

THE UNIVERSITY OF KANSAS
PALEONTOLOGICAL CONTRIBUTIONS

July 24, 1984

Paper 111

EXCEPTIONALLY PRESERVED
NONTRILOBITE ARTHROPODS AND ANOMALOCARIS
FROM THE MIDDLE CAMBRIAN OF UTAH¹

D. E. G. BRIGGS and R. A. ROBISON

Department of Geology, Goldsmiths' College, University of London, Creek Road, London SE8 3BU, and Department of Geology, University of Kansas, Lawrence, Kansas 66045

Abstract—For the first time arthropods with preserved soft parts and appendages are recorded from Middle Cambrian strata in Utah. Occurrences of four nontrilobite taxa are described, including *Branchiocaris pretiosa* (Resser) and *Emeraldella?* sp. from the Marjum Formation, *Sidneyia?* sp. from the Wheeler Formation, and *Leancoilia? hanceyi*, n. sp., from the Spence Shale. A small specimen of the giant predator *Anomalocaris nathorsti* (Walcott) also is described from the Marjum Formation. These occurrences extend upward the observed stratigraphic ranges of *Anomalocaris*, *Branchiocaris*, and questionably *Emeraldella* and *Sidneyia*. *Emeraldella*, *Leancoilia*, and *Sidneyia* hitherto have been recorded from only the Stephen Formation in British Columbia. Further evaluation indicates that *Dicerocaris opisthoeces* Robison and Richards, 1981, is a junior synonym of *Pseudoarctolepis sharpi* Brooks and Caster, 1956.

DURING RECENT years, intensive collecting has produced rare but diverse, soft-bodied or sclerotized Middle Cambrian fossils from several localities in Utah. Most of the taxa are the same as or similar to those previously described from the famous Burgess shale of the Stephen Formation in British Columbia (e.g., Whittington, 1980; Collins, Briggs, and Conway Morris,

1983). Although providing little new morphologic data, the Utah specimens are important because of new information they provide about the geographic and stratigraphic distribution of a rarely preserved part of the Middle Cambrian biota. They support the notions that the Burgess shale biota is unusual only in its preservation (Conway Morris and Whittington, 1979) and probably is representative of upper open-shelf Middle Cambrian environments of west-

¹ Manuscript received March 6, 1984.

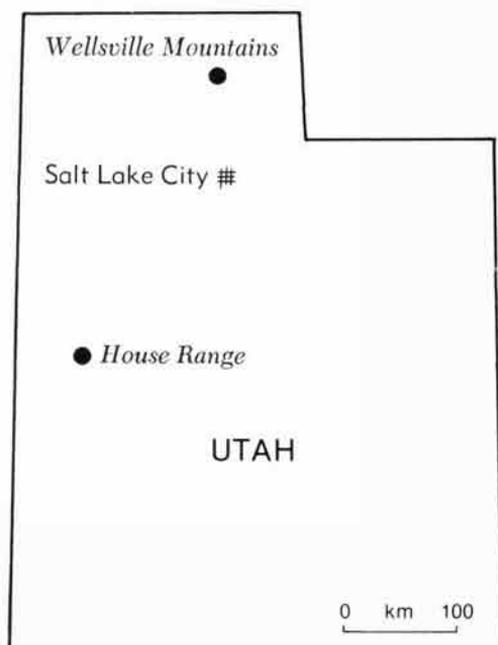


Fig. 1. Areas in Utah (dots) where Middle Cambrian fossils were collected.

ern North America (Conway Morris and Robison, 1982). The purpose of this paper is to document new occurrences of *Anomalocaris* and four taxa of unmineralized arthropods from the House Range and Wellsville Mountains of Utah (Fig. 1).

Few nontrilobite arthropods have previously been described from Cambrian strata of Utah. Most of these are valves of phyllocarids or protocaridids from various Middle Cambrian formations (Walcott, 1886; Brooks and Caster, 1956; Briggs, 1976; Günther and Gunther, 1981; Robison and Richards, 1981). A single specimen of the aglaspid *Beckwithia typa* was described by Resser (1931). Single *Molaria*- and *Mollisonia*-like specimens from the Wheeler Formation and two merostomelike specimens from the Spence Shale were illustrated by Gunther and Gunther (1981). Two specimens from the Wheeler Formation were described by Conway Morris and Robison (1982) as the medusoid *Peytoia* cf. *P. nathorsti*; however, those now are known to be the jaws of *Anomalocaris nathorsti* (Whittington and Briggs, 1982, in press). Specimens described here are the first

with preserved appendages and soft parts to be reported from Utah.

Repositories.—Illustrated specimens are with collections of either the National Museum of Natural History (USNM) or the University of Kansas Museum of Invertebrate Paleontology (KUMIP).

Acknowledgments.—Several of the specimens were collected by Lloyd, Metta, and Val Gunther. Other single specimens were collected by Robert Drachuk, Robert Fife, Jeff Hancey, and Thomas T. Johnson. A preliminary draft of this paper was improved by helpful suggestions from Virginia Ashlock, Desmond Collins, Simon Conway Morris, M. N. Rees, A. J. Rowell, and H. B. Whittington. Illustrations were prepared by Roger B. Williams. Some of the Gunther's collecting expenses were supported by National Science Foundation grant EAR-8201428 to Prof. J. Keith Rigby of Brigham Young University. D. E. G. Briggs' work was carried out while on sabbatical leave at the Field Museum of Natural History, Chicago, under the auspices of the Visiting Scientist Program, with additional support from the Royal Society and Goldsmiths' College Research Fund. Some publication costs were supported by NSF grant EAR-8024066 to R. A. Robison. We are grateful for all of this help.

GEOLOGIC SETTING

Inferred temporal relationships of most stratigraphic units cited in this paper are shown in Figure 2. Lithostratigraphic nomenclature for the House Range conforms to usage by Hintze and Robison (1975). Lithostratigraphic units in the Wellsville Mountains need further study and possible revision of nomenclature.

Middle Cambrian lithofacies in western North America indicate the presence of a broad continental shelf. Thick deposits of shallow-water, platform sediment accumulated along the inner shelf. Commonly, a carbonate shoal complex along the seaward margin of the platform was flanked by a restricted inshore basin on one side and deeper open shelf on the other side (Robison, 1976; Aitken, 1978). During much of the Middle Cambrian two almost mutually exclusive biotopes were separated by probable salinity and temperature barriers over the carbonate shoals. An inner restricted-shelf biofacies generally is characterized by sparse,

SERIES	TRILOBITE ZONES				FORMATIONS	
	restricted-shelf polymeroids	open-shelf polymeroids	open-shelf agnostoids		House Range	Wellsville Mountains
MIDDLE CAMBRIAN	commonly barren	Cedaria	Lejopyge laevigata	upper	Weeks	Bloomington
				lower		
	----- <i>Eldoradla</i> -----	Bolaspidella	Ptychagnostus punctuosus		Marjum	
	commonly barren		Ptychagnostus atavus		Wheeler	
			Ptychagnostus gibbus			
	----- <i>Ehmaniella</i> -----	Oryctocephalus	Ptychagnostus praecurrens		Spence	
	Glossopleura		Peronopsis bonnerensis			
	Albertella					
	Plagiura					

Fig. 2. Inferred temporal relationships of some stratigraphic units in Utah (see Robison, 1976, 1984a). The Burgess shale of the Stephen Formation in British Columbia contains a fauna representative of the *Ptychagnostus praecurrens* and upper *Oryctocephalus* zones. Formation names not relevant to this paper are omitted. Dashed lines denote uncertain position of boundaries. Thicknesses of units are not shown to scale.

low-diversity, polymeroid trilobites. An outer open-shelf biofacies is characterized by common, high-diversity, polymeroid and agnostoid trilobites. Fossils are usually most abundant near the seaward margin of the carbonate platform facies.

In places during the early Middle Cambrian, carbonate shoals were poorly developed and disjunct. This allowed the intermingling of faunas that more commonly were confined to either restricted- or open-shelf environments. An example of such intermingling is the fauna of the Spence Shale in the Wellsville Mountains. The Spence is characterized by abundant fossils and high taxonomic diversity (e.g., Resser, 1939; Campbell, 1974). It has yielded one of the fossils, *Leancoilia? hanceyi*, n. sp., which is described here.

A general marine transgression during the Middle Cambrian widely superimposed a di-

verse open-shelf trilobite fauna containing *Bathyriscus* and *Elrathina* above a restricted-shelf fauna dominated by *Glossopleura*. These faunas have traditionally been assigned to different zones (e.g., Howell and others, 1944; Lochman-Balk and Wilson, 1958). Nevertheless, total stratigraphic ranges of both *Bathyriscus* and *Elrathina* have been observed to overlap completely the range of *Glossopleura* (Robison, 1976). In the Spence Shale of the Wellsville Mountains species of *Bathyriscus*, *Elrathina*, and *Glossopleura* are associated in the same beds (Campbell, 1974; fig. 4). These distribution patterns are part of the basis for proposed abandonment of *Bathyriscus-Elrathina* as a zone name (Robison, 1976). The patterns also are important with regard to interpretations that have been made about the depositional setting of the Burgess shale in British Columbia.

The Burgess shale has been determined to

represent part of a sediment apron that accumulated adjacent to a near-vertical submarine escarpment (Fritz, 1971; McIlreath, 1975, 1977). Using the uppermost occurrences of *Glossopleura* as a time surface, Fritz (1971:1161-1163, fig. 2) calculated that minimum water depth at the front of the escarpment exceeded 200 meters. Based on observed distribution patterns of faunas containing *Glossopleura* and *Bathyriscus-Elrathina*, we suggest that the boundary between these faunas may have greater ecological than temporal significance and inferred water depths during Burgess shale deposition may be exaggerated.

Of the fossils described here, most are from the Wheeler and Marjum formations of the House Range. These formations represent deposition in an open-shelf basin, mostly at depths below storm wave-base, but probably less than 200 meters. Major lithofacies changes in the Wheeler and Marjum formations of the House Range were described by Robison (1964b). Further study of the Marjum by Brady and Koepnick (1979) has documented a transition from shallow platform to deeper shelf-basin lithofacies. Fossils here described from the Marjum are preserved in thin-bedded, hemipelagic lime mudstone and interbedded shale

indicative of a low-energy, gently sloping ramp. Coeval, intertidal, carbonate platform lithofacies are no more than a few kilometers away. Fossils here described from the Wheeler Formation are preserved in similar rocks; however, the platform margin was probably a few tens of kilometers away and the water was probably deeper. Paleogeographic reconstruction (e.g., Bambach, Scotese, and Ziegler, 1980) indicates a position in equatorial latitudes.

Many Wheeler and Marjum beds are unfossiliferous. Others range from sparsely to abundantly fossiliferous. Rare bedding surfaces are covered with well-preserved, articulated remains of arthropods, sponges, echinoderms, and other animals, as well as brachiopod shells and the thalli of various noncalcareous algae. Regularly aligned fossils on the bedding surfaces are indicative of current action at the time of burial. The fossils and associated matrix show many features of the Silurian "smothered-bottom assemblages" described by Brett (1983), which were interpreted as being buried by episodic storm deposition on a gently sloping shelf. More aerobic conditions in the Wheeler and Marjum sediments probably account for the much less common preservation of soft-bodied organisms than in the Burgess shale.

