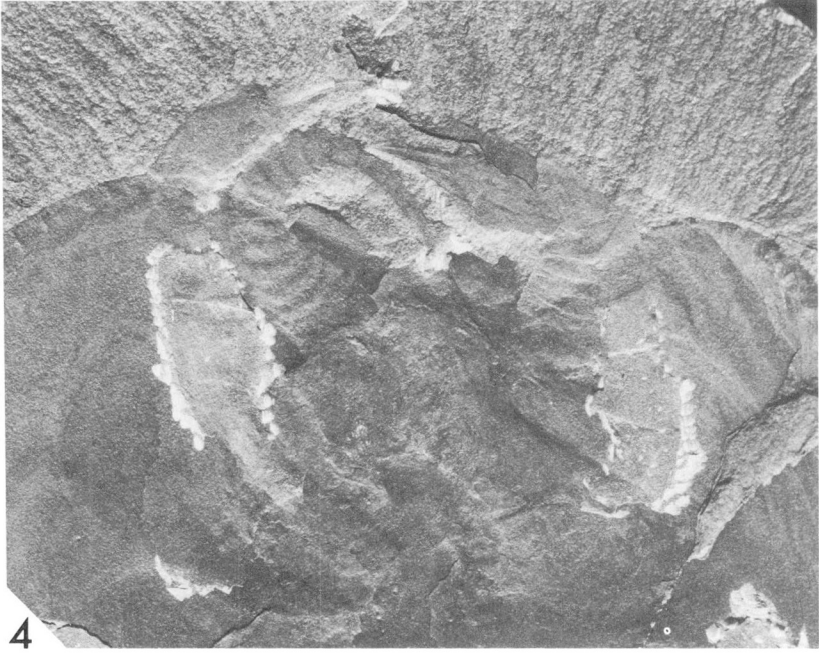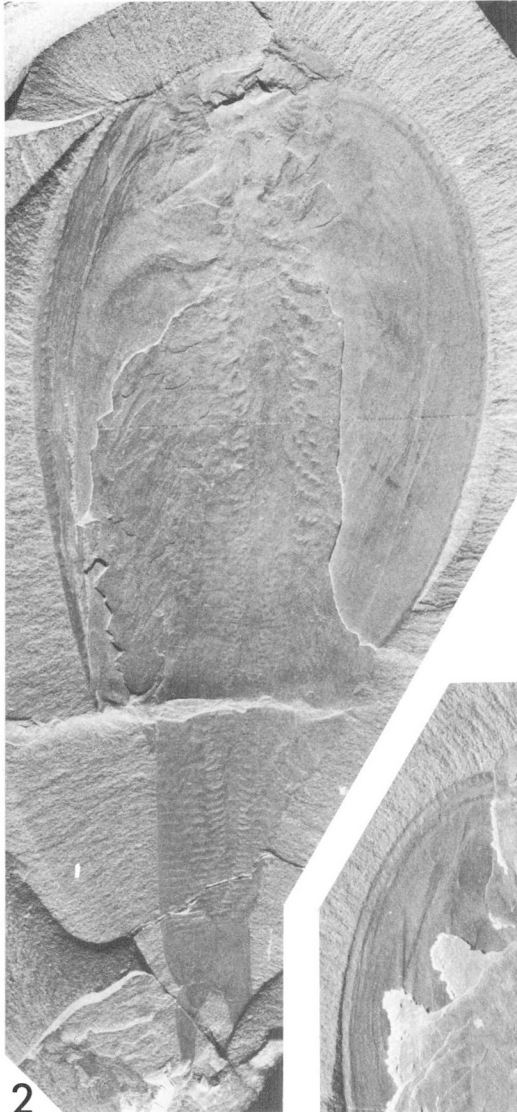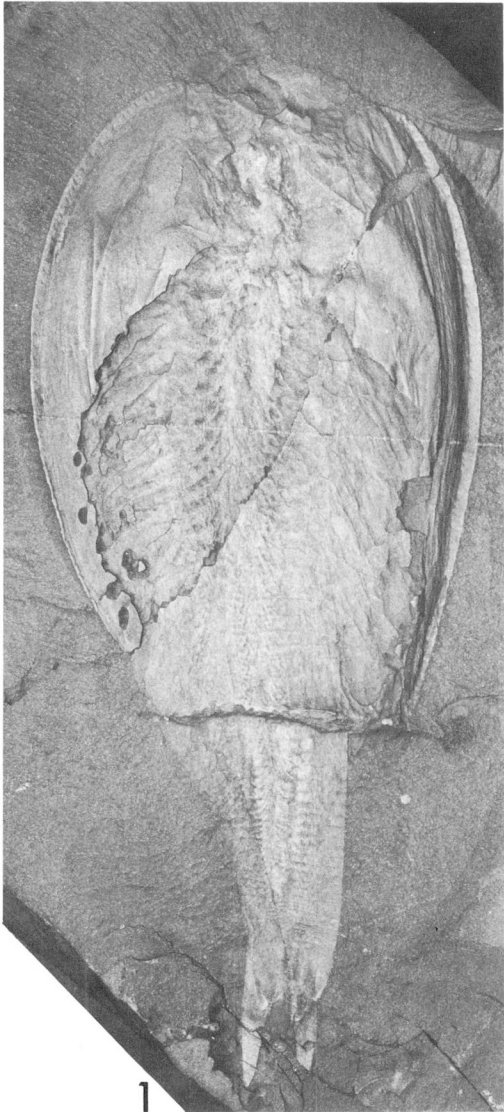
Plate 4
Branchiocaris pretiosa (Resser, 1929)

