

MIDDLE CAMBRIAN ARTHROPODS FROM UTAH

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ABSTRACT—The Middle Cambrian Spence Shale Member (Langston Formation) and Wheeler and Marjum Formations of Utah are known to contain a diverse soft-bodied fauna, but important new paleontological material continues to be uncovered from these strata. New specimens of anomalocaridids include the largest and smallest near complete examples yet reported from Utah. New material of stem group arthropods includes two new genera and species of arachnomorphs: *Nettapezoura basilika* and *Dicranocaris guntherorum*. Other new arachnomorph material includes a new species of *Leancoilia* comparable to *L. protogonia* Simonetta, 1970; *Leancoilia superlata?* Walcott, 1912; *Sidneyia* Walcott, 1911a; and *Mollisonia symmetrica* Walcott, 1912. *L. protogonia* from the Burgess Shale is confirmed as a separate species and is not a composite fossil. The first example of the trilobite *Elrathia kingii* preserving traces of the appendages is described. In addition, new material of the bivalved arthropods *Canadaspis* Novozhilov in Orlov, 1960; *Branchiocaris* Briggs, 1976; *Waptia* Walcott, 1912; and *Isoxys* Walcott, 1890 is described.

INTRODUCTION

THE MIDDLE Cambrian Spence Shale Member (Langston Formation) and Wheeler and Marjum Formations of Utah yield a diverse soft-bodied fauna comprising more than 40 described genera in addition to trilobites and other shelly taxa (reviewed in Robison, 1991; Hagadorn, 2002). The diversity and paleontological significance of these soft-bodied faunas have been recognized for some time (e.g., Robison and Richards, 1981; Briggs and Robison, 1984; Conway Morris, 1985). The fauna from the Spence Member is slightly older than that of the Burgess Shale while the Wheeler and Marjum Formation faunas are slightly younger. The study of Cambrian soft-bodied faunas has greatly enhanced our understanding of some of the key events in animal evolution (e.g., Briggs, 1978; Conway Morris, 1985, 1989, 2000; Whittington, 1985; Briggs and Fortey, 1989; Gould, 1989, 1991; Hou et al., 1995; Budd, 1996, 2002; Chen et al., 1996; Fortey et al., 1996; Edgecombe, 1998; Wills et al., 1998; Babcock et al., 2001). In particular, it has been recognized that several arthropods (as well as other organisms) represent stem groups. Some examples of other taxa also may bridge gaps between now-distinct body plans (e.g., Briggs et al., 2005). Preservation of soft tissues is rare, but an unusually large number of exceptionally preserved faunas are of Cambrian age (Allison and Briggs, 1993; Conway Morris, 1993; Orr et al., 1998; Babcock et al., 2001; Butterfield, 2003), providing unequaled biological insight into this critical interval in evolutionary history.

The soft-bodied and lightly skeletonized elements of the Spence Member and the Wheeler and Marjum Formations were described in scattered initial reports, notably that of Brooks and Caster (1956), and then in a series of papers (Gunther and Gunther, 1981; Robison and Richards, 1981; Briggs and Robison, 1984; Robison, 1985; Conway Morris and Robison, 1986, 1988; Babcock and Robison, 1988; Robison and Wiley, 1995; Briggs et al., 2005). New material described here was collected by several individuals but particularly the Gunther family of Brigham City, Utah, and SLH and RDJ.

Several of the taxa described from Utah are similar to taxa from the Burgess Shale (see Table 1). The same is true of other soft-bodied faunas from present day western North America such as those of the Lower Cambrian Latham Shale from the Marble Mountains of California (Briggs and Mount, 1982), and the Lower and Middle Cambrian soft-bodied faunas from the Pioche Formation of Nevada (Lieberman, 2003). The fauna from the Pioche Formation also contains some taxa very similar to those from the

Lower Cambrian of the Chengjiang area, southwest China (Lieberman, 2003). Arthropods form a large component of the relative abundance and diversity of material previously described from Utah (e.g., Robison and Richards, 1981; Briggs and Robison, 1984; Conway Morris and Robison, 1988), yet our knowledge of the arthropods in these faunas is incomplete. Here we describe two new genera and species of arthropods and present new records of others.

GEOLOGICAL SETTING AND DEPOSITIONAL ENVIRONMENT

The geological setting of the Middle Cambrian of Utah was described by Rees (1986), Robison (1991), Liddell et al. (1997), Elrick and Snider (2002), and Gaines et al. (2005a). The Spence Shale Member and the Wheeler and Marjum Formations represent marine, mixed carbonate-siliciclastic muddy slope and basin deposition on what was a subsiding passive margin of Laurentia (Hintze and Robison, 1975; Rees, 1986; Robison, 1991). All three deposits share a common paleogeographic configuration, located in slope and basin environments directly adjacent to the edges of broad carbonate platforms (Rees, 1986; Liddell et al., 1997). Soft-bodied fossils occur exclusively in the lowest-energy facies found within each unit, and were preserved only during intervals of oxygen-deficient benthic conditions (Gaines and Droser, 2005a, 2005b).

The Spence Member occurs in northeastern Utah and southeastern Idaho, and thickens towards the north (Liddell et al., 1997). Although soft-bodied and biomineralized metazoans are abundant at many localities in the Spence, soft-bodied metazoans occur most prominently in a series of exposures along the western flank of the Wellsville Mountains (Liddell et al., 1997). These soft-bodied faunas occur in the lower, fine-grained parts of multiple meter-scale mudstone to nodular wackestone-packstone parasequences, which represent alternating periods of low and moderate energy deposition in a ramp setting (Liddell et al., 1997). At Spence localities in southeastern Idaho, abundant Burgess Shale-type preservation occurs in a different environmental setting, in monotonous mudstone-dominated facies characteristic of a more distal, consistently low-energy depositional environment; however, soft-bodied fossils found here are exclusively algal (Gaines and Droser, 2005b). The Wheeler and Marjum Formations were deposited in a localized topographic low, termed the House Range Embayment, which was interpreted by Rees (1986) as a fault-bounded trough with an abrupt southern margin. At sections containing soft-bodied assemblages, the Wheeler Formation and the overlying Marjum Formation are dominated by two major facies, both of which accumulated below storm wave base. Vertically persistent, finely laminated mudstones represent deposition in basinal environments, and include all instances of soft-bodied preservation (Gaines and Droser, 2005b; Gaines et al.,

* The order of the first two authors is alphabetical

TABLE 1.—Broad scale stratigraphic and geographic distribution of soft-bodied arthropod taxa considered in this study along with relevant reference where appropriate. 'X' = present; 'HR' = House Range; 'DM' = Drum Mountains, where the soft-bodied material is found in what is sometimes referred to as the Pierson Cove Fm.; '#' = same species present in other strata; '\$' = same genus present in other strata; 'EC' = Early Cambrian; and 'MC' = Middle Cambrian.

Taxon	Utah Strata (MC)			Other Faunas			References
	Spence Mbr.	Wheeler Fm.	Marjum Fm.	Chengjiang (EC)	Kaili (MC)	Burgess Shale (MC)	
Anomalocaridids	X	HR	X	\$	\$	\$	Robison (1991); Briggs and Robison (1984); Briggs et al. (1994); Hou et al. (1995, 2004); Zhao et al. (2005)
<i>Nettapezoura basilika</i> n. sp.			X				
<i>Dicranocaris guntherorum</i> n. sp.		DM	X				
<i>Sidneyia</i> sp.	X	?HR				\$	Briggs and Robison (1984)
<i>Leanchoilia superlata?</i> Walcott	X			\$	\$	#	Briggs and Robison (1984); Zhao et al. (1999); Hou et al. (2004)
<i>Leanchoilia?</i> sp. cf. <i>protogonia</i> Simonetta			X	\$	\$	#	Whittington (1981); Zhao et al. (1999); Hou et al. (2004)
<i>Mollisonia symmetrica</i> Walcott	X	DM, HR			\$	#	Walcott (1912); Robison (1991); Zhang et al. (2002)
<i>Canadaspis</i> cf. <i>perfecta</i> Walcott	X	DM		\$	\$	#	Briggs (1978); Robison and Richards (1981); Yuan and Huang (1994); Hou and Bergström (1997)
<i>Waptia</i> cf. <i>fieldensis</i> Walcott	X			\$		#	Briggs et al. (1994); Hou et al. (2004)
<i>Branchiocaris pretiosa?</i>	?X	DM	X	?\$	\$	#	Briggs and Robison (1984); Zhao et al. (1999); Hou et al. (2004)
<i>Isoxys</i> sp. Walcott	X			\$	\$	\$	Briggs et al. (1994); Zhao et al. (1999); Hou et al. (2004)

2005). Interbedded mudstones and thin-bedded fine-grained limestones characterize deposition at the distal end of a carbonate ramp (Rees, 1986; Elrick and Snider, 2002). Other Cambrian soft-bodied faunas, including that of the Burgess Shale, occur in similar depositional configurations, in deep water settings at pronounced breaks in broad (~200 km) carbonate platforms. The Burgess Shale, however, is unique in that it was deposited on the edge of a submarine escarpment, rather than at the distal margin of a carbonate ramp.

Low energy of the depositional environments and event-dominated fine-grained sedimentation (Rogers, 1984; Conway Morris and Robison, 1986; Liddell et al., 1997; Gaines and Droser, 2003, 2005a) provided conditions favoring excellent preservation of both soft-bodied organisms and their biomineralized counterparts, although under different microtaphonomic conditions. Data from the Wheeler Formation, Marjum Formation, and Spence Member indicate that variable benthic redox conditions are represented within each of the deposits and include intervals of sustained benthic anoxia (Gaines and Droser, 2005b). Microstratigraphic data indicate that soft-bodied preservation occurs exclusively in horizons interpreted to have accumulated under anoxic bottom waters, while in situ benthic faunas colonized the substrate when bottom water oxygen content was sufficiently high (Gaines and Droser, 2005a, 2005b). Similar patterns have also been reported from the Burgess Shale and Chengjiang deposits (Allison and Brett, 1995; Hu, 2005).

A majority of the fossils considered in this study come from the seven localities detailed immediately below; additional localities bearing single specimens of interest here are detailed in the systematic paleontology portion of this paper.

"Cataract Canyon": Langston Formation, Spence Shale Member; west side of the Wellsville Mountains, NE $\frac{1}{4}$ NE $\frac{1}{4}$ sec. 23, T10N, R2W, Brigham City 7.5' Quadrangle, Box Elder County, Utah.

"Miners Hollow": Langston Formation, Spence Shale Member; west side of the Wellsville Mountains, N $\frac{1}{2}$ SE $\frac{1}{4}$ sec. 14, T10N, R2W, Brigham City 7.5' Quadrangle, Box Elder County, Utah. Also see localities CF-1 and CF-3 of Sumrall and Sprinkle (1999).

"Red Wash": Marjum Formation; House Range, exposed in ledges along the south side of a large dry wash about 4 km south

of the Wheeler Amphitheater, SW $\frac{1}{4}$ NW $\frac{1}{4}$ sec. 24, T17S, R13W, Marjum Pass 7.5' Quadrangle, Millard County, Utah. See Locality 716 of Robison and Richards (1981).

"Sponge Gully": Marjum Formation; House Range, in a dry stream bed about 700–800 m east of the western road between Marjum Pass and the Wheeler Amphitheater and about 4.7 km east-northeast of Marjum Pass, approximately 41 to 48 m above the Wheeler/Marjum contact, NW $\frac{1}{4}$ SE $\frac{1}{4}$ SE $\frac{1}{4}$ sec. 4, T18S, R13W, Marjum Pass 7.5' Quadrangle, Millard County, Utah. See locality of Rogers (1984) and Locality 347 of Conway Morris and Robison (1986).