SYSTEMATIC DESCRIPTIONS

ANOMALOCARIS Whiteaves, 1892

ANOMALOCARIS NATHORSTI (Walcott), 1911

Figures 3, 4

Simonetta and Delle Cave (1983) described some specimens as "unassignable to any known phylum," but did not identify or name them. Whittington and Briggs (in press) have given a full description and synonymy.

New material.—Posterior portion of a complete individual, USNM 374593, part and counterpart.

Description.—The specimen is compacted dorsoventrally, in parallel aspect. The counterpart comprises the posterior portion of the animal only; the anterior portion is concealed beneath the matrix on the part. The surface of

the specimen near the point where it disappears beneath the matrix is rough compared to that of the remainder, and the matrix does not flake off it readily. Therefore, it has not proved possible to reveal the remainder of the animal by preparation.

The trunk bears a series of paired lobes, each overlapping that immediately in front of it. The lobes are broad based and subtriangular in outline, and each tapers to a rounded distal extremity. Eight lobes are preserved on the left side, corresponding to lobes 4 to 11 on complete specimens from the Burgess shale (Whittington and Briggs, in press). Lobes 5 to 8 preserve fine linear rays running roughly parallel to their axes.

A wide dark feature runs along the axis of the trunk, tapering slightly posteriorly (outline clearly evident on the part), which presumably

represents the gut. The counterpart preserves a series of lateral extensions of this dark trace, corresponding roughly in position to the lateral lobes and presumably segmentally arranged. These extensions, which have not been observed in specimens from the Burgess shale, reach the base of the lobes, and the dark area appears to overrun the margin of the specimen posteriorly. This posterior expansion may be due to seepage of material from the alimentary system (compare dark stain in *Marrella splendens*, Whittington, 1971; also other Burgess shale animals). The gut appears to bifurcate at the anterior extremity of the preserved trace, but this is an effect of preservation. A series of large irregular patches of a nodular mineral flanks the gut trace; these patches also correspond in position to the lateral lobes and presumably are segmentally arranged, although some coalesce. Similar patches are preserved in some specimens from the Burgess shale (Whittington and Briggs, in press). The trunk terminates in a short, narrow projection that is poorly preserved. The nature of a short curved feature on the left side of this projection is unknown.

The length of the specimen from the anterior margin of lobe 4 to the posterior termination is 51 mm. This probably represents just under half the total length (see restoration, Whittington and Briggs, in press), indicating an individual just over 100 mm long.

Discussion.—Although only a portion of the specimen is preserved, the outline of lateral lobes, presence of lobe rays, and direction and degree of overlap between lobes are sufficient to identify the specimen as *Anomalocaris nathorsti*. Recent work by Whittington and Briggs (1982, in press) has shown that *Anomalocaris* is the largest known Cambrian predator, reaching lengths of up to half a meter. The head bears a pair of raptorial appendages and a circular jaw previously known in isolation and interpreted as the medusoid *Peytoia*. Although the appendages are similar to those of arthropods (Briggs, 1979), the unique combination of characters suggests that *Anomalocaris* represents a separate phylum. There are two species, *A. canadensis*, of which only one relatively complete specimen is known (in addition to isolated limbs), and *A. nathorsti*, of which several specimens are known. The two species are distinguished by the nature of the head appendages (Briggs, 1979; Whittington and Briggs, 1982, in press). In the

absence of evidence for these, the specimen cannot be positively identified. Rays on the lobes have been observed only in the better known *A. nathorsti*, however, and the Utah specimen is therefore assigned to this species in the absence of evidence to the contrary.

Although isolated limbs of *A. canadensis* and *A. nathorsti* (appendage F of Briggs, 1979) are well known from Lower and Middle Cambrian localities in western North America (Briggs, 1979; Briggs and Mount, 1982; Collins, Briggs, and Conway Morris, 1983; Whittington and Briggs, in press), such limbs have not been discovered in Utah. Conway Morris and Robison (1982), however, recorded the jaw of *Anomalocaris* (then interpreted as the medusoid *Peytoia*) from the middle part of the Wheeler Formation (*Ptychagnostus atavus* Zone) of the House Range. They also recorded a second possible medusoid from the Spence Shale of the Wellsville Mountains. The latter specimen, which is under study together with additional material of the same organism, is neither a medusoid nor the jaw of *Anomalocaris*; its affinities are presently unknown.

Occurrence and associated biota.—The new specimen of *A. nathorsti* is preserved in moderately hard, pale-yellowish-brown, platy parting, laminated, calcareous clayshale. It was collected about 60 m above the base of the Marjum Formation (Fig. 2) in the central House Range (Fig. 1) by Thomas T. Johnson. The locality (347 of R. A. Robison; 3 of Rigby, 1983:243), informally called Sponge Gully, is in a dry stream gully about 4.7 km east-northeast of Marjum Pass in the NW $\frac{1}{4}$ /SE $\frac{1}{4}$ /SE $\frac{1}{4}$ sec. 4 (unsurveyed), T. 18 S., R. 13 W. (Marjum Pass 7 $\frac{1}{2}$ -minute quadrangle map, U. S. Geological Survey, 1972).

A diverse, well-preserved biota has been collected from the Sponge Gully site. Associated with *A. nathorsti* are sponges (*Choia carteri*, *Choia utahensis*, *Diagonella hindei*, *Diagonella* sp., *Hamptonia bowerbanki*, *Leptomitius metta*, *Protospongia? elongata*, *Testispongia venula*, *Valospongia gigantis*; see Rigby, 1983), trilobites (*Bolaspidella* n. sp., *Hypagnostus parvifrons*, *Modocia typicalis*, *Modocia* n. sp., *Naraoia compacta*, *Pseudoperonopsis? sp.*, *Ptychagnostus occultatus*, *Ptychagnostus punctuosus*; see Robison, 1964a, 1984a,b), other arthropods (*Branchiocaris pretiosa*, *Tuzoia guntheri*; see Robison and Richards, 1981; this paper), a priapulid (*Ottoia prolifica*),

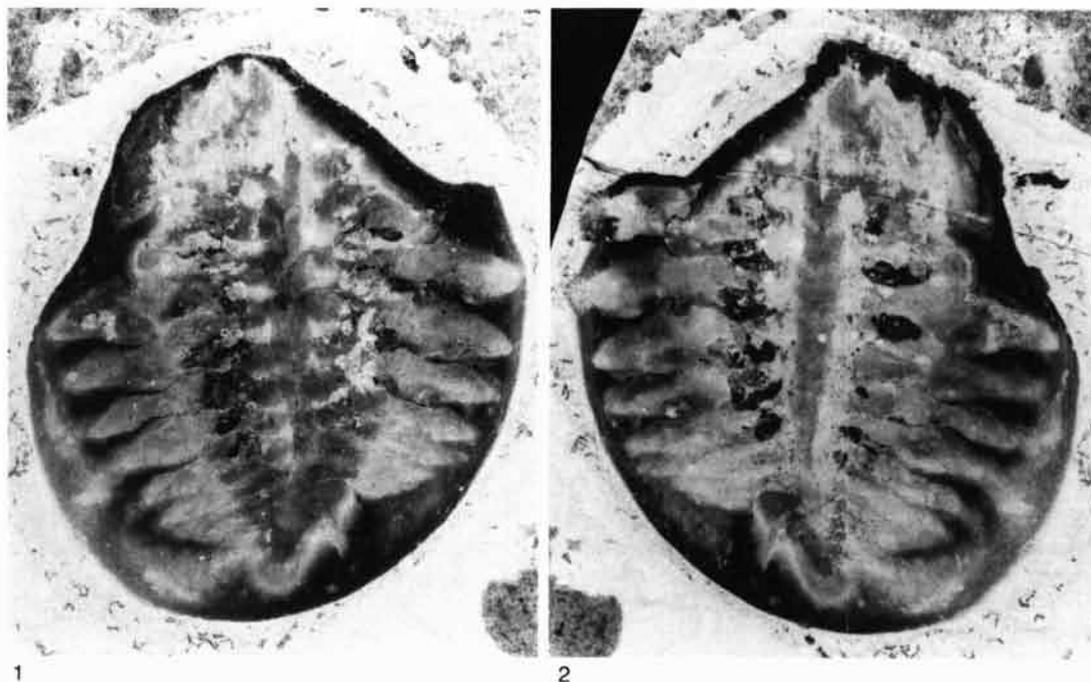


Fig. 3. *Anomalocaris nathorsti* (Walcott); posterior body, USNM 374593; from locality 347, Marjum Formation, House Range; 1, counterpart; 2, part; both $\times 1$.

undetermined lingulide brachiopods, trace fossils (*Planolites* sp.), and algae (*Morania fragmenta*; see Fig. 9.3).

The specimen described here extends the observed stratigraphic range of *A. nathorsti* upward into the lower part of the *Ptychagnostus punctuosus* Zone (Fig. 2).

BRANCHIOCARIS Briggs, 1976

**BRANCHIOCARIS PRETIOSA (Resser),
1929**

Figures 5-9

Briggs (1976) has given a full description and synonymy.

New material.—Three specimens, KUMIP 204795-204797, each including part and counterpart, and each showing soft parts. Several carapaces, including KUMIP 204792-204794.

Description.—KUMIP 204796 and 204797 are compacted in lateral aspect, affording right and left lateral views, respectively (Figs. 5, 1, 2; 7, 1, 2). The compaction of KUMIP 204796 is slightly oblique, revealing part of the folded

right valve in the hinge region. KUMIP 204795 is preserved in parallel aspect, the two valves symmetrical about the hinge line (Figs. 7, 3, 9, 1). Only KUMIP 204796 preserves evidence of the cephalic appendages and probably the distal tips of the pair of 'principal' appendages (Briggs, 1976: text-fig. 2), which project beyond the carapace. A large subcircular feature in the exfoliated anteroventral part of the left valve of KUMIP 204797 probably represents the carapace adductor muscle or its scar. Paired dark linear traces running approximately normal to the axis may correspond to divisions of the anterior part of the trunk. They are also evident where some of the right valve has been removed in the anterior part of the trunk of KUMIP 204796. They may coincide with the 'proximal element' of the limbs observed in specimens from the Burgess shale (Briggs, 1976:10). Similar dark traces are evident in KUMIP 204795. In the posterior part of the trunk of KUMIP 204796 and 204797 the intersomite boundaries are apparent. There are at least 30 trunk divisions. Large flaplike ap-

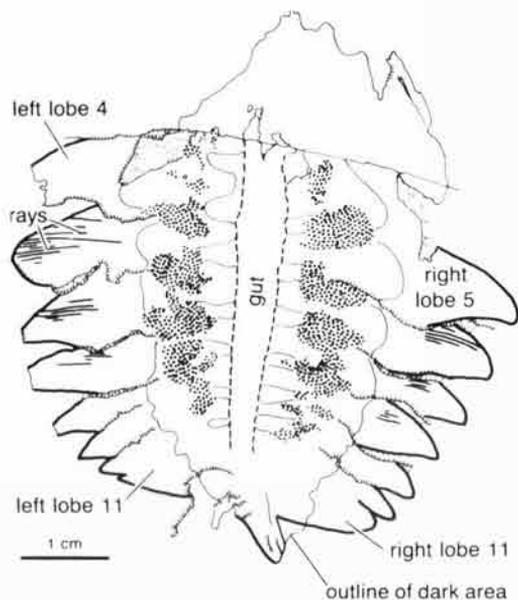


Fig. 4. *Anomalocaris nathorsti* (Walcott), USNM 374593, explanatory drawing of part (compare Fig. 3,2); stipple denotes nodular mineralized patches.

pendages of the left side of KUMIP 204797 are apparent, overlapping posteriorly. The outline of the more anterior of these flaps is fairly clear: gently convex anteriorly, and curving to run approximately parallel to the valve margin. Only the telson extends beyond the posterior margin of the valves (but is not evident in KUMIP 204795); KUMIP 204796 shows both telson spines or processes. A dark trace in the axial region of both KUMIP 204795 and 204796 may represent the gut. KUMIP 204795 shows lateral extensions of this trace in the anterior part of the trunk, which may represent digestive glands. A dark area lying dorsal of the process projecting from the ventral margin of the telson in KUMIP 204797 may indicate the position of the anus.