Figures 1–4. USNM 189029, lateral; figure 1, northwest, ×1.5; figure 2, reflected, west, ×1.5, after removal of part of the carapace; figure 3, north, ×3, after removal of part of the carapace; figure 4, reflected, southwest, ×4, showing spines on somite boundaries; *see* Textfigure 6.
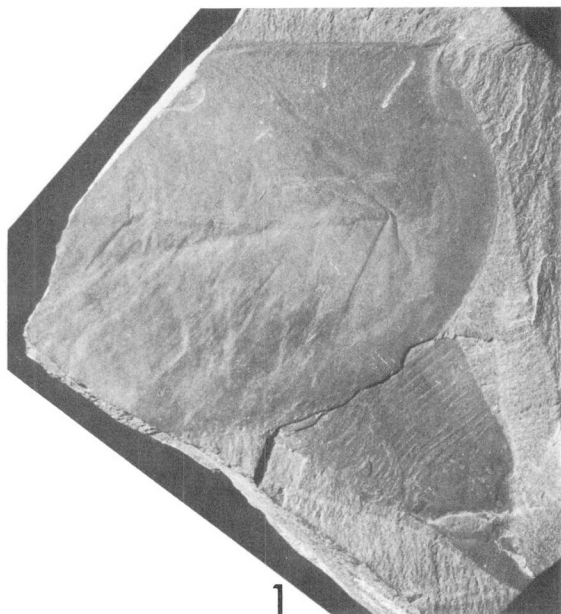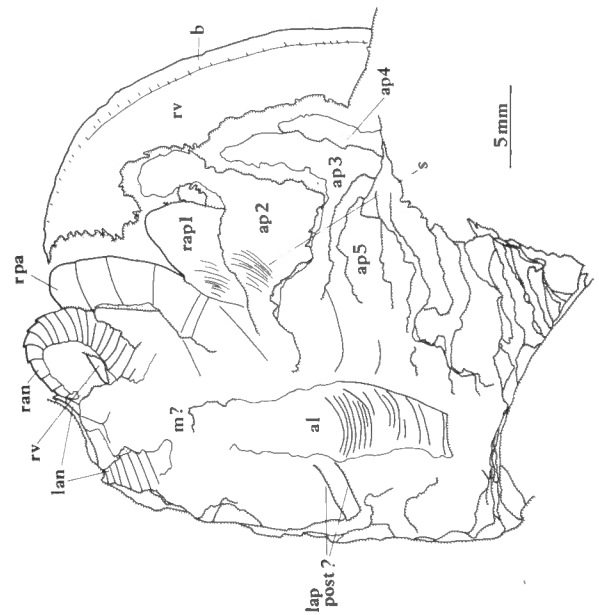
PLATE 4
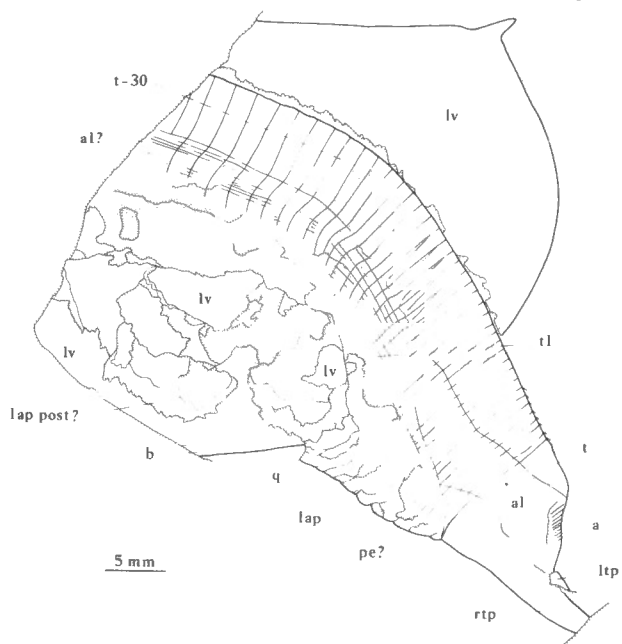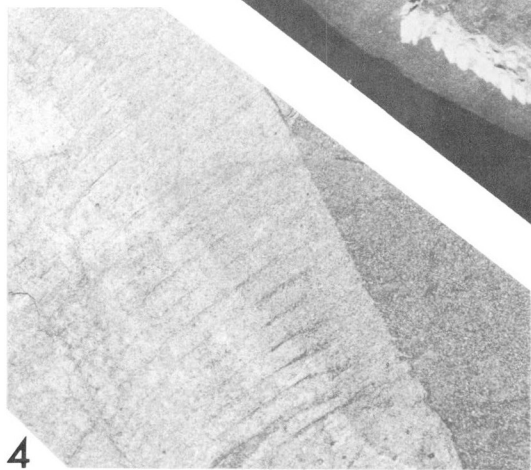
Textfigure 7