"Carpoid Quarry": Wheeler Formation; southwest Antelope Mountain, House Range, about 10 km northeast of Marjum Pass, SE $\frac{1}{4}$ NE $\frac{1}{4}$ sec. 35, T17S, R13W, Marjum Pass 7.5' Quadrangle, Millard County, Utah.

"Swasey Spring": Wheeler Formation; east side of the House Range, sec. 24, T16S, R13W, Marjum Pass 7.5' Quadrangle, Millard County, Utah. See Locality 114 of Robison and Richards (1981).

"Phyllocarid Flats": Upper Wheeler Formation; Drum Mountains, about 300 m SE of the fork of a dry stream valley, SE $\frac{1}{4}$ NE $\frac{1}{4}$ sec. 20, T15S, R10W, Drum Mountains Well, 7.5' minute Quadrangle, Millard County, Utah. Site F4 on Phyllocarid Flats; approximately 46 m stratigraphically below the top of a massive limestone containing stromatolites about 315 m above the base of the Wheeler Formation. Site D3A: approximately 36 m stratigraphically below the top of the massive stromatolitic limestone.

SYSTEMATIC PALEONTOLOGY

Collections from the following institutions were examined: University of Kansas Natural History Museum and Biodiversity Research Center (KUMIP); Royal Ontario Museum (ROM); Smithsonian Institution (USNM); Department of Geology and Geophysics, University of Utah (UU); and Yale Peabody Museum of Natural History (YPM). Morphological terminology follows Briggs (1978), Briggs and Robison (1984), Wills et al. (1998), Briggs and Collins (1999), and Lieberman (2003).

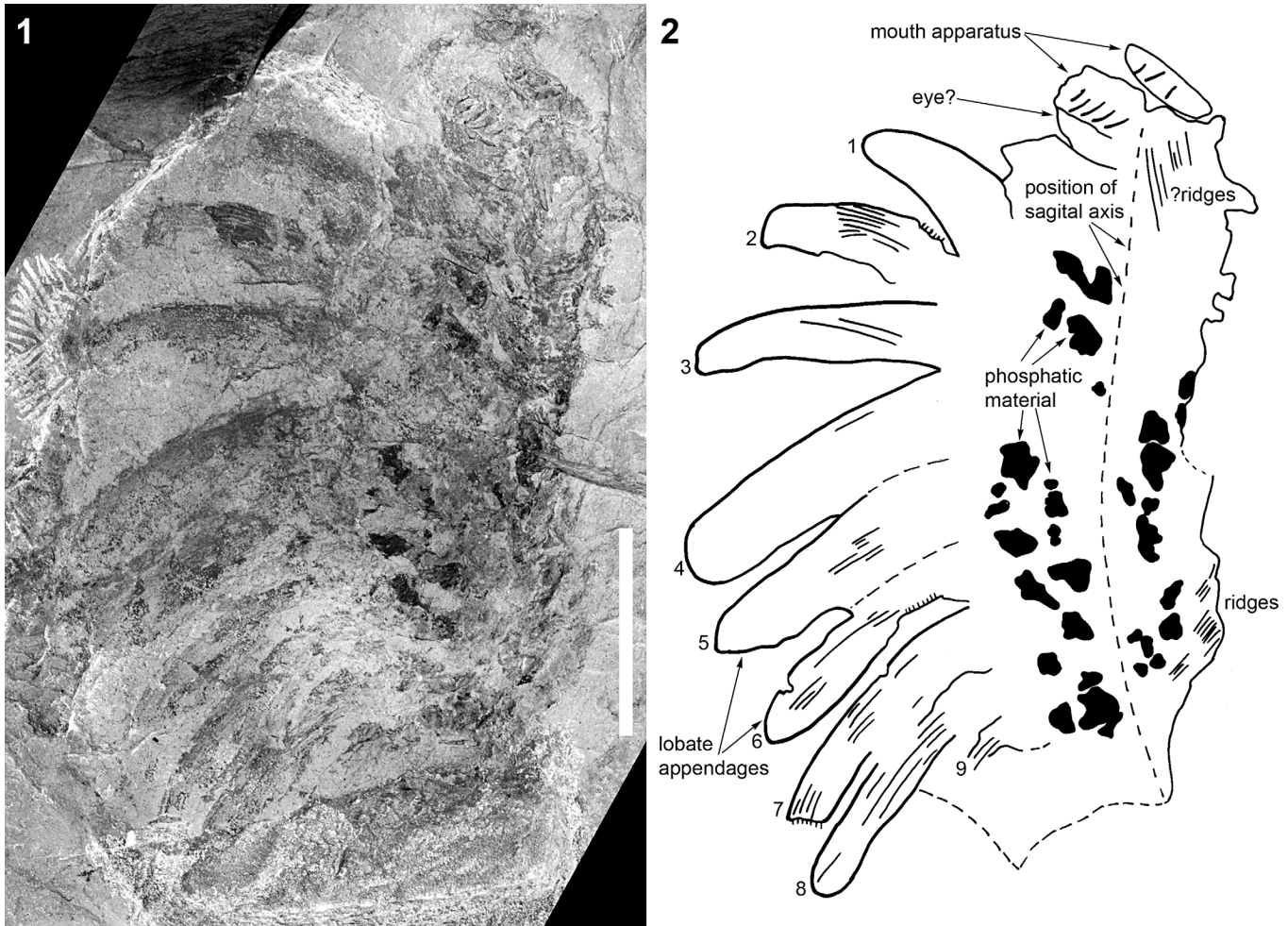


FIGURE 1—*Anomalocaris* sp. Whiteaves, 1892, KUMIP 314037, Spence Shale Member, Langston Formation, Miners Hollow, Wellsville Mountains, Box Elder County, Utah. 1, lateral-oblique view of nearly complete specimen; scale bar equals 3 cm. 2, camera lucida drawing of specimen; lobate appendages are numbered.

Stem group EUARTHROPODA
 Class DINOCARIDA Collins, 1996
 Order RADIODONTA Collins, 1996
 Family ANOMALOCARIDIDAE Raymond, 1935
 Figures 1–3

Discussion.—Anomalocaridids are part of the stem lineage leading to crown group euarthropods (Budd, 1993, 1996, 1998a, 1998b; Dewel and Dewel, 1998; Wills et al., 1998; see Hou et al., 2006 for a contrary view) and thus fall within the Paneuarthropoda (Budd and Jensen, 2000; Budd, 2001).

Material examined/occurrence.—A number of specimens of anomalocaridids have been described from the Middle Cambrian of Utah (Briggs and Robison, 1984; Conway Morris and Robison, 1988; Robison, 1991). Here we focus on significant new specimens that have not been illustrated previously: KUMIP 314037 (Fig. 1), a nearly complete specimen preserved in lateral oblique view and KUMIP 312405, a mouth apparatus and pair of associated anterior appendages, both from Miners Hollow; KUMIP 314078 (Fig. 2.1), a large mouth apparatus, part and counterpart, and KUMIP 314086 (Fig. 2.2), a small anterior appendage, both from Swasey Spring; and KUMIP 314087 (Fig. 3), a nearly complete but poorly preserved specimen in lateral view, from the Carpod Quarry.

Description and discussion of specimens.—KUMIP 314037 (Fig. 1) preserves much of the trunk in a lateral oblique orientation to bedding. At the anterodorsal margin a pair of strongly sclerotized ridged structures represents the presumed left and right sides of the mouth apparatus. The left side is better preserved, and it is represented by at least five (possibly six) ridges, perhaps corresponding to the plates. The long axis of the mouthparts is

inclined anteroventrally and presumably displaced from its original position; the full outline of the structure is not preserved. A large sub-circular structure overlaps the left side of the mouth apparatus and shows a marked color differentiation from adjacent parts of the body. It is similar in size and position to the eye of *Anomalocaris* (see Collins, 1996, figs. 6, 9).

Nine lobate appendages are evident on the left side. They are similar in outline, each consisting of an elongate, gently curved, distally rounded flat lobe. They increase gradually in length backwards to the fourth appendage which is 42 mm long and about 10 mm wide; the sixth and seventh are incomplete distally. Only the proximal part of the ninth lobe is preserved. The second lobe shows parallel ridges and grooves along a considerable extent of its length that correspond to strengthening rays *sensu* Whittington and Briggs (1985) or veins *sensu* Chen et al. (1994). These ridges are well preserved across half the width of the lobe. They are not imbricated or distally splayed. Other lobes show traces of ridges and grooves with the same spacing as those on the second. The overall paddle-like shape of the lobes differs from those of *Laggania nathorsti* (Walcott, 1911b) which are more triangular (see Whittington and Briggs, 1985). The outline corresponds more closely to that of the single flap from the Middle Cambrian of Nevada in Lieberman (2003, fig. 6.5) and to the more posterior flaps of *Anomalocaris saron* Hou, Bergström, and Ahlberg, 1995 from Chengjiang, but the outline of the lobes varies with orientation to bedding (see Whittington and Briggs, 1985). The geometry of the ridges in this Utah specimen differs from that in

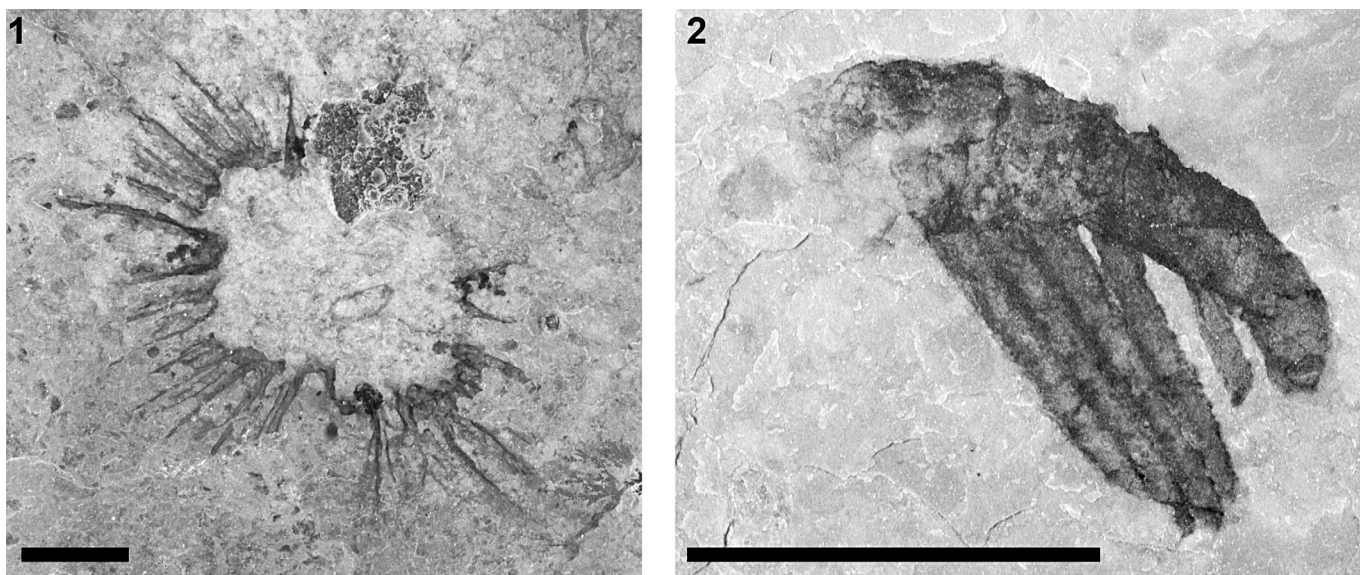


FIGURE 2—*Anomalocarididae* gen. et sp. indet., Wheeler Formation, near Swasey Spring, House Range, Utah. 1, KUMIP 314078, mouth apparatus, scale bar equals 1 cm. 2, KUMIP 314086 (part), anterior appendage, scale bar equals 1 cm.

other anomalocaridids: they parallel the margins of the lobe rather than terminating along the anterior margin (see e.g., Hou et al., 1995, fig. 5).