The greatest length of the valves parallel to the hinge line is 58 mm (KUMIP 204795), 63 mm (204797), and 64 mm (204796). The total sagittal length (from the anterior of the hinge line to the distal extremity of the hinge processes) is about 68 mm in KUMIP 204797 and 67 mm in KUMIP 204796. The length of the 30 somites anterior of the telson in KUMIP 204797 is about 43 mm. Laterally compacted

carapaces from the same locality (Fig. 9,2-4) range in length from 36 to 65 mm. All display a small angular projection of the hinge line both anteriorly and posteriorly, and are almost symmetrical about the midline, expanding slightly anteroventrally.

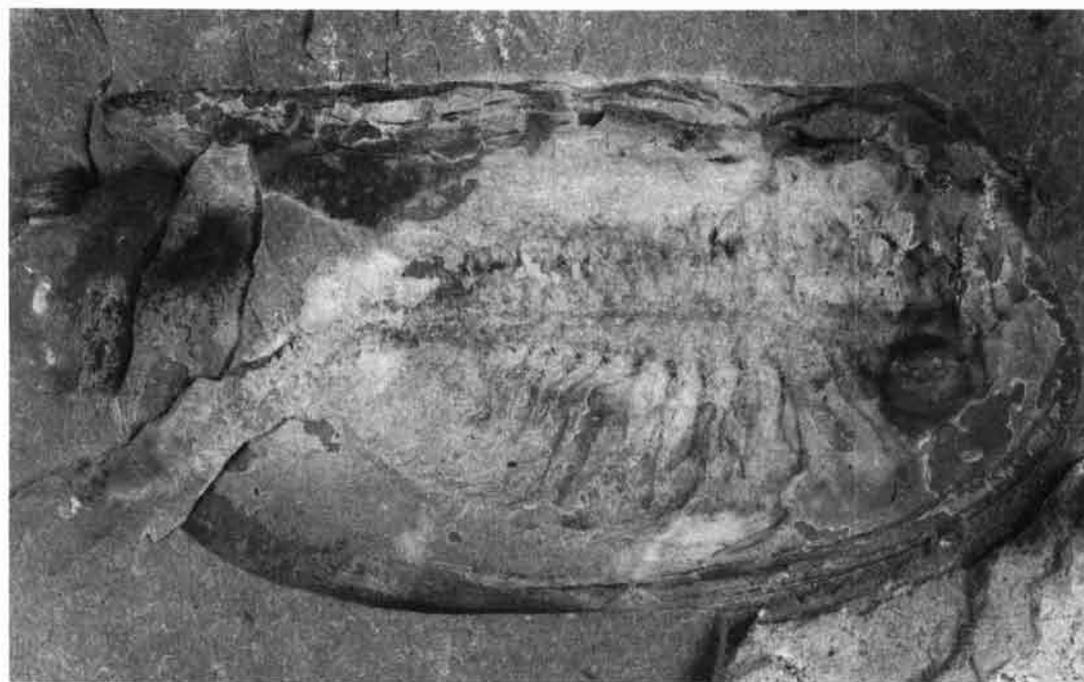
Discussion.—Five known specimens of *Protocaris pretiosa* (Resser, 1929) from the Middle Cambrian Burgess shale of British Columbia formed the basis for a redescription by Briggs (1976) who assigned the arthropod to a new genus, *Branchiocaris*. A large number of smaller specimens, apparently juveniles of the same species (Briggs, in preparation), have since been discovered on Mount Stephen at a new locality (9 of Collins, Briggs, and Conway Morris, 1983) in a geologic setting similar to the Burgess shale quarries. This locality yields also *Glossopleura* (D. H. Collins, personal communication, 1983). The specimens described here are the first of *Branchiocaris* with soft parts discovered outside British Columbia.

The features preserved are sufficient to identify the specimens beyond reasonable doubt as conspecific with the material from British Columbia. The exact number of trunk somites is not known. Although more than 30, there appear to be significantly fewer than the 46 recorded in the two most completely preserved Burgess shale specimens (Briggs, 1976:8-9). Length of the 30 somites immediately anterior of the telson in KUMIP 204797 is also greater relative to that of the carapace than in the three Burgess shale specimens in which this parameter can be measured. The sample is small, however, and some variability is to be expected in a multisegmented arthropod (as in recent branchiopod crustaceans and myriapods, for example). In the absence of more distinct morphological differences, the specimens from Utah are assigned to the same species as specimens from British Columbia.

Briggs (1976) redescribed the holotype of *Dioxycais argenta* Walcott from the Ophir Shale (lower Middle Cambrian, *Glossopleura* Zone) of the Wasatch Range, Utah, and pointed out the similarity in valve outline between it and *Branchiocaris*. He retained the latter as a separate genus, however, as *Dioxycais* is based on a single poorly preserved valve lacking any trace of soft parts, and bivalved arthropods with different soft-part morphologies may have very similar carapaces (for example, *Perspicaris recon-*



1



2

Fig. 5. *Brachioecaris pretiosa* (Resser); KUMIP 204797 from locality 347, Marjum Formation, House Range; 1, counterpart; 2, part; both $\times 2$.

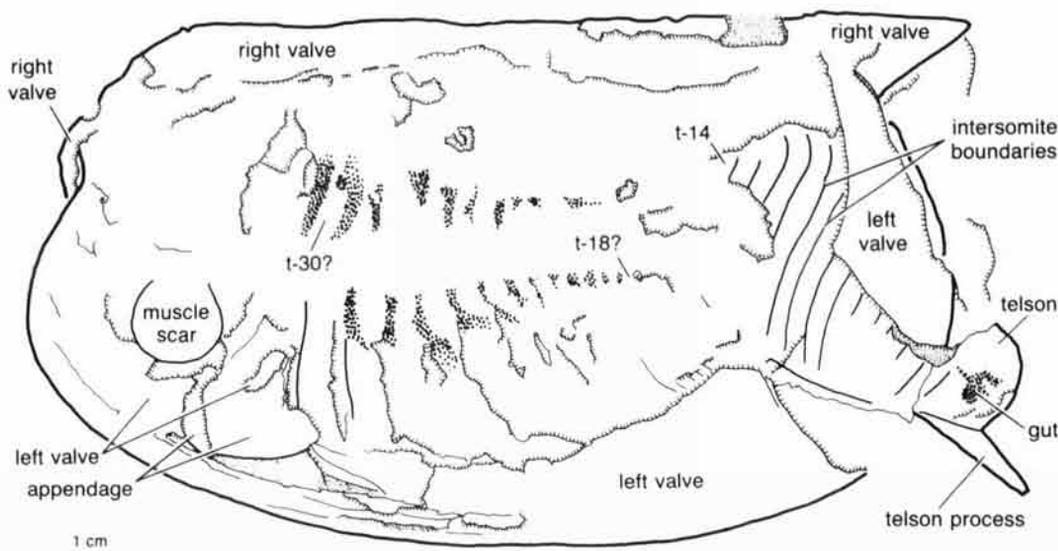


Fig. 6. *Branchiocaris pretiosa* (Resser), KUMIP 204797, explanatory drawing of counterpart; t-14 denotes 14th somite anterior of the telson, other such numbers denote other somites (compare Fig. 5, I).

dita and *Canadaspis perfecta*; Briggs, 1977, 1978).

On the basis of carapace outline, Robison and Richards (1981:6) referred two specimens from the upper Wheeler Formation (*Ptychagnostus atavus* Zone) of the Drum Mountains, Utah, to *Branchiocaris?* sp. The discovery of new specimens of *B. pretiosa* with soft parts now allows the range of the genus and species to be extended with confidence to Utah. It also prompts a reconsideration of the possibility that *B. pretiosa* may be a synonym of *Dioxycares argenta*.

Briggs (1976) confined *Dioxycares argenta* to the holotype, but noted that a number of additional valves from other localities in the Middle Cambrian of Utah and British Columbia may also belong to the genus. Robison and Richards (1981:7, 8) also tentatively assigned additional specimens to *D. argenta* from the Spence and Ute formations of the Wellsville Mountains, Utah. They pointed out the similarity in outline between *D. argenta* and *Pseudoarctolepis sharpi* Brooks and Caster, 1956, apart from the apparent lack of prominent lateral spines in the former. They considered (1981:7) that *Dioxycares* differs from *Branchiocaris* "by

having larger terminal hinge processes, particularly at the posterior end." This is difficult to demonstrate on the basis of the holotype alone, however, as "the posterior end of the hinge or fold is poorly preserved and partly destroyed as a result of some earlier worker's misguided preparation" (Briggs, 1976:14).

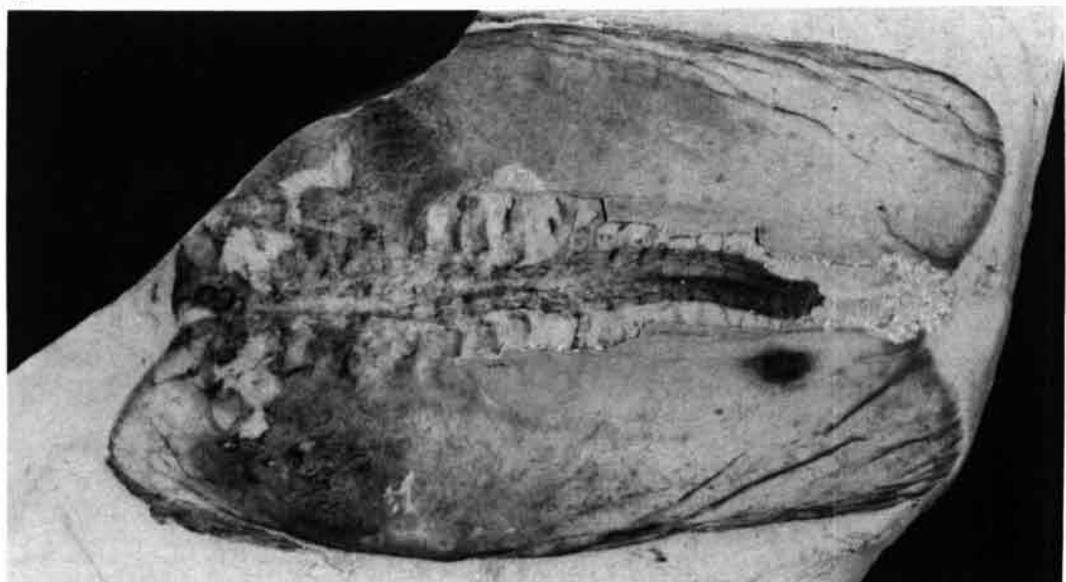
The type locality of *D. argenta* is probably paved over by a highway (Briggs, 1976), and therefore a more complete description based on new topotype specimens is not likely. To avoid potential confusion between *Dioxycares* and *Branchiocaris*, which are now both known from the Middle Cambrian of Utah, we restrict the name *D. argenta* to the poorly preserved holotype (USNM 15401), which is indeterminate by present taxonomic standards. Briggs (1977: 613) took a similar action in dealing with the poorly preserved lectotype of *Canadaspis ovalis* from the Burgess shale. This action has the additional merit of focusing attention on the much more completely known arthropods from the Burgess shale and Marjum Formation. We assign isolated valves from the locality yielding the soft-bodied Utah specimens to *Branchiocaris pretiosa*, and similar isolated valves from else-



1



2



3

Fig. 7. (Explanation on facing page.)