Plate 5
Branchiocaris pretiosa (Resser, 1929)

Figures 1–3. USNM 189030, part and counterpart, parallel; figure 1, part, north, ×2.5; figure 2, part, northwest, ×4, after removal of part of the carapace, *see* Textfigure 7; figure 3, counterpart, east, ×2.5.
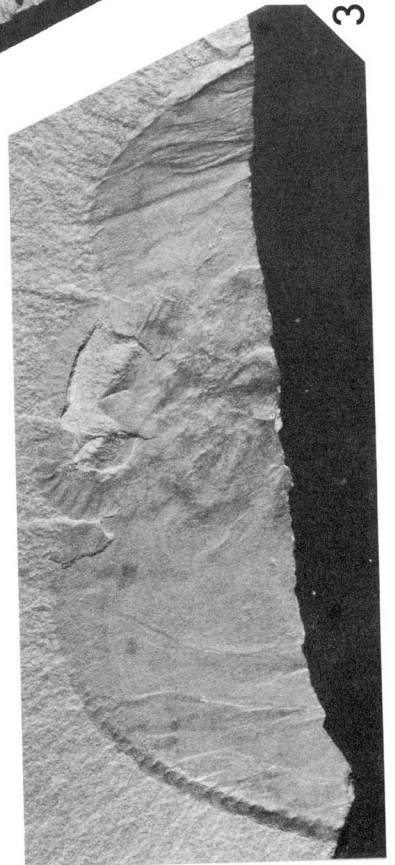
PLATE 5
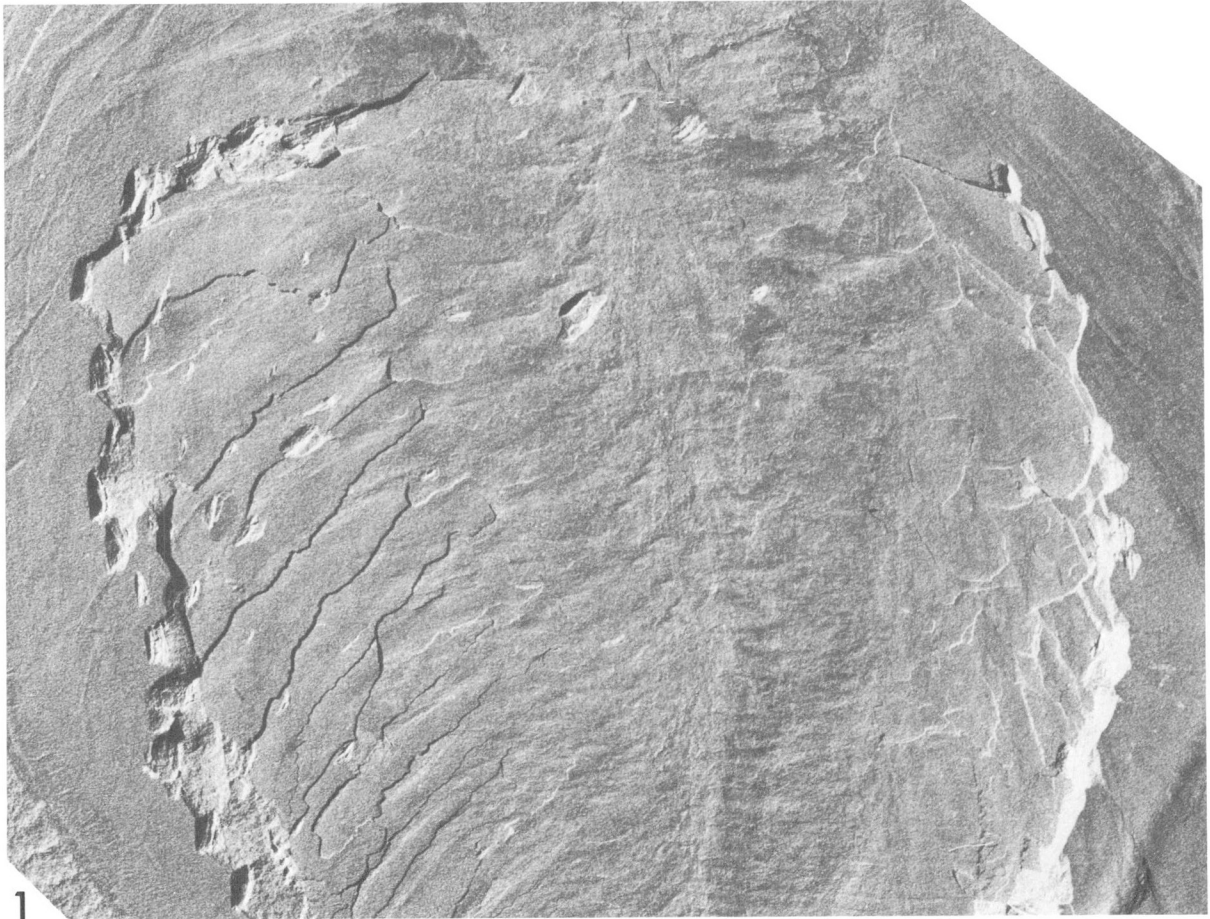
Plate 6

Branchiocaris pretiosa (Resser, 1929)

Figure 1. USNM 80483, part, oblique, north, ×4, to show elements of appendages, original of Resser, 1929, Pl. 4, fig. 2; *see* Textfigure 4.

Dioxycaris argenta (Walcott, 1886)

Figures 2, 3. USNM 15401, part and counterpart, lateral; figure 2, part, reflected, north, ×1.5; figure 3, counterpart, reflected, north ×1.5.

PLATE 6