The lobes resemble exopodites, but there is no indication of endites or gnathobases along the inner proximal margin, nor of a segmented endopodite-like branch (ramipod-like branch sensu Hou et al., 1995) or supporting rod. In this respect this specimen differs from *Parapeytoia yunnanensis* and *Cucumericrus decoratus* Hou, Bergström, and Ahlberg, 1995. The attachment of the flaps to the body is not associated with any proximal modifications. They are almost as wide proximally as at their widest point, and appear to attach directly to the ventrolateral body wall, corresponding to the condition in anomalocaridids. The flaps overlap posterior to anterior but to a lesser extent in this specimen than in other anomalocaridids. No flaps can be identified confidently posterior of the ninth. The curve of the attachments of trunk limbs 6–9 corresponds to the shape of the trunk. The position of one or two of the right posterior limbs, apparently directed anteriorly, is picked out by traces of the rays.

A series of patches of black mineralized material is present along the axis of the specimen. These patches are aligned roughly with the limbs, suggesting that they are segmentally arranged. The patches are composed of closely-packed fibers, about 0.1 mm wide. EDX analysis shows that the mineral is phosphatic, presumably apatite. The distribution, composition, and gross structure of this mineral shows striking similarities to patches of mineral that

have been interpreted as mid-gut glands in Burgess Shale arthropods (Butterfield, 2002). Similar structures are evident in *Laggania nathorsti* from the Middle Cambrian Marjum Formation of the House Range (Briggs and Robison, 1984) and from the Burgess Shale, where they are sometimes preserved as mineralized strips (see Whittington and Briggs, 1985; Collins, 1996; Butterfield, 2002). Their distribution and structure is unlike that of muscle tissue described from the anomalocaridid *Pambdelurion whittingtoni* (Budd, 1998a, 1998b).

Previously identified anomalocaridid remains from the Middle Cambrian of Utah in general, and the Spence in particular, have been assigned to *L. nathorsti* (e.g., Briggs and Robison, 1984; Conway Morris and Robison, 1988; Robison, 1991), a species that Whittington and Briggs (1985) assigned to *Anomalocaris*, Chen et al. (1994) referred to *Peytoia*, and Collins (1996) to *Laggania* (final resolution of this issue awaits the description of new material from the Burgess Shale in the collections of the Royal Ontario Museum). KUMIP 312405 (not figured) preserves a pair of anterior appendages about 17 mm long, with a morphology similar to that in *L. nathorsti* ('Appendage F' of Briggs, 1979; Whittington and Briggs, 1985; Collins, 1996), associated with a mouth apparatus. The large specimen described here differs from *L. nathorsti* in the shape of the flaps, the conformation of the ridges on the flaps, and possibly the number of flaps and position and nature of the mouth apparatus, although some of these differences may be taphonomic. This specimen cannot be assigned

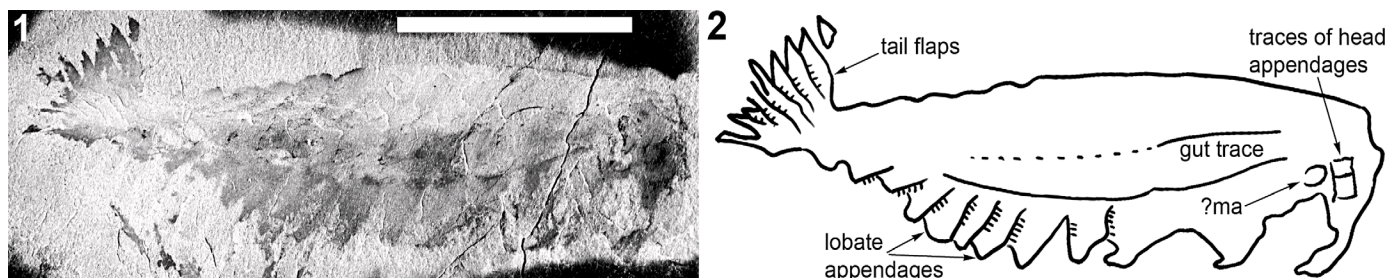


FIGURE 3—1, *Anomalocaris* sp. Whiteaves, 1892, KUMIP 314087, Wheeler Formation, Carpod Quarry, southwest Antelope Mountain, House Range, Millard County, Utah. Lateral-oblique view of nearly complete specimen; scale bar equals 1 cm. 2, camera lucida drawing of specimen. Abbreviation: ma, mouth apparatus.

to a species in the absence of evidence of the anterior appendages. With a preserved length of about 110 mm it is the largest near complete anomalocaridid yet reported from Utah.

KUMIP 314078 (Fig. 2.1): This specimen, a part and counterpart near parallel to bedding, is a large mouth apparatus: the maximum width is approximately 6.4 cm; the interior space, measured diagonally, approximately 2.8 cm. Not all the oral plates are preserved, but about 25 are evident and extrapolation suggests that the remaining seven could be accommodated. The geometry and position of the teeth can not be determined. Anomalocaridid mouth apparatuses have been reported previously from the Wheeler Formation (Conway Morris and Robison, 1982, 1988), including smaller examples preserved in a similar manner to KUMIP 314078 (Conway Morris and Robison, 1982, pl. 1, figs. 1–5). Because of the incomplete state of preservation, assignment to species is not possible.

KUMIP 314086 (Fig. 2.2): This specimen is a small, ventrally curved anterior appendage roughly 1.5 cm long; at least eight segments are evident. Four relatively long ventral spines, and a shorter more distal one are evident; they reach a maximum length of 0.9 cm. Traces of structures that may correspond to auxiliary spines are faintly visible on some of the ventral spines. A similar appendage, also from the Wheeler Formation, was described by Conway Morris and Robison (1988, fig. 26.3). This appendage is similar to that of *Laggania nathorsti* ('Appendage F' of Briggs, 1979; Whittington and Briggs, 1985; Collins, 1996).

KUMIP 314087 (Fig. 3): This specimen, which is preserved in lateral-oblique aspect, shows a series of flap-like lobes on the right side of the animal, which overlap from posterior to anterior. At least ten lobes are visible directed posteroventrally. The tail bears at least eight dorsally directed triangular flaps. Their anterior margin is gently convex, but the posterior margin is obscured. The flaps may belong to both sides of the tail. The shape and the posterior- to anterior-overlap direction of the lateral lobes, and of the tail flaps, is characteristic of anomalocaridids and not *Opabinia* Whittington, 1975 (see Whittington and Briggs, 1985; Budd, 1996). The morphology of the tail is similar to that in *Anomalocaris canadensis*, although only three pairs of flaps are recorded in that species (Collins, 1996, p. 285) and any identification must be tentative in the absence of the head appendages. Previous considerations of *Anomalocaris* have emphasized its status as a giant predator (e.g., Whittington and Briggs, 1985; Briggs, 1994). This is the smallest complete specimen so far described from North America, with a length of just 29 mm.

Remarks.—Anomalocaridids represent a remarkable array of Cambrian stem-group arthropods that comprised the first large animal predators (Whittington and Briggs, 1985; Briggs, 1994; Chen et al., 1994; Hou et al., 1995; Collins, 1996; Budd, 1998a, 1998b, 2001). Originally based on material of *Anomalocaris* Whittaves, 1892 from the Middle Cambrian of Mount Stephen and from the Burgess Shale (Walcott Quarry), the group has since been expanded to include several taxa, and representatives have been found in Early Cambrian localities from Laurentia, e.g., California (Briggs and Mount, 1982), Pennsylvania (Briggs, 1979), Nevada (Lieberman, 2003), and Greenland (Budd, 1998a), and also eastern Europe (Dzik and Lendzion, 1988), Australia (McHenry and Yates, 1993; Nedin, 1995), and China (Chen et al., 1996; Hou et al., 2004). Representatives have also been reported from the Middle Cambrian of the Northwest Territories, Canada (Butterfield and Nicholas, 1996), Utah (Briggs and Robison, 1984; Conway Morris and Robison, 1988; Robison, 1991), Nevada (Lieberman, 2003), and from the Kaili biota in China (Zhao et al., 2005). The specimens described in this paper include the largest and smallest near complete specimens yet reported from Utah.

Phylum EUARTHROPODA
Subphylum ARACHNOMORPHA

Discussion.—Arachnomorpha is used in the sense of Wills et al. (1998), and Cotton and Braddy (2004, p. 169) and is equivalent to Arachnata sensu Edgecombe and Ramsköld (1999).

Genus NETTAPEZOURA new genus

Type species.—*Nettapezoura basilika* new species.

Other species.—None (monotypic).

Etymology.—*Netta*—duck, *peza*—foot, *oura*—tail (all f. Gr), reflecting the shape of the telson.

Discussion.—The position of this taxon within the Arachnomorpha has yet to be determined by cladistic analysis.

NETTAPEZOURA BASILIKA new species

Figure 4

Etymology.—“*basilikos*” from Greek, meaning “regal” or “royal”, because this species must have been one of the apex predators of the Middle Cambrian.

Holotype/type locality and horizon.—UU 04083.02 a,b (Fig. 4), complete part and counterpart, from about 45 m above the base of the Marjum Formation, Sponge Gully, central House Range, Millard County, Utah.

Other material.—No other material can be assigned with confidence to this taxon.

Diagnosis.—Cephalic shield semicircular; cephalon bearing at least two pairs of long segmented appendages (endopodites). Trunk of 11 somites; no clear trilobation; pleurae large and broadly triangular in aspect, not in contact with those anterior or posterior. Trunk appendages present on seven, possibly eight trunk somites consisting of stacked lamellae (~30) with convex outer margins attached to a leaf-like lobe, made up of ~20 elongate radiating elements. Posterior three somites apodous, tube-like, forming a separate tagma (abdomen). Posterior margin of telson projecting medially into a spine flanked by concave embayments; lateral margins extending into similar pointed projections.

Description.—UU 04083.02 a,b is preserved in a parallel oblique attitude to bedding (Fig. 4.1, 4.2). The left side of the body is preserved in near parallel aspect. The right side is oriented at a higher angle to bedding so that the right lateral margin of the cephalic shield is folded in a concertina fashion and the tergites and telson are foreshortened on this side. The preserved outline is further modified by dorsal flexure of the trunk posteriorly.

Cephalic shield.—The cephalic shield is semicircular in outline. The width (in UU 04083.02 a,b, the only known specimen) is about 4.5 cm (estimated as twice the width from the axis to the left hand margin), about twice the length (sagittal). The axial region may have been slightly raised. The margin was smoothly convex; there is no evidence of any indentation to accommodate an appendage or eye stalk. The posterior margin was straight or weakly concave posteriorly; it is not clearly demarcated in the axial region of the specimen. Near the mid-length of the cephalic shield, towards the midline, there are several scattered small, dark areas of mineralization. These do not share the characteristic internal texture of the features described by Butterfield (2002, 2003) in *Leancoilia* and their distribution is not consistent with an interpretation as midgut glands.

Preparation of the left side of UU 04083.02 revealed the outline of two segmented appendages toward the rear of the cephalic shield (Fig. 4.3) interpreted as endopodites; there is no evidence of corresponding exopodites in these cephalic appendages. The more anterior appendage reveals three distal podomeres. The podomeres expand slightly distally except for the terminal one. The penultimate podomere extends into two spines that flank the shorter terminal podomere, which appears to taper to a point. The more posterior of the two appendages extends beyond the margin of the carapace about twice as far as the other. Five podomeres are exposed, each expanding slightly distally, apart from the terminal one. The second, third and fourth decrease slightly in length; the fourth projects distally into spines that apparently flank a pointed terminal podomere. Up to four short structures, which project from beneath the cephalic shield anterior to these two limbs, may represent other appendages or even a stalked eye. It has proved impossible to prepare these projections further distally in order to test this possibility.