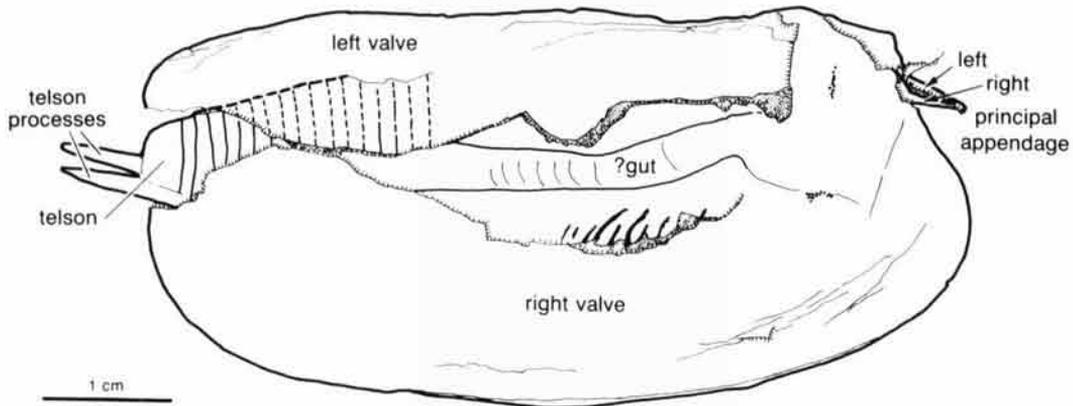


Fig. 8. *Branchiocaris pretiosa* (Resser), KUMIP 204796, explanatory drawing of part; dashed lines denote details added from counterpart (compare Fig. 7.1).

where to *?Branchiocaris pretiosa*.

From further evaluation of the three specimens originally assigned to *Dicerocaris opisthoeces* Robison and Richards, 1981, we conclude that they represent juveniles of *Pseudoarctolepis sharpi*. Apparent differences between specimens, particularly in the position and orientation of lateral spines, have actually resulted from different orientations of carapaces to bedding and compaction in shale of the Wheeler Formation. Therefore, *D. opisthoeces* is a junior synonym of *P. sharpi*.

Occurrence and associated biota.—The new specimens of *Branchiocaris pretiosa* are all preserved in pale-yellowish-brown to medium-gray, platy parting, laminated, calcareous clay-shale. All were collected from the lower Marjum Formation in the House Range by Lloyd and Metta Gunther. The locality, stratigraphic occurrence, and associated biota are the same as described herein for *Anomalocaris nathorsti*.

Specimens of *B. pretiosa* showing soft parts are known from British Columbia in the Burgess shale of the Stephen Formation on Fossil Ridge (*Ptychagnostus praecurrens* Zone; Briggs, 1976); specimens of *Branchiocaris* from the Stephen Formation of Mount Stephen (locality 9 of Collins, Briggs, and Conway Morris, 1983) may be conspecific. D. H. Collins (personal communication) reports that *Glossopleura* also is

present at the Mount Stephen locality. In Utah, *B. pretiosa* is present in the Marjum Formation (*Ptychagnostus punctuosus* Zone) of the House Range. Isolated valves of *?B. pretiosa* are known from British Columbia in the Eldon Formation of Mount Bosworth (upper *Oryctocephalus*, = *Bathyriscus-Elrathina*, Zone; Briggs, 1976). In Utah isolated valves are known from the Spence Shale (*Glossopleura* Zone; Robison and Richards, 1981) and Bloomington Formation (lower? *Bolaspidella* Zone; Briggs, 1976) of the Wellsville Mountains, the Ute Formation (*Glossopleura* Zone; Robison and Richards, 1981) of the Bear River Range, and the Wheeler Formation (*Ptychagnostus atavus* Zone; Robison and Richards, 1981) of the Drum Mountains.

EMERALDELLA Walcott, 1912

EMERALDELLA? sp.

Figure 10

Material.—KUMIP 204791, part and counterpart.

Description.—The specimen comprises a part and incomplete counterpart compacted dorso-ventrally in parallel-oblique aspect. The cuticle is moderate-reddish-brown, presumably due to oxidized iron, and has exfoliated in places from the underlying matrix, which is a pale-reddish-brown clayshale. The exoskeleton consists of a

Fig. 7. *Branchiocaris pretiosa* (Resser) from locality 347, Marjum Formation, House Range. 1, 2, KUMIP 204796, part (after preparation) and counterpart, both $\times 1.7$. 3, KUMIP 204795, part (after preparation; compare Fig. 9.1), $\times 2.0$.

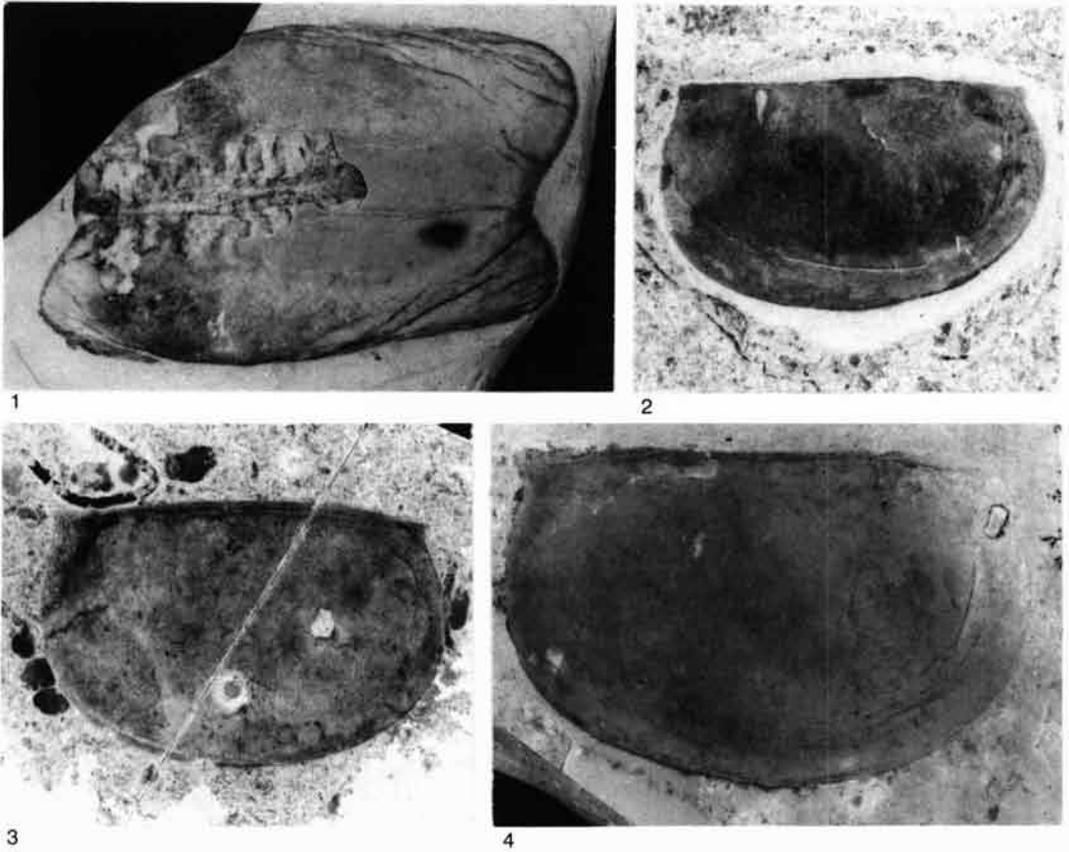


Fig. 9. *Branchiocaris pretiosa* (Resser) from locality 347, Marjum Formation, House Range. 1, KUMIP 204795, part (before preparation; compare Fig. 7.3), $\times 1.2$. 2, KUMIP 204792, counterpart of laterally compacted carapace, $\times 1.4$. 3, KUMIP 204793, counterpart of laterally compacted carapace associated with *Morania fragmenta* Walcott (dark spots) and possible coprolites (dark curved strands), $\times 1.1$. 4, KUMIP 204794, counterpart of laterally compacted carapace, $\times 1.1$.

cephalic shield and 11 trunk tergites. Internal structures are indicated by color variations, and there is evidence of poorly preserved limbs.

The cephalic shield is semicircular in outline. An axial structure, delimited by darker red color, bifurcates anteriorly into two anterolaterally directed spurs. To the left of the axis are two subcircular gaps in the cuticle, the nature of which is unknown. Faint traces of four appendages extend beyond the margin of the cephalic shield on the right side, at least the posterior two being long and slender.

Lateral margins of trunk tergites are not clear because most are either exfoliated or compacted against the limbs beneath. The outline of pleural regions on the left side of the two anteriormost tergites is evident on the counter-

part; they terminate in a straight lateral margin subparallel to the axis of the trunk. Although the outline of the more posterior pleurae is obscured, the tergites appear to increase in width to about the fourth, the trunk then tapering gradually to about the seventh and more rapidly in the posterior somites. The telson is not clearly preserved.

The darker red axial structure in the cephalic shield continues posteriorly through the trunk as a linear feature flanked by circular to ovoid structures in at least the first six trunk somites. These may represent the gut trace and laterally extending digestive glands (compare *Naraoia*; Whittington, 1977; Robison, 1984b). Abaxial of the gut trace are paired nodular features that apparently coincide with inter-

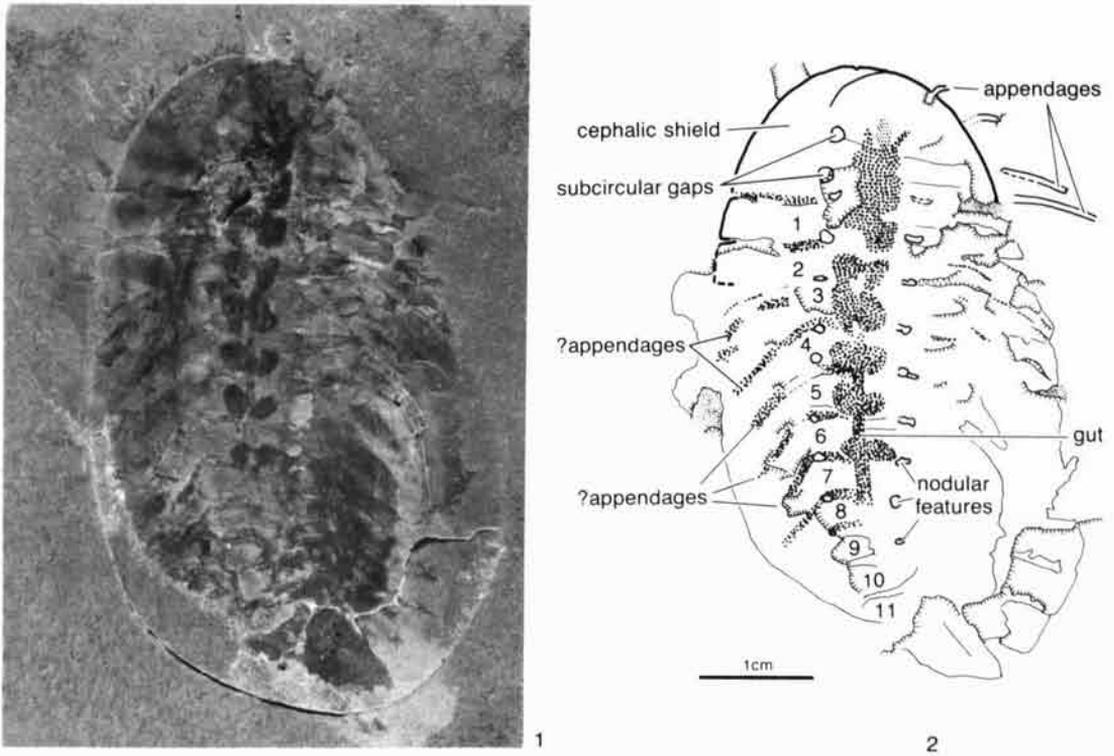


Fig. 10. *Emeraldella?* sp.; KUMIP 204791 from locality 716, Marjum Formation, House Range; 1, part. $\times 1.5$; 2, explanatory drawing.

somite boundaries from the posterior margin of the cephalic shield to the posterior margin of the ninth tergite. These nodular features may represent sites of muscle attachment. Linear features outlined in darker red, particularly on the left side of the trunk, extend laterally from the axis and then curve posterolaterally, almost reaching the margin of the tergites. They do not appear to represent intersomite boundaries, which were presumably oriented more normal to the axis, and may represent a segmented inner branch of the trunk appendages. Indistinct outlines evident below the exfoliated cuticle on the anterior and posterior right of the trunk may represent outer rami of the appendages.

Discussion.—Lack of evidence for the nature of appendages and telson of this arthropod makes the determination of its affinities difficult. The cephalic shield, 11 trunk tergites, and biramous appendages eliminate all but the aglaspidids (Raasch, 1939; Briggs, Bruton, and

Whittington, 1979), *Alalcomenaeus* (Whittington, 1981), *Emeraldella* and *Leancoilia* (Bruton and Whittington, 1983) of known Cambrian arthropods. The aglaspidids have a phosphatic cuticle that is characteristically tuberculate, and the head shield is wider than succeeding trunk tergites. New material of *Alalcomenaeus* from the Stephen Formation of British Columbia (locality 9 of Collins, Briggs, and Conway Morris, 1983) shows that it has 11 and not 12 trunk somites, but the cephalic shield is more rectangular in outline than in the Utah specimen, and bears eyes, and the trunk tapers rather than expanding posteriorly. *Emeraldella* and *Leancoilia* are superficially similar in dorsal view (disregarding the head appendages and telson). The head shield of *Leancoilia*, however, is larger and tapers forward; that of *Emeraldella* is short, semicircular, and similar to the Utah specimen. In addition, *Emeraldella* has long segmented cephalic limbs projecting beyond the margins of the exoskeleton in a fashion similar

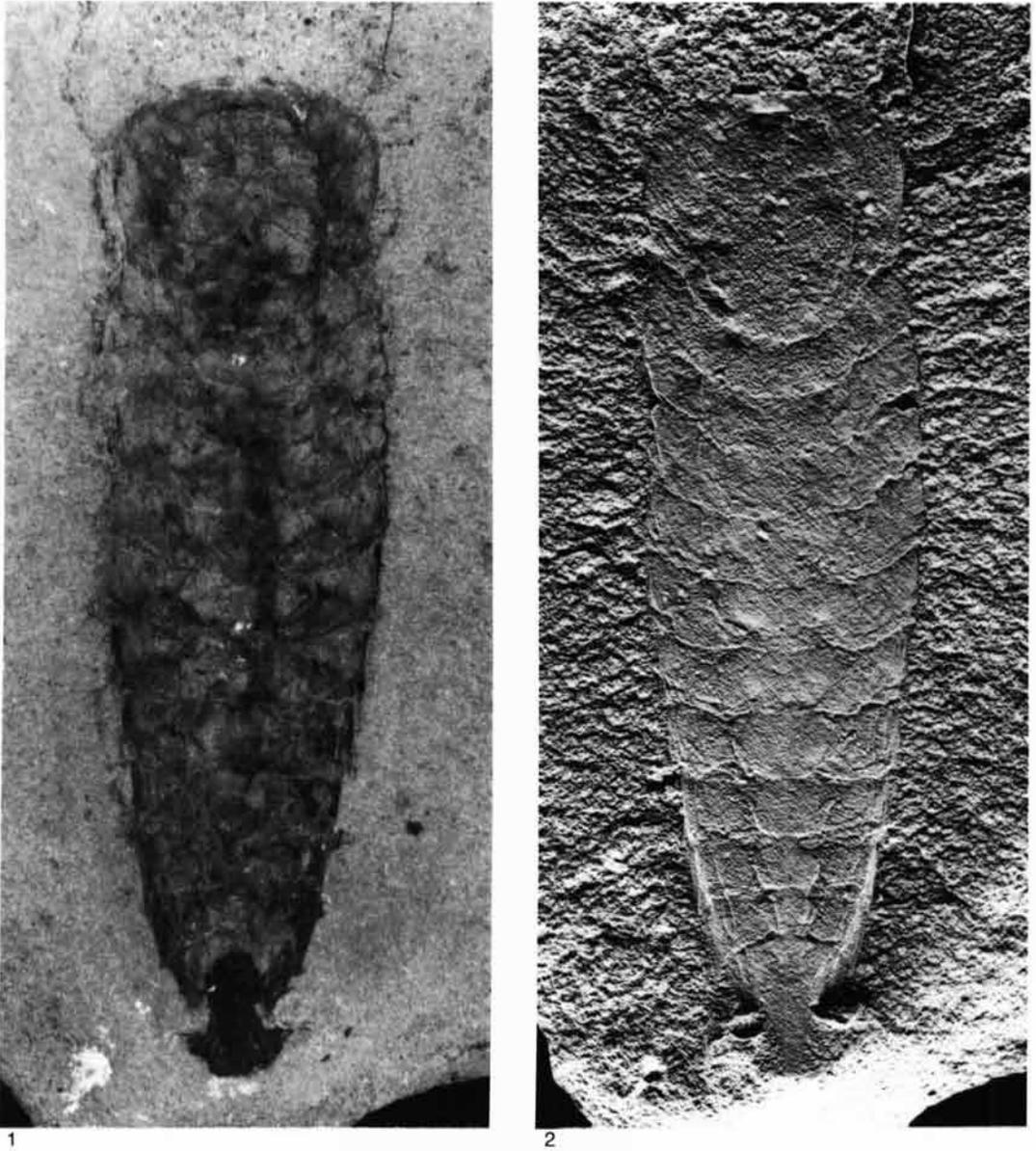


Fig. 11. *Leancoilia? hanceyi*, n. sp.; holotype, USNM 374592; Spence Shale, Wellsville Mountains; $\times 2.2$. 1, Part photographed under alcohol. 2, Part lightly coated with magnesium oxide and photographed in low-oblique light.

to those preserved in the Utah specimen (compare Bruton and Whittington, 1983: pl. 5, fig. 23), and unlike the head appendages of *Leancoilia*. Although the Utah specimen cannot be identified with confidence, it shows a greater similarity to *Emeraldella brocki* than to any other known Cambrian arthropod.

Occurrence and associated biota.—The specimen of *Emeraldella?* is preserved in hard, pale-red-dish-brown, platy parting, laminated, calcareous clayshale. It was collected about 300 m above the base of the Marjum Formation (Fig. 2) in the House Range (Fig. 1) by Val Gunther. The locality (716 of R. A. Robison; 1 of Rigby,

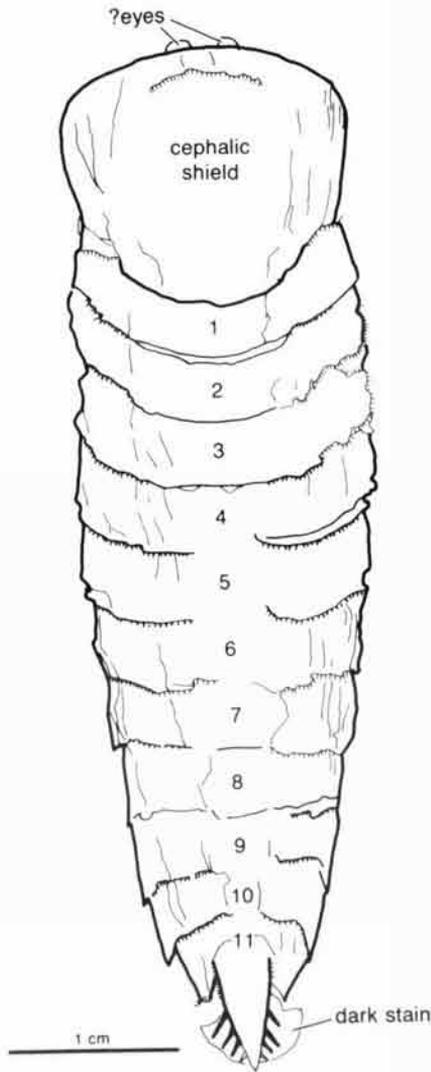


Fig. 12. *Leanchoilia? hanceyi*, n. sp., USNM 374592, explanatory drawing of part (compare Fig. 11).

1983:243), informally called Red Wash, is about 4 km due south of Wheeler Amphitheater in lower ledges along the south side of a large wash in the SW $\frac{1}{4}$ NW $\frac{1}{4}$ sec. 24 (unsurveyed), T. 17 S., R. 13 W. (Marjum Pass 7 $\frac{1}{2}$ -minute quadrangle map, U. S. Geological Survey, 1972).

The lithology and biota at the Red Wash locality are similar to those at Sponge Gully, about 6.5 km south; however, the stratigraphic

position is about 240 m higher in the Marjum Formation. Associated with *Emeraldella?* sp. at the Red Wash locality are sponges (*Choia hindei*, *Diagonella cyathiformis*, *Hamptonia bowerbanki*, *Leptomitus metta*; see Rigby, 1983), trilobites (*Bolaspidella* n. sp., *Hypagnostus parvifrons*, *Mocodia typicalis*, *Pseudoperonopsis?* sp., *Ptychagnostus germanus*, *Schmalensecia* sp., *Utaspis marjumensis*; see Robison, 1964a, 1984a), other arthropods (*Perspicaris?* *ellipsopelta*, *Tuzoia guntheri*; see Robison and Richards, 1981), undetermined lingulide brachiopods, trace fossils (*Planolites* sp.), and algae (*Morania fragmenta*).

If this tentative identification could be confirmed, it would represent the first record of *Emeraldella* outside the Walcott quarry (Bruton and Whittington, 1983:559) in British Columbia. Also, it would extend the observed biostratigraphic range of *Emeraldella* from the *Ptychagnostus praecurrens* Zone to the upper *Ptychagnostus punctuosus* Zone (Fig. 2).

LEANCHOILIA Walcott, 1912

LEANCHOILIA? HANCEYI, n. sp.

Figures 11, 12

Etymology.—The species is named for Jeff Hancey of Farmington, Utah, who collected the holotype.

Holotype.—Part and incomplete counterpart, USNM 374592, the only known specimen.