Trunk.—The trunk consists of 11 segments and a telson. There is no distinct axial region. In segments one to five there are black stains towards the midline that become more nodular in appearance posteriorly; they lack the texture and distribution characteristic of arthropod midgut glands sensu Butterfield (2002, 2003). The relative width (tr.) of the tergites is difficult to determine due to the attitude of the specimen to bedding and the incomplete

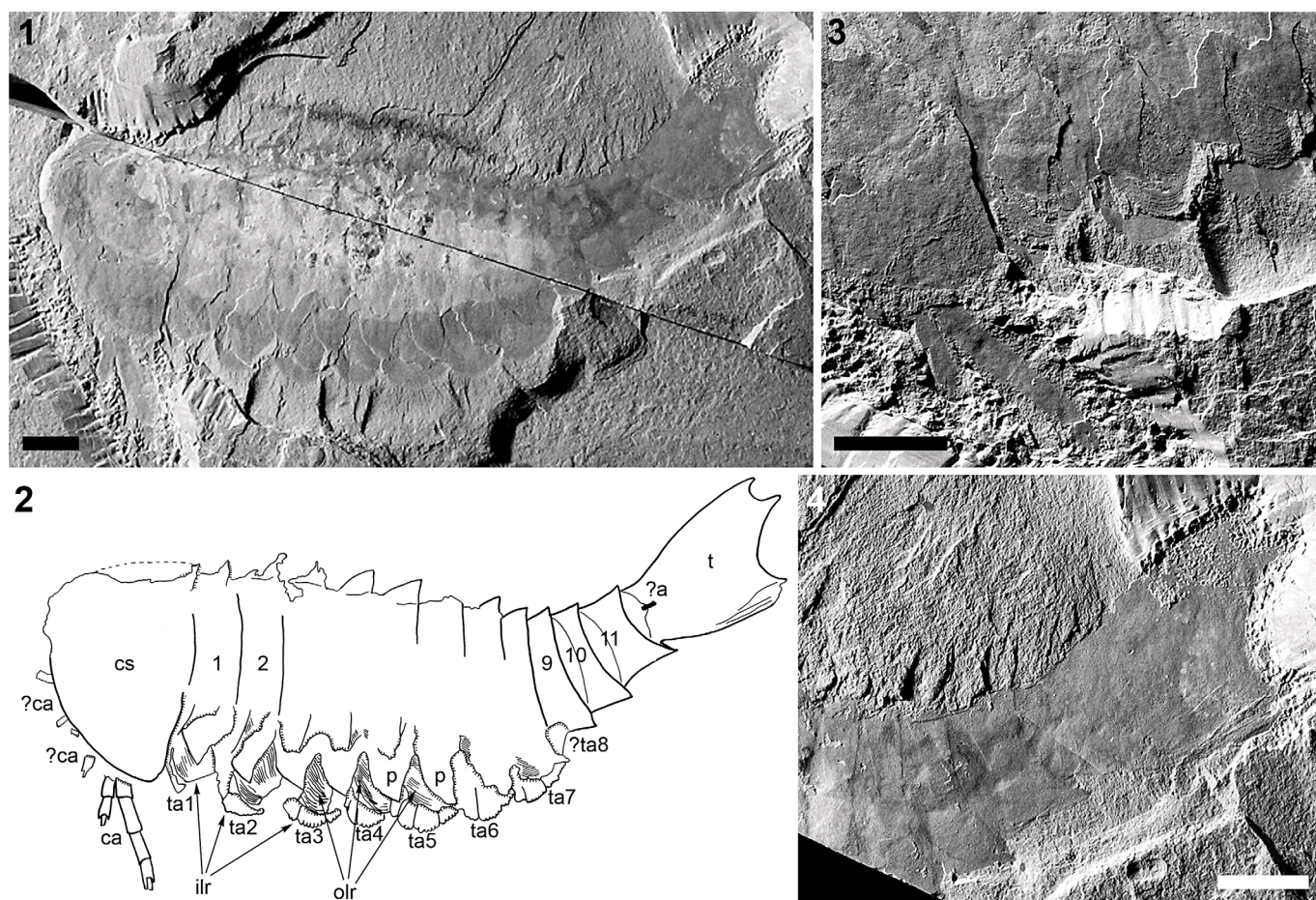


FIGURE 4—*Nettapezoura basilika* n. sp., holotype, UU 04083.02 a, Marjum Formation, Sponge Gully, House Range, Millard County, Utah. 1, near lateral view of left side of complete specimen (part); scale bar equals 1 cm. 2, camera lucida drawing of specimen; abbreviations are as follows: a, anus; ca, cephalic appendages; cs, cephalic shield; ilr, inner leaf-like ramus; olr, outer lamellate ramus; p, pleuron; t, telson; and ta, trunk appendage; trunk segments are numbered. 3, detail of cephalic appendages and trunk appendages 1–3; scale bar equals 1 cm. 4, detail of trunk segments 9–11 and telson; scale bar equals 1 cm.

outline of the right side, but the trunk appears to taper posteriorly from the sixth somite. The outline of the tergites is often incomplete due to the way the specimen has split, and their posterior margin may be obscured in the axial region. The posterior margins of the anterior tergites are straight to gently convex posteriorly; those of the more posterior tergites are gently concave posteriorly. The tergites abut or overlap posteriorly in the axial region; laterally they separate but the outline of the sub-triangular pleural extensions is obscured in places by splitting or by the appendages, which overlies them on the counterpart.

Appendages are present on segments one to seven and probably also eight (but the area associated with tergite eight may be part of limb seven). The appendages are exposed on the left side where they extend beyond the lateral margins of the tergites (reflecting in part the attitude of the specimen to bedding), and adaxially where they are revealed by splitting. The trunk appendages, which consist of two elements, are interpreted as exopodites, and are very different in morphology to the appendages exposed in the posterior part of the cephalic shield.

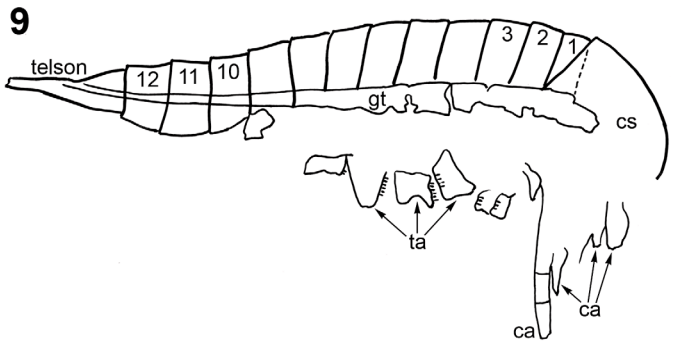
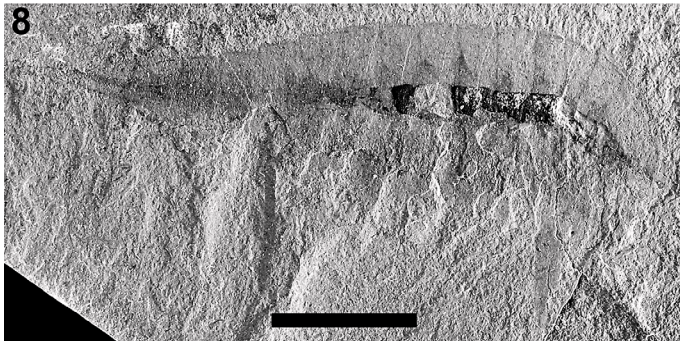
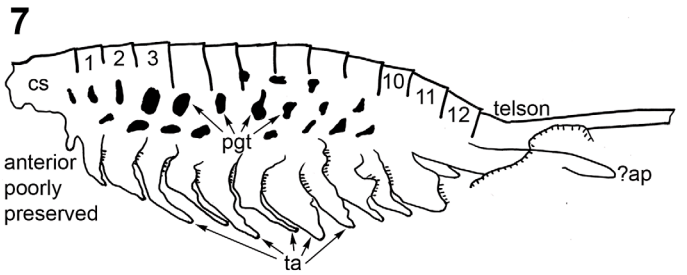
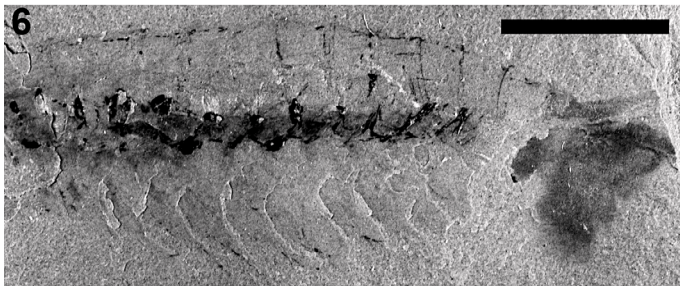
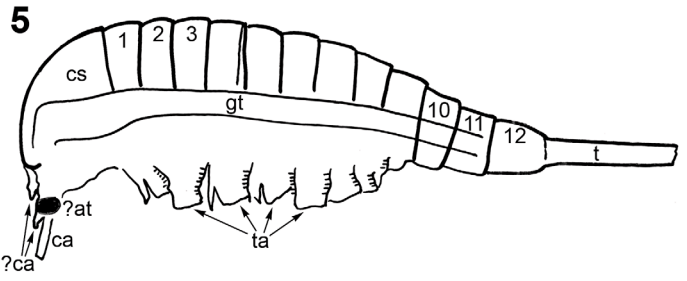
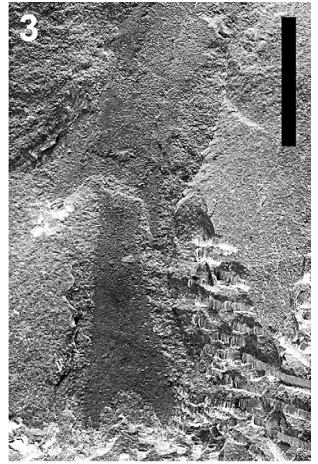
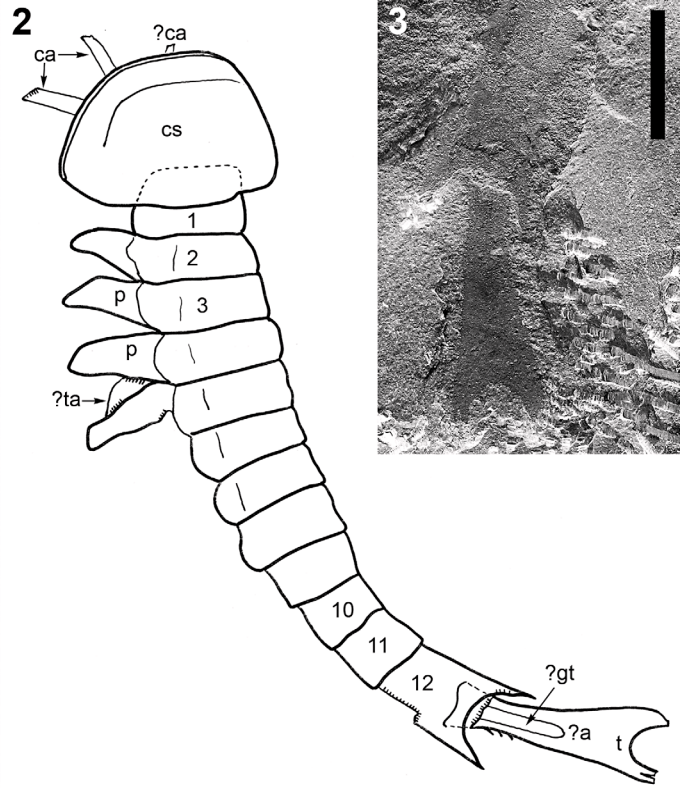
The outer element of the trunk appendages consists of a series of lamellae, those beneath extending progressively farther beyond those that lie above them. The outer margin of the lamellae is convex, roughly parallel to the lateral margin of the corresponding tergite. The overall outline of the lamellae is unknown as only their outer margin is exposed; they may be long and narrow like the gill filaments in *Sidneyia* (Bruton, 1981). Counting and extrapolation indicates that each exopodite bore at least 30 lamellae (based on L3); it is not possible to determine whether or not this number varied along the length of the specimen.