Description.—The specimen is compacted in parallel aspect (dorsoventrally). The exoskeleton is elongate and divided into a cephalic shield, a trunk of 11 tergites, and a telson. Attitude of the longitudinal axis of the specimen to the bedding (i.e., tilt to the horizontal) is not known and in the absence of additional specimens the effect of this orientation on the preserved configuration cannot be assessed.

The cephalic shield is subrectangular in outline, the width slightly expanding anteriorly. The anterior margin is gently convex, the posterior more strongly so. The central part of the cephalic shield (about 60 percent of the width) is exfoliated and may be part of a more convex axis that extends the length of the trunk. A pair of small semicircular features projecting beyond the anterior margin of the cephalic shield may represent eyes.

Trunk tergites expand slightly in both width and length as far as the fourth or fifth, these dimensions decreasing gradually beyond that point. The posterior margin of the tergites is gently concave anteriorly at the front of the trunk, becoming gradually straight at about the sixth tergite, and then convex anteriorly in tergites immediately in front of the telson. Folding of the compacted cuticle parallel to the lateral margin of the trunk indicates a wide axial region that becomes relatively narrower posteriorly (Fig. 11, 2). An even greater concentration of folding adjacent to the trunk margin suggests that the pleural regions may even fold underneath in the anterior tergites at least; sharp angular terminations are evident in tergites 10 and 11.

The outline of the telson is partially obscured by a dark stain (Fig. 11, I), which probably represents organic material exuded from the anus (compare *Marrella splendens*; Whittington, 1971). The telson is triangular in shape, tapering to a point, and bearing at least four pairs of lateral spines, graded in length. Additional spines may have been removed at a break in slope along the anterolateral margins of the telson.

A dark linear stain, which is clearly evident when the specimen is immersed in alcohol (Fig. 11, I), may represent a gut trace. This, together with the stain around the telson, suggests that the specimen represents a carcass rather than an exuvia, and that although appendages are not evident, they may be preserved beneath the exoskeleton.

The specimen is 59.5 mm in length from the anterior margin of the cephalic shield to the tip of the telson. Maximum width is 17.5 mm at the fourth trunk tergite.

Discussion.—In the absence of additional specimens (to allow three-dimensional restoration) and information about appendages, the affinities of this arthropod remain equivocal. A head shield, 11 trunk tergites, and a short spiny telson are also present in *Alalcomenaeus cambricus* (Whittington, 1981; Briggs, in preparation) and *Leancoilia superlata* (Bruton and Whittington, 1983). Both of these arthropods have a pair of large branched head appendages, which although not evident, may have been present in the specimen described here.

Alalcomenaeus cambricus is poorly known (Whittington, 1981) and may prove to be syn-

onymous with *Actaeus armatus*, which is based on a single imperfectly preserved specimen. A large collection of *A. cambricus* from the Middle Cambrian Stephen Formation of Mount Stephen (locality 9 of Collins, Briggs, and Conway Morris, 1983) is presently under study (Briggs, in preparation) and shows that this arthropod had 11 tergites. *A. cambricus* is much narrower than *Leancoilia*, and therefore similar to the specimen described here, and has a more rectangular cephalic shield. It also possesses eyes. The telson, however, is paddle shaped, expanding to a straight posterior margin fringed with spines. *Leancoilia superlata* has a telson essentially identical to that in the Utah specimen, but its head shield is pointed anteriorly, and extends into a dorsally curved 'snout.' The anterior margin of the cephalic shield in *L. superlata* would appear less pointed in specimens preserved tilted posteriorly to the bedding, and such tilting would also increase the anterior concavity of the posterior margin of the tergites. However, the shield of *L. superlata* would not become as blunt anteriorly as in the Utah specimen. The ratio of maximum width (at the 4th or 5th tergite) to length (from the anterior margin of the cephalic shield to the distal tip of the telson) is much greater in *L. superlata* than in the Utah specimen. The ratio in specimens of *L. superlata* preserved in parallel or parallel-oblique aspect figured by Bruton and Whittington (1983: pl. 13, fig. 79, 81), together with additional material in Walcott's collection, ranges from 37 to 53 percent. That in the Utah specimen is 29 percent. If the possibility of lateral expansion during compaction is discounted (Walton, 1936; Briggs and Williams, 1981), this difference must be a function of the original width and convexity of the arthropod.

Bruton and Whittington (1983:578) discussed additional species of *Leancoilia* and concluded that none appears valid. One of these, *L. persephone* Simonetta, 1970, is characterized by a much narrower trunk than *L. superlata* and therefore merits comparison with the present specimen. Of the six specimens assigned to *L. persephone* by Simonetta (1970:38), Bruton and Whittington (1983:578) considered four (USNM 155635, 155646, 155652, 155653) to be unidentifiable. We concur with this assessment, although USNM 155653 shows a poorly preserved elongate telson with spines and a rounded anterior margin to the cephalic shield.

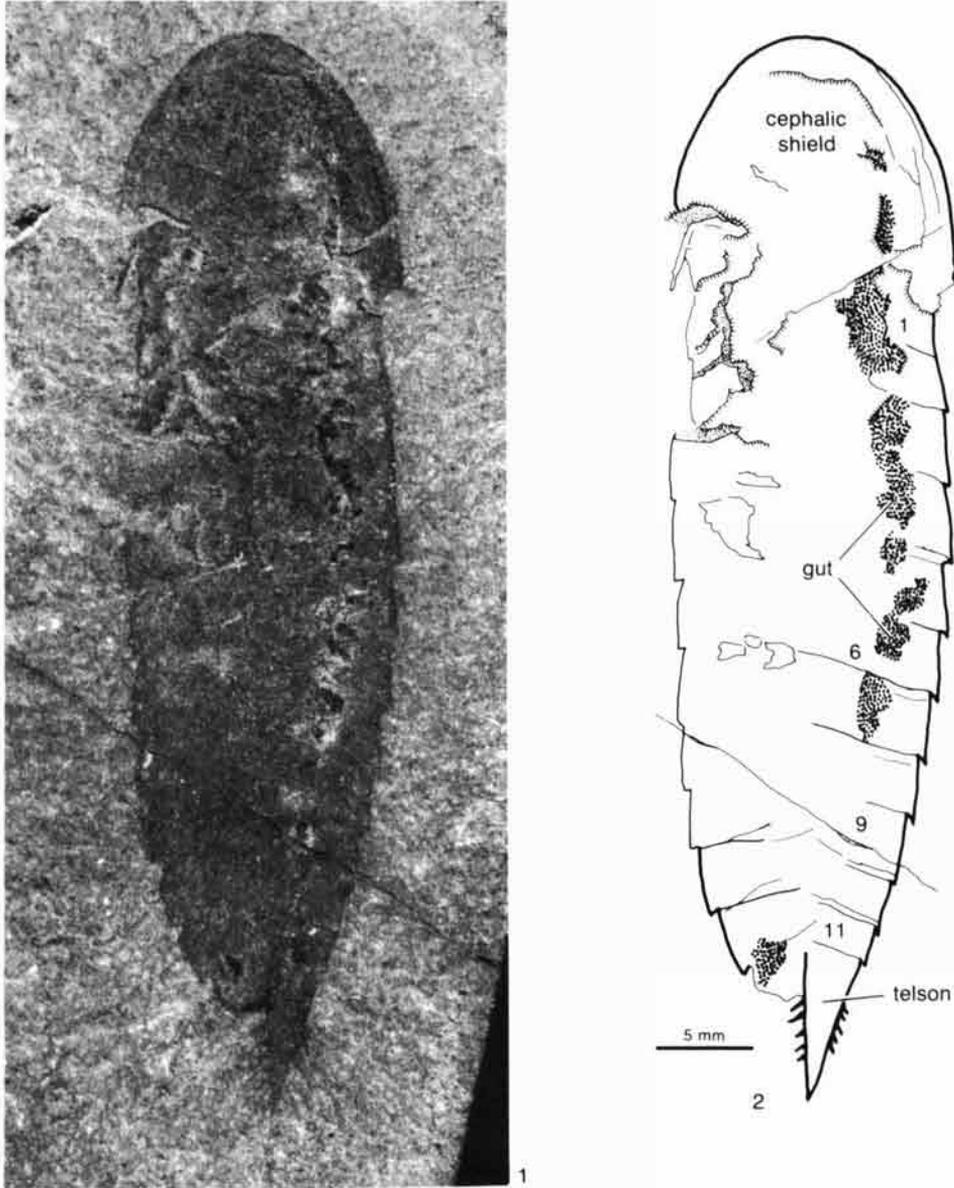


Fig. 13. *Leanochoilia superlata* Walcott; USNM 155651 from Walcott quarry (35k) (holotype of *Leanochoilia persephone* Simonetta, 1970), Burgess shale, Stephen Formation, British Columbia; 1, counterpart in oblique light, $\times 2.5$; 2, explanatory drawing.

It is probably an obliquely compacted *L. superlata*. Both of the other two specimens, USNM 155649 and the holotype 155651, show the characteristic telson, and part of a great appendage is evident on the former. The trunk in both appears relatively narrow, but only the

counterparts are known (the specimens have split along the dorsal surface of the exoskeleton) and the outlines are not well defined. The better preserved of the two (Fig. 13, USNM 155651) illustrates the nature of the preservation. The cephalic shield is rounded anteriorly, there are

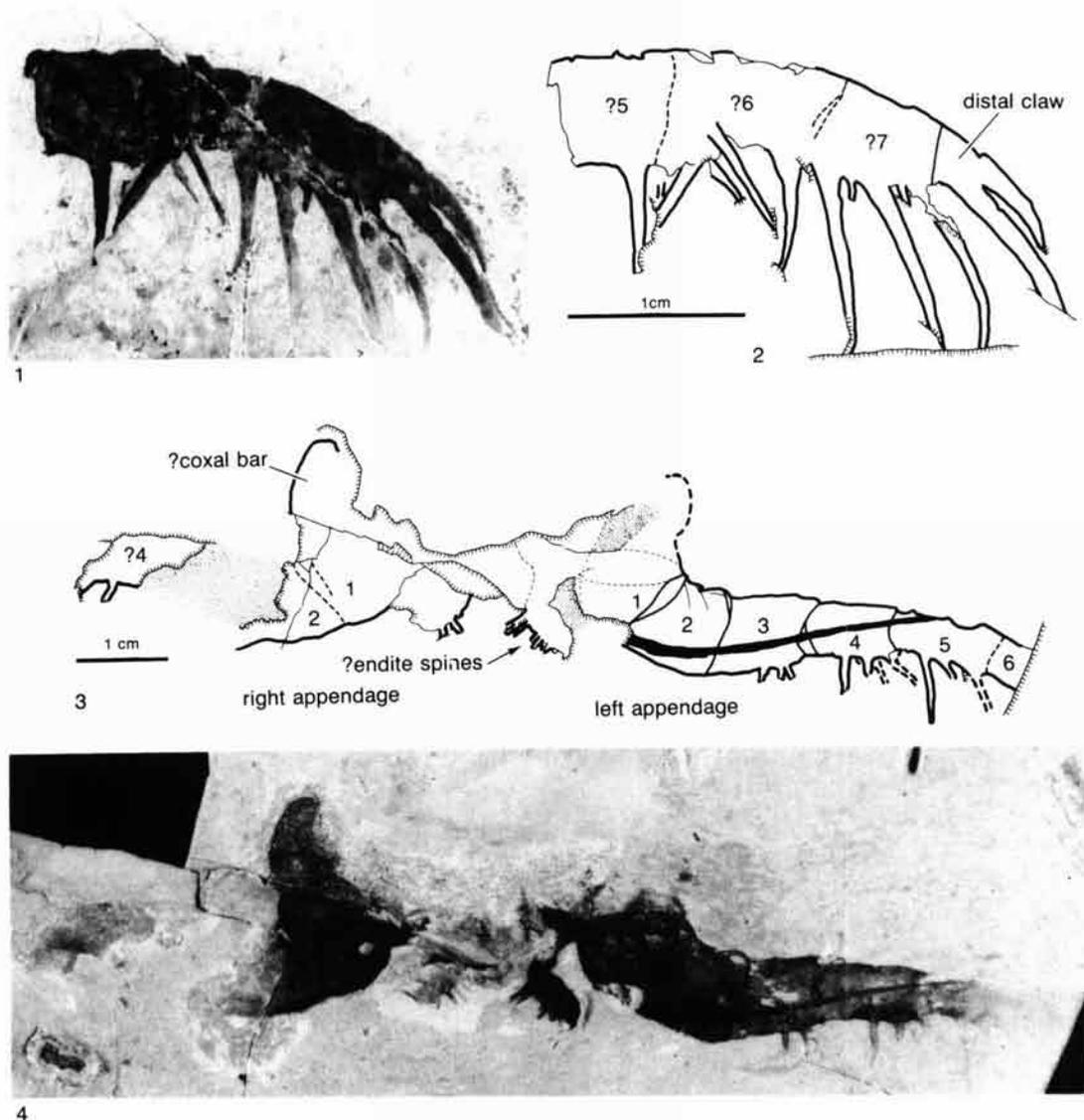


Fig. 14. *Sidneyia?* sp. from locality 114, Wheeler Formation, House Range. 1, KUMIP 204799, $\times 2.3$. 2, Explanatory drawing of KUMIP 204799. 3, Explanatory drawing of KUMIP 204798. 4, KUMIP 204798, $\times 1.3$.

11 tergites, and the telson is clearly that of *Leaenchoilia*. The gut trace (dark nodular masses, presumably apatite) and telson, however, are significantly displaced to the left (right in counterpart) indicating a pronounced obliquity of compaction, and the outline of the right margin of the trunk is indistinct suggesting that it is partly obscured in the matrix of the unknown part. Thus, the narrowness of the trunk is an effect of preservation. There is no evidence of

the anterior cephalic snout characteristic of *Leaenchoilia* but it may also be preserved in the matrix of the part, due to the oblique compaction. We agree with Bruton and Whittington that *L. persephone* should be synonymized with *L. superlata*. The Utah specimen, however, shows no evidence of oblique compaction and we therefore designate it a new species, and tentatively assign it to *Leaenchoilia*.

Occurrence and associated biota.—The single

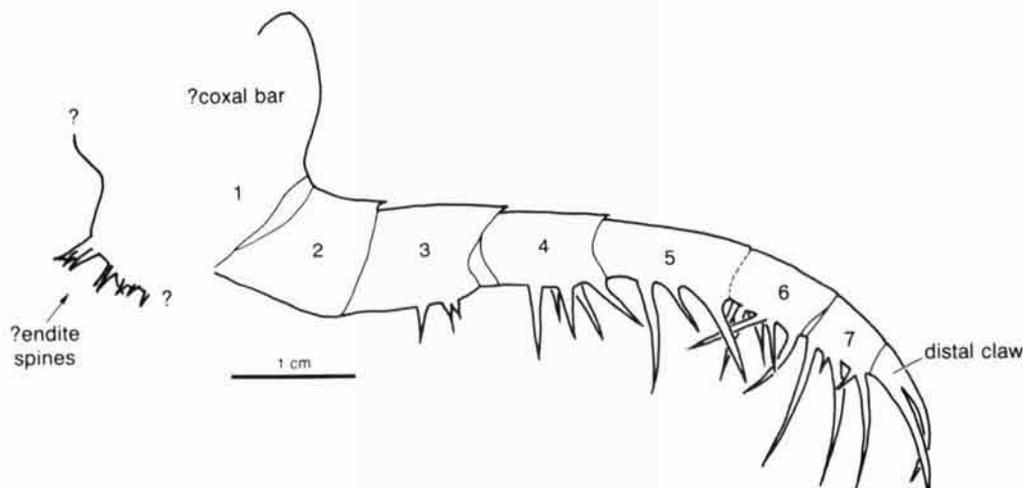


Fig. 15. *Sidneyia?* sp.; reconstructed limb based on KUMIP 204798 and 204799.

specimen of *L.?* *hanceyi* is preserved in hard, medium-dark-gray, flaggy parting, noncalcareous mudshale. It was collected near the middle of the Spence Shale (Fig. 2) in Cataract Canyon on the west side of the Wellsville Mountains (Fig. 1). The locality is in the NE $\frac{1}{4}$ NE $\frac{1}{4}$ sec. 23, T. 10 N., R. 2 W. (Brigham City 7 $\frac{1}{2}$ -minute quadrangle map, U. S. Geological Survey, 1955), about 4 km north of Brigham City, Box Elder County, Utah.

The Spence Shale of the Wellsville Mountains contains a diverse biota representing the agnostoid *Peronopsis bonnerensis* Zone and intermingled taxa of the polymeroid *Glossopleura* and *Oryctocephalus* zones. Descriptions of the Spence biota from Cataract Canyon and nearby localities are recorded in several publications. Resser (1939) described several species of trilobites as well as a few species of brachiopods, hyolithes, priapulids, and echinoderms. Robison (1965), Robison and Sprinkle (1969), and Sprinkle (1973) described additional echinoderms. Robison (1969) described two different annelids together with some associated trace fossils. Campbell (1974) documented 54 species of trilobites and 3 species of echinoderms from the Spence Shale in Antimony Canyon, which is about 2 km south of Cataract Canyon. Satterthwait (1976) described representatives of the algae *Margaretia* and *Marpolia*. Many specimens of the alga *Morania fragmenta* are on pieces of mudshale with the part and counterpart of

L.? *hanceyi*. Rigby (1980) described the sponge *Vauxia magna* and an undescribed specimen resembling *Vauxia gracilentia* has been subsequently collected (KUMIP 113279). Robison and Richards (1981) described representatives of the larger bivalve arthropods *Canadaspis* and *Tuzoia*. Conway Morris and Robison (1982) described a specimen superficially resembling the jaw of *Anomalocaris nathorsti*. Also, many representatives of the Spence biota from the Wellsville Mountains have been illustrated by Gunther and Gunther (1981).

SIDNEYIA Walcott, 1911

SIDNEYIA? sp.

Figures 14, 15

Material.—Two incomplete specimens of appendages, KUMIP 204798 and 204799, each including part and counterpart.

Description of KUMIP 204798.—This specimen (Fig. 14, 3, 4) preserves a pair of segmented appendages in lateral aspect. The designation left and right is based on the assumption that the gnathobasic spines (see below) are situated nearer to the anterior than to the posterior face of the limb (compare Bruton, 1981, fig. 106a); the part then affords a view of the anterior face of the appendages. Most of the left appendage, apart from the distal and proximal extremities, is preserved. Partial preparation of the part has revealed some gnathobasic spines and part of

the questionable fourth podomere of a second appendage, which appears to be preserved facing the more complete one. The symmetrical arrangement of the two limbs about a midline suggests that they may represent both members of an opposing pair. The rest of the arthropod is not preserved. The cuticle ranges in color from dark brown to dusky yellow.

Near the proximal end of each appendage the ventral margin bears a row of short spines that face ventrolaterally toward the opposing limb. These probably functioned in capturing and processing food and may therefore be termed gnathobasic. The cuticle connecting the row of spines to the limb is incompletely preserved. Preparation of the area dorsal and proximal of these spines has failed to reveal more spines, such as might have been borne by a coxa (Bruton, 1981: figs. 46-48); however, preservation is poor and they may have been destroyed. A dorsal extension of the proximal part of the right limb (Fig. 14,4) may represent a coxal bar. A number of lines are preserved traversing the cuticle in this proximal area in the left limb (Fig. 14,3) and it is difficult to determine which represent articulations. The boundary between podomeres is assumed, however, to coincide with a pronounced angle, concave dorsally, in the dorsal margin of the limb. By analogy with *Sidneyia* (Bruton, 1981), this articulation is considered to represent that between podomere 1 (attached to the coxa) and the remainder of the limb.

The distal margins of podomeres 2, 3, and 4 are clearly evident (Fig. 14,4). Double structures are presumably the result of overlap between podomeres. The dorsal margin is stepped at the articulations and this may indicate the former position of spines. Podomeres taper distally as the limb narrows, and increase slightly in length in podomeres 2 to 5. Podomeres 3 to 5 bear ventral spines that appear to increase in length toward the distal end of the limb, but their terminations are not evident. The articulation between podomeres 5 and 6 is not clear.

A dark linear trace running from the proximal part of the ventral margin of podomere 2, through 3 and 4 to the mid-dorsal margin of podomere 5 (Fig. 14,4) may represent a muscle. It is not clear why a single muscle should be preserved nor why it extends through a greater

number of podomeres than similar muscles in living arthropods, but there is no obvious alternative interpretation for the structure.

Description of KUMIP 204799.—This specimen (Fig. 14,1,2) preserves the distal portion of a slightly larger appendage apparently similar to that described above. The limb curves ventrally and the ventral side is armed with elongate spines of varying width. Articulations between podomeres are not clear except for one separating the two distalmost spines from the rest of the fragment. By analogy with *Sidneyia* (Bruton, 1981), however, this specimen may represent podomeres 5, 6, and 7 and the distal claw. Figure 15 is a composite reconstruction based on this assumption, using both specimens.

Discussion.—As Briggs (1979:657) has pointed out, individual limbs of arthropods may provide little evidence of affinity. Of known Cambrian arthropods, however, the specimens illustrated here show a striking similarity to the limbs of *Sidneyia inexpectans*. The only other Cambrian arthropod with a similar limb is *Emeraldella brocki* (Bruton and Whittington, 1983: fig. 65), but the distal podomere in that arthropod is elongate and terminates in a 'foot' of four short spines. The preserved basal spines in KUMIP 204798 (Fig. 14,3,4) may represent either the endite or ventral part of the gnathobasic lobe. The dorsal flexure between podomeres 1 and 2, the configuration of podomeres, and the presence of ventral spines and a terminal 'claw' are all features of *Sidneyia* (Bruton, 1981:637, figs. 46-48). The reconstructed limb (Fig. 15) shows more and longer ventral spines than does any limb figured by Bruton, although there is some variability in *Sidneyia* appendages from the Burgess shale (compare Bruton, 1981: figs. 46-48).

The size of both Utah specimens indicates a larger individual than those from the Burgess shale. Approximate scaling based on Bruton's (1981) reconstruction, assuming body length is about 3.8 times limb length, suggests a body more than 27 cm long. This is some three times larger than the upper end of the size range observed in the Burgess shale (Bruton, 1981: 625).

The most complete of the *Sidneyia*-like appendages (KUMIP 204798) was collected by Robert Drachuk. A less complete specimen

(KUMIP 204799) was collected by Robert Fife. Both specimens subsequently came into the possession of Lloyd Gunther, who contributed them to the University of Kansas Museum of Invertebrate Paleontology.