A leaf-like structure extends ventrally beyond the stacked lamellae. The lamellae appear to be attached to this structure along a transverse line that runs roughly parallel to the somite boundaries. Unlike the lamellae, the leaf-like structure is preserved as a single layer, although it may be folded anteriorly in places where it presumably curved at a higher angle to the bedding

(L1, L2). The outline of the leaf-like structure is convex but the margin is scalloped and occasional lines subdivide the structure radially, suggesting that it was composed of individual radiating elements. The number of radiating elements is difficult to determine, but enumeration of the scallops and extrapolation indicate that, if present, there were at least 20.

The last three somites of the trunk (9–11) lack appendages and each is narrower than that preceding it (Fig. 4.4). They are tubular (unlike the more anterior somites with tergites) and insert one into another, and do not open ventrally. The dorsal curvature of the posterior part of the trunk is reflected in the dual boundaries between somites: one convex anteriorly representing the dorsal junction, the other concave anteriorly corresponding to the ventral (see Briggs and Collins, 1999: text-fig. 15). The telson inserts into the 11th somite anteriorly and expands posteriorly; the lateral margins are gently convex and extend into a point (Fig. 4.4). The posterior margin extends into a median point flanked by two concave indentations (the overall outline reminiscent of a duck's foot). There is no evidence of caudal appendages and no spines are evident around the margin of the telson. No relief is evident on the surface (apart from some folding on the left side). A depression in the anterior part of the telson may indicate the position of the anus.

Discussion.—While it is undesirable to erect a new taxon based on one example, this well-preserved specimen displays a unique combination of characters that clearly distinguish it from other Cambrian arthropods thus far described. The division of the body into a cephalic shield and 11 trunk somites is shared with a number of arachnomorphs: *Alalcomenaeus* Simonetta, 1970, *Leancoilia* Walcott, 1912, *Emeraldella* Walcott, 1912, and *Sanctacaris* Briggs and Collins, 1988. These taxa also share a strong differentiation of the limbs of the cephalic shield from those of the trunk. *Nettapezoura* differs from these taxa, however, in the



presence of three apodous tube-shaped somites at the rear, and in the shape of the telson. Such a separate tagma occurs in *Sidneyia*, but it has 12 trunk somites, the last of which bears appendages that combine with the telson to form a tail flap. The two posteriormost limbs of the cephalon of *Nettapezoura* appear to be simple endopodites ('walking appendages') like those that occur in a number of taxa such as *Emeraldella* (Bruton and Whittington, 1983). There is no evidence that they were biramous. The trunk appendages of *Nettapezoura* are reminiscent of those of *Sidneyia*, in that they consist of a series of lamellae overlying a flap-like structure. They are likewise interpreted as representing an exopodite (Bruton, 1981; see Boxshall, 2004, fig. 4A). In *Nettapezoura*, however, the flap-like structure is made up of a series of elongate radiating elements and there is no evidence that the trunk appendages included a segmented endopodite like those of *Sidneyia*.

Genus DICRANOCARIS new genus

Type species.—*Dicranocaris guntherorum* new species.

Included species.—None (monotypic).

Etymology.—*Dikranon*—pitchfork, *caris*—shrimp (f. Latin).

Discussion.—This arthropod displays a combination of characters that are unknown in any other Cambrian arthropod, particularly the unique morphology of the telson.

DICRANOCARIS GUNTHERORUM new species

Figure 5

Molaria?-like trilobitomorph. GUNTHER AND GUNTHER, 1981, p. 62, pl. 48b. *Alalcomenaeus* cf. *cambricus* Simonetta. ROBISON, 1991, p. 86, fig. 7.10.

Etymology.—In honor of the Gunther family, Brigham City, UT, who has contributed so much to our knowledge of Cambrian soft-bodied faunas.

Holotype/type locality and horizon.—UU 06011.03 (Fig. 5.1–5.3), a complete individual preserved in parallel oblique aspect, from the Wheeler Formation, site D3A, Phyllocarid Flats, Drum Mountains, Millard County, Utah.

Other material examined/occurrences.—The following eight specimens may also represent this taxon. Three specimens are from the Wheeler Formation: KUMIP 135148 (Fig. 5.4, 5.5), a complete individual preserved in lateral aspect from a quarry in the Wheeler Amphitheater, (SE¼ sec. 2, T17S, R13W, Marjum Pass 7.5' Quadrangle); KUMIP 312406, a poorly preserved parallel-oblique specimen figured by Gunther and Gunther [1981, pl. 48b] before it was prepared, and KUMIP 314079 (Fig. 5.6, 5.7), part and counterpart of a complete individual preserved in lateral aspect, both from Carpod Quarry. UU 06011.02 a,b (Fig. 5.8, 5.9), part and counterpart of a complete individual preserved in lateral aspect, from Sponge Gully. The other four specimens, all poorly preserved, are from the Marjum Formation: KUMIP 312402, incomplete, is questionably from Red Wash and KUMIP 312400, part and counterpart in parallel aspect showing the outline of the telson, is from near Red Wash (east and downstream of); KUMIP 312401, incomplete, is questionably from "Modocia flats," (probably about S½, sec. 2 (unsurveyed), T18S, R13W, Marjum Pass 7.5' Quadrangle); and KUMIP 312403, part and counterpart incomplete, is from Sponge Gully.

Diagnosis.—Short semi-circular head shield, 12 trunk somites with narrow, well defined axis and long, projecting pleurae at least anteriorly, last somite longer than the rest, bearing a long telson that expands to about twice its width and bifurcates distally.

Description.—The holotype (Fig. 5.1–5.3) is preserved in parallel oblique aspect—the left side in outline, the right folded beneath. The posterior part of the trunk is flexed dorsally.

The holotype is 10 cm long (sag.). The maximum width of the cephalic shield was about 3 cm (based on twice the measured width of the left side). Preservation of detail is poor, but there is evidence of at least two cephalic

appendages, and perhaps one of the trunk appendages. The cephalic shield is semicircular in outline, with a narrow shallow groove around the anterior margin. It was about twice as wide as long, and about 0.15 of the total length of the arthropod. The axial area is raised slightly posteriorly, although this may be the result of overlap with the trunk (it is considered unlikely that this raised area represents an additional trunk somite; cf. *Yoholia* Walcott, 1912). The posterior margin of the cephalon is convex posteriorly. Two appendages emerge from beneath the anterior left of the cephalic shield and project some 6 mm beyond it. The full extent of neither is apparent. A short projection nearer the axis of the cephalic shield may represent an additional appendage. These appendages preserve no details of segmentation. The total number of appendages in the cephalon is unknown.

The trunk consists of 12 somites and a telson. Only the axial part of the tergites is well preserved, and it shows some positive relief. It is clear that the trunk narrows gradually posteriorly. Long narrow pleurae are evident on tergites two to five projecting laterally at a lower level than the axial part. The outline of these pleurae is poorly preserved but they appear to taper rapidly distally so that successive tergites are only in contact in the axial region. The anterior margin of each pleura is convex and the posterior straight to concave. It is not known whether the pleurae of the first tergite were absent or reduced. The pleurae on the right side are presumably folded beneath the trunk. It is not known whether segments six to 11 bore pleurae, as they would be concealed within the matrix. However, tergites nine to 11 lack any prominent relief, their preserved lateral margins are straighter, and at least the last three may represent tubes without pleurae, i.e., an apodous tagma. The somites posterior of seven are longer than the more anterior ones. Segment 12 is about twice as long as 11 and expands posteriorly, extending into lateral projections that flank the proximal part of the telson. An area lying between and below the pleura of tergites four and five may represent a trace of a trunk appendage; no details of its morphology can be discerned.

The telson inserts into the concave posterior margin of somite 12 and a ridge at the rear of this somite indicates its line of attachment (Fig. 5.3). The telson is very narrow proximally, about half the width of segment 12, but it expands distally more than twofold, extending into two lateral projections, probably terminating in spines, that flank a concave indentation. There is an indication of short spines near at the anterior left of the telson, but it is not clear whether these are real. The position of the anus is unknown, but if a darkened axial area represents a gut trace, it lies about the mid-length of the telson.

Three specimens in lateral aspect (KUMIP 135148, Fig. 5.4, 5.5; KUMIP 314079, Fig. 5.6, 5.7; and UU 06011.02, Fig. 5.8, 5.9) show a relatively short rounded cephalic shield, a segmented trunk bearing flap-like appendages (KUMIP 135148 preserves evidence that they were biramous) and an elongate telson. All show evidence of a mineralized gut trace. Both KUMIP 135148 and UU 06011.02 preserve evidence of a long cephalic appendage. Details are difficult to distinguish due to the nature of the preservation, but a number of other appendages (to DEGB) or structures (to BSL and JRH) are clearly evident anterior of this one in UU 06011.02. It is not clear how many of the trunk somites bear appendages (the structure at the rear of KUMIP 314079 resists interpretation), but probably 9 or 10. Details of the outline of the appendages are largely obscured.

Discussion.—The carapace outline resembles that of *Sanctacaris* and *Alalcomenaeus* but these taxa, like *Leancoilia*, have 11 rather than 12 trunk somites. Among the few described Cambrian taxa with 12 trunk somites are *Sidneyia* and *Habelia*, but the new form differs in the morphology of the telson. All three lateral specimens appear to have 12 trunk somites. Some laterally flattened specimens of *Alalcomenaeus cambricus* (e.g., ROM 45598; Briggs and Collins, 1999, text-fig. 3 and pl. 2, fig. 3) show a fold near the base of the telson where it expands into the flattened paddle, which might be mistaken for a somite boundary. In UU 06011.02 and KUMIP 135148, however, there is a clear boundary at the posterior margin of the 12th segment where the telson inserts. Furthermore, if somite 12 were included in the length of the telson it would be much longer relative to the length

FIGURE 5—1–3, *Dicranocaris guntherorum* n. gen and sp., holotype, UU 06011.03, Wheeler Formation, site D3A, Drum Mountains, Millard County, Utah. 5–9, ?*Dicranocaris guntherorum* n. gen and sp. (see text for locality information for these specimens). Abbreviations: a, anus; ap, appendage; at, agnostid trilobite; ca, cephalic appendages; cs, cephalic shield; gt, gut trace; p, pleuron; pgt, phosphatic gut trace; t, telson; and ta, trunk appendage; trunk segments are numbered. 1, parallel oblique view of holotype (UU 06011.03); scale bar equals 1 cm. 2, camera lucida drawing of holotype. 3, detail of trunk segment 12 and telson of holotype; scale bar equals 1 cm. 4, KUMIP 135148, lateral view of complete individual; scale bar equals 1 cm. 5, camera lucida drawing of KUMIP 135148. 6, KUMIP 314079 (part), left-lateral view of complete individual (anterior end poorly preserved); scale bar equals 1 cm. 7, camera lucida drawing of KUMIP 314079 (the additional length in the cephalic shield and telson are evident on the counterpart). 8, UU 06011.02 a, lateral view of complete individual; scale bar equals 1 cm. 9, camera lucida drawing of UU 06011.02 a.

of the specimen than is the telson in *A. cambricus*. These three specimens, which range in length from ~40–55 mm, are therefore interpreted as small specimens of *Dicranocaris*. KUMIP 135148 and UU 06011.02 preserve evidence of a long cephalic appendage. Any similarity to the ‘great appendage’ of *Alalcomenaeus* is difficult to determine based upon the specimens of *Dicranocaris* that are currently known. In KUMIP 135148, the long cephalic appendage appears to be attached near the anterior end of the specimen, while in UU 06011.02 this structure lies further posteriorly than that in *A. cambricus* (where it is derived from the front of the head; Budd, 2002). Thus, DEGB argues that the cephalic appendage of UU 06011.02 cannot be homologous with the ‘great appendage’ of Cambrian taxa such as *Alalcomenaeus*. Because of its similarities to *Sanctacaris* and *Alalcomenaeus* we treat *Dicranocaris* as an arachnomorph pending more detailed phylogenetic work. Its affinities are difficult to determine, however, in the absence of well preserved appendages.

Genus SIDNEYIA Walcott, 1911a

Discussion.—This taxon is treated as an arachnomorph based on its position in phylogenetic analyses in Edgecombe and Ramsköld (1999), Wills et al. (1998), and Cotton and Braddy (2004).

SIDNEYIA sp. Figure 6

Material examined/occurrence.—KUMIP 314033 (Fig. 6), an incomplete dorsal exoskeleton from Miners Hollow.

Description/discussion.—This specimen is large but poorly preserved. Ten divisions are evident, presumably corresponding to the cephalon and nine tergites. The maximum preserved width is ~90 mm. The tergites are much wider than long and convex anteriorly, with a more pronounced convexity in the axis. Their lateral terminations are straight to rounded. The first five tergites widen from the anteriormost posteriorly; the posterior three narrow slightly. A dark axial area likewise widens posteriorly and narrows in the last three tergites. This axial area is displaced to the left, reflecting a slight tilt to the bedding that is also evident in compaction wrinkling at the extremity of the pleurae on the same side. There is no evidence of preserved appendages. The outline of the tergites is the same as that in *Sidneyia* from the Burgess Shale—indeed the specimen is strikingly similar to that figured by Bruton (1981, pl. 5, fig. 37). Extrapolating on the basis of Bruton’s reconstruction indicates a specimen about 18 cm long—i.e., the largest *Sidneyia* known. Because of the incomplete preservation it is not possible to determine unequivocally whether or not this specimen is conspecific with *S. inexpectans* from the Burgess Shale.

Briggs and Robison (1984) referred appendages from the Wheeler Formation in the House Range of Utah to *Sidneyia* sp. A specimen (USNM 518270, formerly Princeton University 41005) from the Kinzers Fm. of Pennsylvania referred to *Sidneyia* sp. by Resser and Howell (1938, pl. 13, fig. 3) consists of three posteriormost trunk segments that project laterally into pleural spines, and a telson and caudal furca totally different from the tail in *Sidneyia inexpectans*. An additional specimen from the Kinzers Fm. (YPM 94007) preserves the first seven tergites of the thorax, maximum width ~70 mm, and is similar in appearance and proportions to *S. inexpectans*, but the posterior trunk appendages and telson are unknown. *Sidneyia sinica* Zhang and Shu in Zhang et al., 2002, which is based on a single specimen from the Early Cambrian Chengjiang Lagerstätte of south China, is incorrectly assigned to *Sidneyia*. The posteriormost appendages arise from the rear margin of the telson, not from the posterior abdominal somite, as they do in *S. inexpectans*.

Genus LEANCHOILIA Walcott, 1912

Discussion.—Here we describe new material of *Leancoilia* from Utah, which likely represents *Leancoilia superlata*. We describe a new specimen of *Leancoilia protogonia* from the Burgess Shale, which demonstrates that the holotype is not a composite (contra Whittington, 1981) and that *L. protogonia* is a separate species. This allows us to compare a new arthropod from Utah with *L. protogonia* and show that, while it is most similar to *L. protogonia*, it is not conspecific.

The phylogenetic position of *Leancoilia* remains controversial. We place it within the Arachnomorpha based on the phylogenetic analyses of Wills et al. (1998) and Cotton and Braddy (2004). Budd (2001), however, argued that *Leancoilia* lies near the top of the stem group of euarthropods as part of his great appendage arthropods. Budd’s (2002) phylogenetic analysis of a variety of Cambrian euarthropods (omitting modern taxa), however, resolved *Leancoilia* in a relatively basal position, grouped with *Alalcomenaeus*, one node up the tree relative to *Parapeytoia*.

LEANCHOILIA SUPERLATA? Walcott, 1912 Figure 7

Undetermined arthropod 1, CONWAY MORRIS AND ROBISON, 1988, p. 33–34, figs. 23, 24.

Material examined/occurrence.—KUMIP 204783 (Conway Morris and Robison, 1988, figs. 23, 24, p. 34, 35), in parallel aspect; KUMIP 314028 (Fig. 7.1), complete part and counterpart in oblique aspect; KUMIP 314029 (Fig. 7.2), nearly complete part and counterpart in lateral aspect; KUMIP 314031 (Fig. 7.3), a partially complete part and counterpart preserved in dorsal aspect; these four specimens are from Miners Hollow. (KUMIP 314029 is from about 25 ft [7.6 m] from the top of the Spence.) Questionably KUMIP 314030, preserved in dorsal aspect, from the Spence Shale Member (in float) at Cataract Canyon.

Description/discussion.—None of the specimens considered here preserves evidence of the appendages. However, a number of characters support an assignment to *Leancoilia*. The cephalic shield is relatively large, its anterior margin rounded in outline, and faintly upturned anteriorly in lateral view. At least ten trunk somites are evident and they show a weakly developed axial lobe. Although the trunk is incomplete posteriorly in KUMIP 314028 (Fig. 7.1) the rounded anterior margin of the cephalon suggests that this specimen is *Leancoilia* rather than *Alalcomenaeus*. Many of the trunk segments preserve patches of phosphate that are similar in texture to those interpreted as gut glands in *Leancoilia* from the Burgess Shale (Butterfield 2002, 2003), although these structures also occur in other taxa. The posterior margins of the pleurae, where evident, are weakly and evenly concave posteriorly. Their lateral margins roughly parallel the sagittal line or are weakly rounded. The termination of the trunk is evident only in KUMIP 314029 (Fig. 7.2) where it appears to extend into a triangular telson.

Conway Morris and Robison (1988, p. 33–35, figs. 23, 24) referred KUMIP 204783 to Undetermined Arthropod 1 (see also appendix in Robison, 1991), but the additional morphological data from the associated specimens described here suggests that it can be assigned to *Leancoilia*.

The Utah specimens are similar to *L. superlata* Walcott, 1912 from the Burgess Shale (see Bruton and Whittington (1983) for an extensive synonymy, but note that *Leancoilia protogonia* is retained here), but without information on the appendages, it is impossible to confirm that they are conspecific. The anterior margin of the cephalic shield in these specimens differs from that in *Leancoilia? hanceyi* Briggs and Robison, 1984, also known from the Spence Shale, which is blunter and makes a more pronounced angle with the lateral margins. The specimens assigned here to *L. superlata?* also differ from a specimen from the Marjum Formation assigned by Briggs and Robison (1984) to *Emeraldella?* sp. which has a much broader cephalic shield and long slender cephalic appendages.

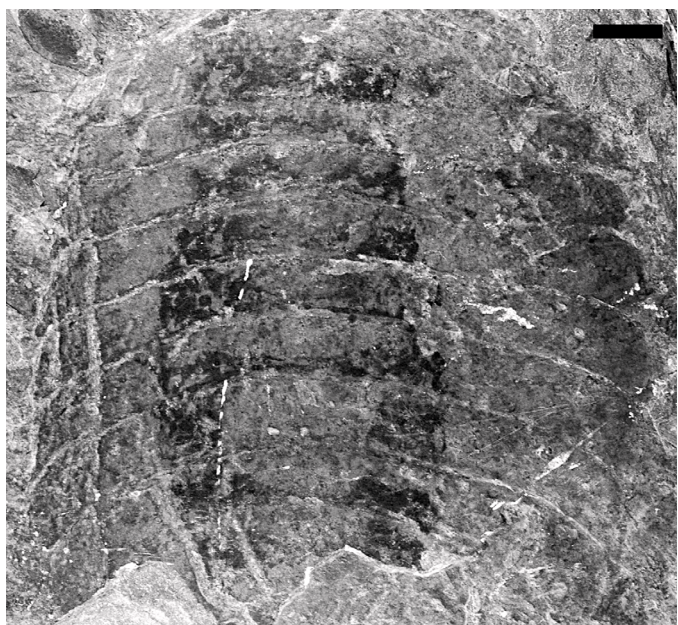


FIGURE 6—*Sidneyia* sp. Walcott, 1911a, KUMIP 314033, Spence Shale Member, Langston Formation, Miners Hollow, Wellsville Mountains, Box Elder County, Utah. Dorsal view of incomplete specimen; scale bar equals 1 cm.

LEANCHOILIA PROTOGONIA Simonetta, 1970

Figure 8.1

Leanchoilia protogonia Simonetta, 1970, p. 38, pl. 4, fig. 2; SIMONETTA AND DELLE CAVE, 1975, pl. 1, fig. 6, pl. 31, fig. 1; BRUTON AND WHITTINGTON, 1983, p. 578.

'*Leanchoilia protogonia*', a composite fossil. WHITTINGTON, 1981, pp. 331–332, 334, 351, figs. 116, 120–122.

Material examined/occurrence.—USNM 155648, holotype, from the Walcott Quarry. ROM 57152, a part and counterpart of a complete specimen, from a level 40 cm below the Walcott Quarry, Greater Phyllopod Bed, Walcott Quarry Shale Member, Burgess Shale Formation, west slope of Fossil Ridge, Yoho National Park, British Columbia.

Diagnosis.—*Leanchoilia* with an elongate telson bearing 6 pairs of lateral spines, the more posterior long and curved, and a long slender median spine.

Description.—ROM 57152 (Fig. 8.1), a new specimen of *L. protogonia*, is preserved in lateral aspect. The head shield is gently convex dorsally, and shows no evidence of an upturn at the anterior extremity. The proximal part of the great appendage projects beyond the head shield; the distal flagellae are not evident, but the morphology is otherwise characteristic of the great appendage of *Leanchoilia* (Whittington and Bruton, 1983) and *Alalcomenaeus* (Briggs and Collins, 1999). The trunk consists of 11 somites; details of the appendages are not clear. The telson is elongate and tapers gradually posteriorly. There is a long narrow median spine, and at least six lateral spines are evident on the left side. The specimen is 18 mm long from the anterior margin of the cephalic shield to the posterior extremity of the telson, excluding the median spine. The holotype (see Whittington, 1981) is 27 mm long. The cephalic shield and telson are similar in length and each about 0.5 the length of the trunk tergites.