Occurrence and associated biota.—Both of the *Sidneyia*-like appendages are preserved in light-gray, platy parting, laminated, calcareous clay-shale. They were collected about 100 m below the top of the Wheeler Formation (Fig. 2) on the east side of the House Range (Fig. 1). The locality is on the crest of a low, north-trending ridge in section 24 (unsurveyed), T. 16 S., R. 13 W. (Swasey Peak 7½-minute quadrangle map, U. S. Geological Survey, 1972), and about 700 m south of a stock-watering trough

that is supplied by water piped from Swasey Spring.

The locality has yielded abundant fossils of the *Ptychagnostus atavus* Zone. Associated taxa have been listed by Robison (in press) and include 13 species of trilobites, one other arthropod (*Pseudoarctolepis sharpi*), jaws of *Anomalocaris nathorsti*, and a new species of the onychophoran *Aysheaia*, an undetermined species of inarticulate brachiopod, a new species of the sponge *Choia*, and 2 species of noncalcareous algae. Several of the invertebrate species have been described by Robison (1971, 1982), Robison and Richards (1981), and Conway Morris and Robison (1982). The paleoecology has been discussed by Robison (in press).

REFERENCES

- Aitken, J. D. 1978. Revised models for depositional grand cycles, Cambrian of the southern Rocky Mountains, Canada. *Canadian Petroleum Geology, Bulletin* 26(4): 515-542.
- Bambach, R. K., C. R. Scotese, and A. M. Ziegler. 1980. Before Pangea: the geographies of the Paleozoic world. *American Scientist* 68:26-38.
- Brady, M. J., and R. B. Koepnick. 1979. A Middle Cambrian platform-to-basin transition, House Range, west-central Utah. *Brigham Young University Geology Studies* 26:1-7.
- Brett, C. E. 1983. Sedimentology, facies and depositional environments of the Rochester Shale (Silurian; Wenlockian) in western New York and Ontario. *Journal of Sedimentary Petrology* 53:947-971.
- Briggs, D. E. G. 1976. The arthropod *Branchiocaris* n. gen., Middle Cambrian, Burgess shale, British Columbia. *Geological Survey of Canada, Bulletin* 264:1-29.
- . 1977. Bivalved arthropods from the Cambrian Burgess shale of British Columbia. *Palaeontology* 20: 595-621.
- . 1978. The morphology, mode of life, and affinities of *Canadaspis perfecta* (Crustacea: Phyllocarida), Middle Cambrian, Burgess shale, British Columbia. *Philosophical Transactions of the Royal Society of London (B)*281:439-487.
- . 1979. *Anomalocaris*, the largest known Cambrian arthropod. *Palaeontology* 22:631-664.
- , D. L. Bruton, and H. B. Whittington. 1979. Appendages of the arthropod *Aglaspis spinifer* (Upper Cambrian, Wisconsin) and their significance. *Palaeontology* 22:167-180.
- , and J. D. Mount. 1982. The occurrence of the giant arthropod *Anomalocaris* in the Lower Cambrian of southern California, and the overall distribution of the genus. *Journal of Paleontology* 56:1112-1118.
- , and S. H. Williams. 1981. The restoration of flattened fossils. *Lethaia* 14:157-164.
- Brooks, H. K., and K. E. Caster. 1956. *Pseudoarctolepis sharpi*, n. gen., n. sp. (Phyllocarida), from the Wheeler Shale (Middle Cambrian) of Utah. *Journal of Paleontology* 30:9-14.
- Bruton, D. L. 1981. The arthropod *Sidneyia inexpectans*, Middle Cambrian, Burgess shale, British Columbia. *Philosophical Transactions of the Royal Society of London (B)*295:619-653.
- , and H. B. Whittington. 1983. *Emeraldella* and *Leanchoilia*, two arthropods from the Burgess shale, Middle Cambrian, British Columbia. *Philosophical Transactions of the Royal Society of London (B)*300: 553-585.
- Campbell, D. P. 1974. Biostratigraphy of the *Albertella* and *Glossopleura* zones (lower Middle Cambrian) of northern Utah and southern Idaho. Unpublished Master of Science thesis, University of Utah, 292 p.
- Collins, Desmond, D. E. G. Briggs, and Simon Conway Morris. 1983. New Burgess shale fossil sites reveal Middle Cambrian faunal complex. *Science* 222: 163-167.
- Conway Morris, Simon, and R. A. Robison. 1982. The enigmatic medusoid *Peytoia* and a comparison of some Cambrian biotas. *Journal of Paleontology* 56:116-122.
- , and H. B. Whittington. 1979. The animals of the Burgess shale. *Scientific American* 241:122-133.
- Fritz, W. H. 1971. Geologic setting of the Burgess shale, vol. 2, p. 1155-1170. In E. L. Yochelson (ed.), *Proceedings of the North American Paleontological Convention*, Chicago, 1969. Allen Press (Lawrence).
- Gunther, L. F., and V. G. Gunther. 1981. Some Middle Cambrian fossils of Utah. *Brigham Young University Geology Studies* 28(1):1-81.
- Hintze, L. F., and R. A. Robison. 1975. Middle Cambrian stratigraphy of the House, Wah Wah, and adjacent ranges in western Utah. *Geological Society of America, Bulletin* 86:881-891.
- Howell, B. F., and others. 1944. Correlation of the Cambrian formations of North America. *Geological Society of America, Bulletin* 55:993-1003.

- Lochman-Balk, Christina, and J. L. Wilson. 1958. Cambrian biostratigraphy in North America. *Journal of Paleontology* 32:312-350.
- McIlreath, I. A. 1975. Stratigraphic relationships at the western edge of the Middle Cambrian carbonate facies belt, Field, British Columbia. *Geological Survey of Canada, Paper 75-1(A)*: 557-558.
- . 1977. Accumulation of a Middle Cambrian, deep-water limestone debris apron adjacent to a vertical, submarine carbonate escarpment, southern Rocky Mountains, Canada. *Society of Economic Paleontologists and Mineralogists, Special Publication 25*:113-124.
- Raasch, G. O. 1939. Cambrian Merostomata. *Geological Society of America, Special Papers 19*:1-146.
- Resser, C. E. 1929. New Lower and Middle Cambrian Crustacea. *Proceedings of the United States National Museum* 76(9):1-18.
- . 1931. A new Middle Cambrian merostome crustacean. *Proceedings of the United States National Museum* 79(33):1-4.
- . 1939. The Spence Shale and its fauna. *Smithsonian Miscellaneous Collections* 97(12):1-29.
- Rigby, J. K. 1980. The new Middle Cambrian sponge *Vauxia magna* from the Spence Shale of northern Utah and taxonomic position of the Vauxiidae. *Journal of Paleontology* 54:234-240.
- . 1983. Sponges of the Middle Cambrian Marjum Limestone from the House Range and Drum Mountains of western Millard County, Utah. *Journal of Paleontology* 57:240-270.
- Robison, R. A. 1964a. Late Middle Cambrian faunas from western Utah. *Journal of Paleontology* 38:510-566.
- . 1964b. Upper Middle Cambrian stratigraphy of western Utah. *Geological Society of America, Bulletin* 75:995-1010.
- . 1965. Middle Cambrian eocrinoids from western North America. *Journal of Paleontology* 39:355-364.
- . 1969. Annelids from the Middle Cambrian Spence Shale of Utah. *Journal of Paleontology* 43:1169-1173.
- . 1971. Additional Middle Cambrian trilobites from the Wheeler Shale of Utah. *Journal of Paleontology* 45:796-804.
- . 1976. Middle Cambrian trilobite biostratigraphy of the Great Basin. *Brigham Young University Geology Studies* 23(2):93-109.
- . 1982. Some Middle Cambrian agnostoid trilobites from western North America. *Journal of Paleontology* 56:132-160.
- . 1984a. Cambrian Agnostida of North America and Greenland: Part I, Ptychagnostidae. *University of Kansas Paleontological Contributions, Paper 109*:1-60.
- . 1984b. New occurrences of the unusual trilobite *Naraoia* from the Cambrian of Idaho and Utah. *University of Kansas Paleontological Contributions, Paper 112*:1-8.
- . In press. Affinities of *Aysheaia* (Onychophora), with description of a new Cambrian species. *Journal of Paleontology*.
- , and B. C. Richards. 1981. Larger bivalve arthropods from the Middle Cambrian of Utah. *University of Kansas Paleontological Contributions, Paper 106*:1-28.
- , and James Sprinkle. 1969. Ctenocystoidea: new class of primitive echinoderms. *Science* 166:1512-1514.
- Satterthwait, D. F. 1976. Paleobiology and paleoecology of Middle Cambrian algae from western North America. Unpublished Doctor of Philosophy dissertation, University of California, Los Angeles, 121 p.
- Simonetta, A. M. 1970. Studies on non trilobite arthropods of the Burgess shale (Middle Cambrian). *Palaeontographica Italica* 66(new series 36):35-45.
- , and Laura Delle Cave. 1983 (1982). New fossil animals from the Middle Cambrian. *Bolletino di Zoologia (Naples)* 49:107-114.
- Sprinkle, James. 1973. Morphology and evolution of blastozoan echinoderms. *Museum of Comparative Zoology, Harvard University, Special Publication*, 283 p.
- Walcott, C. D. 1886. Second contribution to the studies on the Cambrian faunas of North America. *United States Geological Survey, Bulletin* 30. 369 p.
- . 1911. Cambrian geology and paleontology II: Middle Cambrian Merostomata. *Smithsonian Miscellaneous Collections* 57(2):17-40.
- . 1912. Cambrian geology and paleontology II: Middle Cambrian Branchiopoda, Malacostraca, Trilobita, and Merostomata. *Smithsonian Miscellaneous Collections* 57(6):145-228.
- Walton, John. 1936. On the factors which influence the external form of fossil plants; with descriptions of the foliage of some species of the Palaeozoic equisetalean genus *Annularia* Sternberg. *Philosophical Transactions of the Royal Society of London (B)*226:219-237.
- Whiteaves, J. F. 1892. Description of a new genus and species of phyllocarid crustacean from the Middle Cambrian of Mount Stephen, British Columbia. *Canadian Record of Science* 5:205-208.
- Whittington, H. B. 1971. Redescription of *Marrella splendens* (Trilobitoidea) from the Burgess shale, Middle Cambrian, British Columbia. *Geological Survey of Canada, Bulletin* 209:1-24.
- . 1977. The Middle Cambrian trilobite *Naraoia*, Burgess shale, British Columbia. *Philosophical Transactions of the Royal Society of London (B)*280:409-443.
- . 1979. Early arthropods, their appendages and relationships, p. 253-268. In M. R. House (ed.), *The Origin of Major Invertebrate Groups*. Systematics Association, London, Special Volume 12, Academic Press (London).
- . 1980. The significance of the fauna of the Burgess shale, Middle Cambrian, British Columbia. *Proceedings of the Geological Association* 91:127-148.
- . 1981. Rare arthropods from the Burgess shale,

Middle Cambrian, British Columbia. Philosophical Transactions of the Royal Society of London (B)292: 329-357.

———, and D. E. G. Briggs. 1982. A new conundrum from the Middle Cambrian Burgess shale, vol. 2, p. 573-575. In Bernard Mamet and M. J. Copeland

(eds.), Proceedings of the Third North American Paleontological Convention, Montreal, 1982. Business and Economic Service Limited (Toronto).

———, and ———. In press. The giant Middle Cambrian animal *Anomalocaris*. Philosophical Transactions of the Royal Society of London (B).