Discussion.—The division of the body into a cephalic shield and 11 trunk somites, the proximal morphology of the great appendage, and particularly the telson morphology with six pairs of elongate lateral spines (Whittington, 1981, fig. 116, did not include the small anteriormost pair in his drawing) and one medial, show that this specimen is conspecific with *Leanchoilia protogonia*. Whittington (1981) argued that the holotype and only known specimen of *L. protogonia* (USNM 155648) is a composite consisting of an unknown organism (the telson) overlying a specimen of *Leanchoilia superlata*. The new specimen described here demonstrates that the holotype is not a composite. Simonetta and Delle Cave (1975, pl. 1, fig. 6) reconstructed *L. protogonia* with 19 somites, but Whittington (1981) correctly reinterpreted the

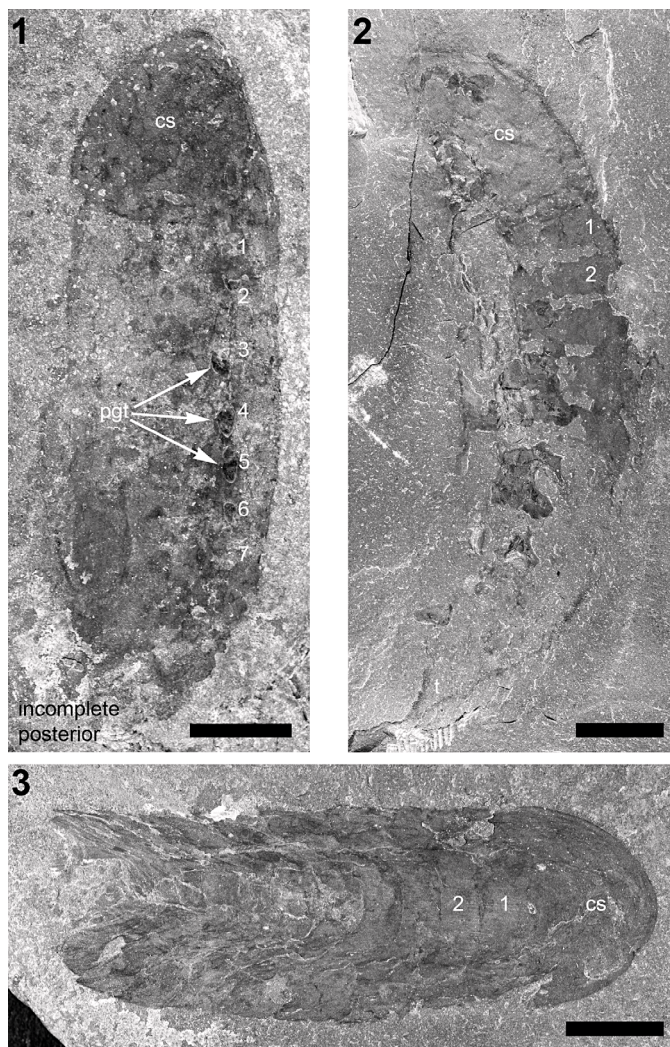


FIGURE 7—1–3, *Leanchoilia superlata*? Walcott, 1912, Spence Shale Member, Langston Formation, Miners Hollow, Wellsville Mountains, Box Elder County, Utah. Abbreviations: cs, cephalic shield; pgt, phosphatic gut trace; t, telson; trunk tergites are numbered. 1, KUMIP 314028 (part), oblique view of specimen with incomplete posterior; scale bar equals 1 cm. 2, KUMIP 314029 (part), lateral view of nearly complete specimen; scale bar equals 1 cm. 3, KUMIP 314031 (counterpart), dorsal view of incomplete specimen; scale bar equals 1 cm.

number as 11. The holotype of *L. protogonia* (Whittington, 1981, pl. 13, figs. 116, 120–122), preserved in parallel aspect, shows that the trunk tapers posteriorly from the head shield and is relatively narrower than that in *Leanchoilia superlata*. Its assignment to *Leanchoilia* is retained here, although the discovery of further material might show that it represents a new genus.

LEANCHOILIA? sp. PROTOGONIA Simonetta, 1970

Figures 8.2, 8.3

Material examined/occurrence.—UU 06011.01 a, b (Fig. 8.2, 8.3), a part and counterpart of a complete specimen preserved parallel to bedding, from Sponge Gully.

Description.—The specimen is preserved in parallel aspect. It is 34.5 mm long from the anterior of the cephalic shield to the posterior extremity of the telson and the maximum width of 9 mm occurs near the posterior margin of the cephalic shield. Only the dorsal exoskeleton is preserved; there is no evidence of the appendages. The axial area of the cephalic shield, as well as the first seven trunk tergites, is raised above the lateral projections of the exoskeleton. The axial area of the cephalic shield tapers forward beyond the triangular lateral extensions and terminates in a near straight anterior margin. A dark area on the left anterolateral edge of the shield may represent an eye;

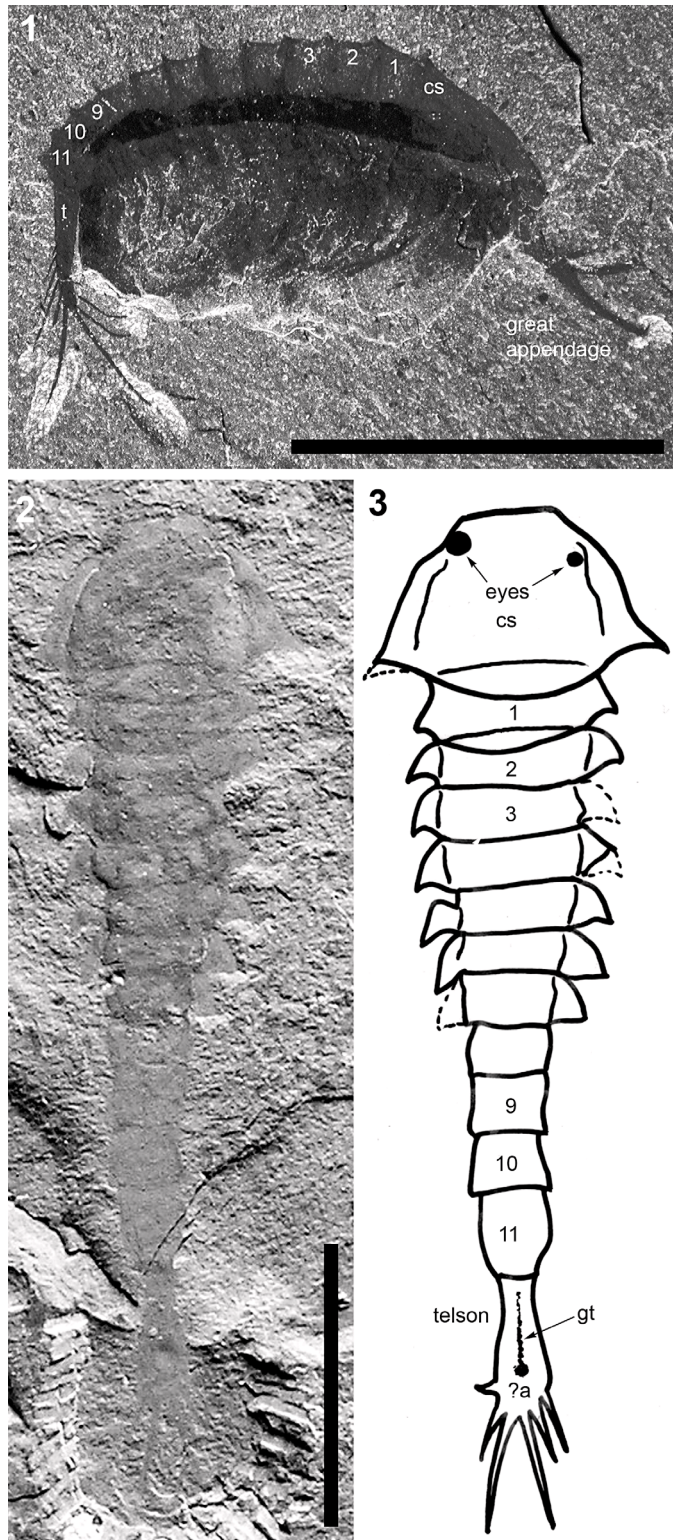


FIGURE 8—1, *Leanchoilia protogonia* Simonetta, 1970, ROM 57152, Burgess Shale Formation, west slope of Fossil Ridge, Yoho National Park, British Columbia; scale bar equals 1 cm. 2, *Leanchoilia?* sp. cf. *protogonia* Simonetta, 1970, UU 06011.01 a, Marjum Formation, Sponge Gully, House Range, Millard County, Utah; scale bar equals 1 cm. 3, camera lucida drawing of UU 06011.01 a. Abbreviations for 1–3: a, anus; cs, cephalic shield; gt, gut trace; and t, telson; trunk segments are numbered.

there is no evidence of an eye on the right side, but its approximate position is estimated in Figure 8.3. The posterior margin of the cephalon is convex posteriorly and overlaps the first of the 11 trunk tergites. The first seven bear small, sub-triangular pleurae. These structures are not evident on the left side of tergite 7, nor in somites 8 to 11, but it is not possible to determine whether or not they were present on the posterior somites (they would lie at a lower level and it is not feasible to prepare them). The first eight trunk somites are similar in length. The last three are longer; the final one, which narrows posteriorly, is the longest. The telson is narrow, club shaped in outline, and bears at least six spines, three on each side of the midline. A faint gut trace is evident in the anterior two thirds of the telson, which terminates in a round depression that may represent the anus.

Discussion.—The division of the body into a cephalic shield and 11 trunk somites is shared with a number of arachnomorphs from the Burgess Shale: *Alalcomenaeus*, *Leanchoilia*, *Emeraldella*, and *Sanctacaris*. It is difficult to determine the outline of the cephalic shield on the basis of a single specimen as it will vary with attitude to bedding (cf. *Alalcomenaeus*: Briggs and Collins, 1999). The triangular lateral projections of the cephalic shield recall those in *Sanctacaris*. The disposition of tergites differs strongly from that in *Leanchoilia superlata* (see Bruton and Whittington, 1983) and also *Leanchoilia? hanceyi* from the Spence Shale (Briggs and Robison, 1984), particularly in the lack of overlap between successive lateral projections. The posterior tapering of the trunk, and the outline of the telson are more similar to those in *Leanchoilia protogonia* than in any other taxon. The telson of *L. protogonia*, however, is relatively longer than that in the specimen described here, and bears a larger number of longer more slender spines. There is no evidence for the presence of eyes in the two specimens of *L. protogonia*. The Utah specimen is clearly a different species, but in the absence of evidence of the appendages it is here referred to as *Leanchoilia?* sp. cf. *protogonia*.

Genus MOLLISONIA Walcott, 1912

Type species.—*M. symmetrica* Walcott, 1912.

Discussion.—The phylogenetic affinities of *Mollisonia* have never been considered in detail because the appendages are unknown. The Utah specimens reveal faint trilobation, the roughly transverse anterior margin of the cephalic shield, the slightly concave posterior cephalic margin, seven thoracic tergites which are divided laterally by pleural furrows, and a large tail shield, subequal in size to the cephalic shield, with three pairs of spines, one lateral and two posterior.

Mollisonia shows some similarities to *Kuamaia* Hou, 1987, which Hou and Bergström (1997) assigned to the Order Helmetiida. *Kuamaia* shares, for example, the roughly subequal cephalic and pygidial shields, seven or eight segments in the thorax, and the pygidial shield with a pair of lateral spines. *Helmetia*, however, has only six thoracic segments and Hou and Bergström (1997) did not consider *Mollisonia* to belong to the Helmetiida. *Mollisonia* shares seven tergites and a spine-fringed posterior shield with *Sinoburius* Hou, Ramsköld, and Bergström, 1991, which Hou and Bergström (1997) assigned to a new Order Sinoburiida, but the shape of the cephalic shield is very different and *Mollisonia* lacks eyes on the dorsal surface. Edgecombe and Ramsköld's (1999) cladistic analysis of Cambrian arthropods grouped *Sinoburius* with *Xandarella* (confirming Hou and Bergström's, 1997 view) but *Mollisonia* is unlike *Xandarella*. The similarity of *Mollisonia* to the helmetiids and sinoburiids suggests that its affinities lie with the arachnomorphs, but until the appendages are discovered and *Mollisonia* is incorporated into a phylogenetic analysis its evolutionary position will remain uncertain.

MOLLISONIA SYMMETRICA Walcott, 1912

Figure 9

Mollisonia symmetrica WALCOTT, 1912, p. 196, pl. 24, fig. 3; STØRMER in Moore, 1959, p. O37, fig. 26.1.

Mollisonia? rara WALCOTT, 1912, p. 198, pl. 24, figs. 6, 7.

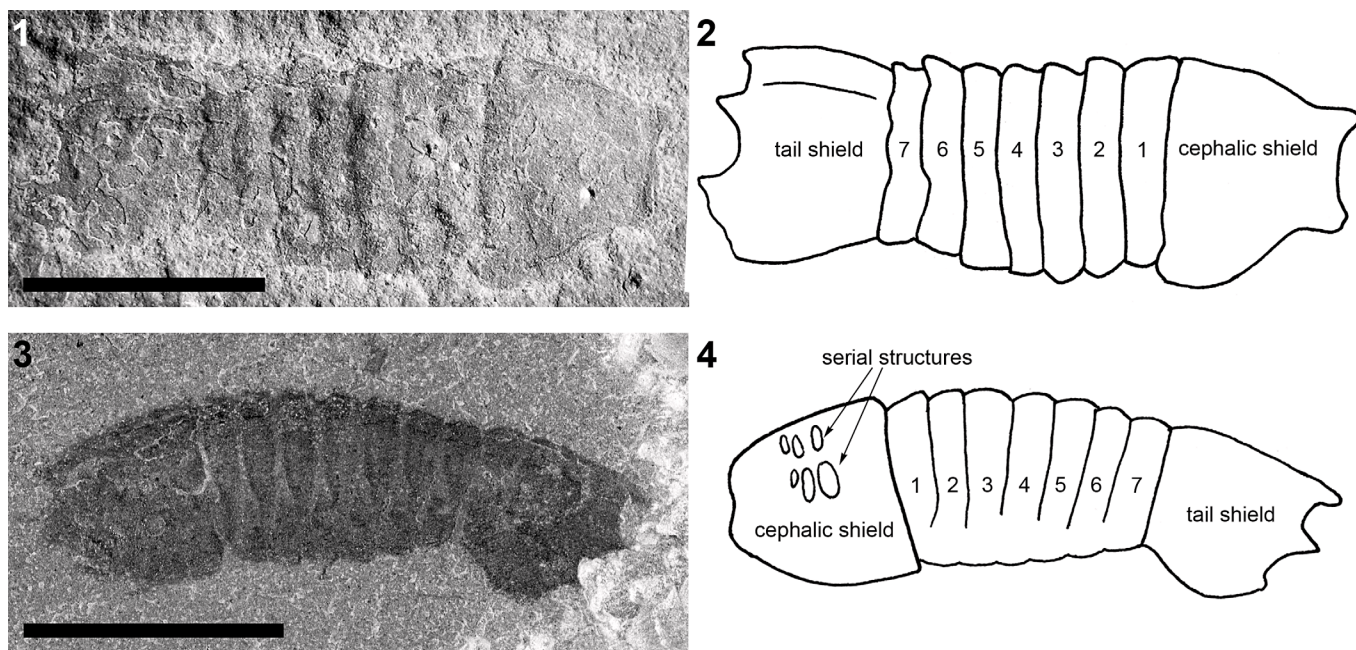


FIGURE 9—*Mollisonia symmetrica* Walcott, 1912. 1, UU 06011.04, Wheeler Formation, site D3A, Drum Mountains, Millard County, Utah. Complete specimen preserved parallel to bedding; scale bar equals 1 cm. 2, camera lucida drawing of UU 06011.04; trunk tergites are numbered. 3, KUMIP 314041, Spence Shale Member, Langston Formation, Miners Hollow, Wellsville Mountains, Box Elder County, Utah. Left-lateral oblique view of complete specimen; scale bar equals 1 cm. 4, camera lucida drawing of KUMIP 314041; trunk tergites are numbered.

Mollisonia-like arthropod. GUNTHER AND GUNTHER, 1981, p. 62, pl. 48a.
Mollisonia sp. ROBISON, 1991, p. 97, fig. 7.2.

Material examined/occurrences.—KUMIP 135149, complete specimen preserved parallel to bedding, from the Wheeler Formation, House Range, Utah (see Robison, 1991, fig. 7.2). UU 06011.04 (Fig. 9.1, 9.2), complete specimen preserved parallel to bedding from Phyllocarid Flats. KUMIP 314041 (Fig. 9.3, 9.4), complete specimen preserved in lateral oblique aspect, 40 m above the base of the Spence Shale Member, from Miners Hollow. USNM 57762, 57763, 83951, 189155, 189183, the Walcott Quarry, Greater Phyllopod Bed, Walcott Quarry Shale Member, Burgess Shale Formation, west slope of Fossil Ridge, Yoho National Park, British Columbia.

Description/discussion.—The new material illustrated herein (Fig. 9) shows a pair of blunt projections along the anterior cephalic margin, and KUMIP 314041 (Fig. 9.3, 9.4) shows three pairs of serially repeated structures in the head shield which are oval in outline, aligned normal to the axis, and diminish in size anteriorly. Based on the new material discussed here it seems likely that the appearance of projections on the anterior margin of the cephalic shield depends on taphonomic factors and how the specimen has been prepared.

Mollisonia symmetrica is based on a unique specimen described by Walcott (1912) from Mount Stephen. It is a weathered impression (concave on the shale) of the dorsal surface (Walcott, 1912, pl. 24, fig. 3). It shows the narrow short first thoracic tergite, followed by six tergites of similar width, and the tail shield with three transverse ridges. The specimens of *Mollisonia? rara* Walcott, 1912 cannot be distinguished from *M. symmetrica* and *M.? rara* is synonymized with it here following Simonetta and Delle Cave (1975). USNM 57662 (Walcott, 1912, pl. 24, fig. 6) is incomplete posteriorly, and USNM 57663 (Walcott, 1912, pl. 24, fig. 6) is obscured anteriorly but shows the characteristic pleural ridges and ridges on the tail shield that terminate in marginal spines. USNM 83951 (Walcott, 1931, pl. 21, fig. 4) and USNM 189155 and 189183 (Simonetta and Delle Cave, 1975, pl. 37, fig. 4, pl. 36, fig. 5) show the complete outline in lateral oblique view. *Mollisonia gracilis* Walcott, 1912 (pl. 24, fig. 5) also has seven trunk tergites but differs from *Mollisonia symmetrica* in being much narrower and showing a narrow median ridge on the tergites and tail shield. It may be a juvenile of *M. symmetrica*, but we

retain it as a separate species here pending a full description of new Burgess Shale material of the genus in the ROM collections.

Mollisonia sp. in Robison (1991) cannot be distinguished from *M. symmetrica* and clearly shows the divisions and marginal spines on the tail shield. *Mollisonia sinica* Zhang, Zhao, Yang, and Shu, 2002, from Middle Cambrian Kaili biota of southwest China, differs from, *M. symmetrica* in the outline of the cephalic shield and the tail shield.

Class TRILOBITA
 Suborder PTYCHOPARIINA
 Order PTYCHOPARIIDA
 Family ALOKISTOCARIDAE Resser, 1939
 Genus ELRATHIA Walcott, 1924
 ELRATHIA KINGII (Meek, 1870)
 Figure 10

Elrathia kingii (Meek). The species has been discussed and figured frequently; see MOORE, 1959, p. O240, fig. 179.1; GUNTHER AND GUNTHER, 1981, p. 32, plate 18; JELL AND ADRAIN, 2003, p. 371.

Material examined/locality.—UU 06011.05 (Fig. 10.1, 10.2) and three additional specimens, from Phyllocarid Flats.

Discussion.—*Elrathia kingii* is arguably the most familiar and abundant trilobite in North America (Gaines and Droser, 2003). UU 06011.05, however, is the first to be reported that preserves traces of the thoracic appendages that underlie the dorsal exoskeleton. It does not provide any information on the morphology of the limbs (except to suggest that they did not extend laterally beyond the pleurae), but appears to confirm that the appendages were attached proximally at the junction between tergites, rather than centrally beneath each tergite (see Edgecombe and Ramsköld, 1999). This is the first evidence described of the limbs of a ptychopariid (Suborder Ptychopariina) trilobite, although the limbs of the olenid *Triarthrus* (Suborder Olenina) are well known (e.g., Whittington and Almond, 1987). The specimen also shows the position of the rostral plate and hypostome.

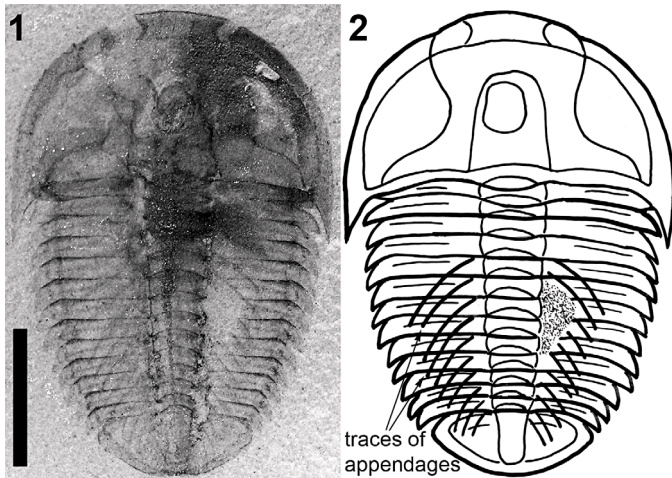


FIGURE 10—*Elrathia kingii* (Meek, 1870), UU 06011.05, Wheeler Formation, site D3A, Drum Mountains, Millard County, Utah. 1, UU 06011.05: view of complete specimen; scale bar equals 5 mm. 2, camera lucida drawing.

Subphylum CRUSTACEA (including stem and crown)
 Order CANADASPIDIDA Novozhilov in Orlov, 1960
 Family CANADASPIDIDAE Novozhilov in Orlov, 1960
 Genus CANADASPIS Novozhilov in Orlov, 1960
 CANADASPIS cf. PERFECTA (Walcott, 1912)

Figure 11

Material examined/locality.—KUMIP 314077 (Fig. 11), part and counterpart, preserved in lateral aspect, upper Wheeler Formation, from the Drum Mountains, about 100 m east of a stream gully in center S½ NE¼ sec. 20, T15S, R10W, Drum Mountains Well 7.5' minute Quadrangle, Millard County, Utah (see Conway Morris and Robison, 1986).

Discussion.—The phylogenetic position of *Canadaspis* has been much debated (see discussions in Briggs, 1978, 1992; Hou and Bergström, 1997; Boxshall, 1998; Walossek and Müller, 1998; Budd, 2001; Lieberman, 2003). The specimen from the Wheeler Formation is the first specimen definitively showing the backward curving shape of the stomach (G. D. Edgecombe, personal commun. to BSL, 2003) as Briggs (1978, 1992) predicted it would be (though this was indeterminate from the Burgess Shale material). The specimen preserves evidence of eight thoracic appendages; the precise number of abdominal segments is indeterminate. Based on the number of thoracic appendages preserved, this specimen is likely referable to *C. perfecta* (see Lieberman, 2003 for a synonymy) rather than to *C. laevigata* (Hou and Bergström, 1991) from the Chengjiang biota although the evidence for 19 body tergites in the latter was not illustrated by Hou and Bergström (1997). The species level assignment is uncertain, however, because of the incomplete preservation of the abdominal segments and telson.

Order WAPTIIIDA Størmer, 1942
 Family WAPTIIDAE Walcott, 1912
 Genus WAPTIA Walcott, 1912

Discussion.—Briggs (1983) suggested that *Waptia* was closely related to *Canadaspis* and a possible relative of the Branchiopoda. Hou and Bergström (1997) and Walossek and Müller (1998), by contrast, argued that the taxon was not a true crustacean. In a phylogenetic analysis performed by Wills et al. (1998) the genus mapped within a set of modern and fossil crustacean taxa and in a more derived position than modern branchiopods. Based on these phylogenetic results, we place the taxon within subphylum Crustacea, class uncertain. Hou and Bergström (1991) erected a new genus *Chuandianella* to accommodate *Mononotella ovata* Li, 1975 from the Lower Cambrian Chengjiang fauna. The discovery of the trunk and head appendages led them to compare the taxon



FIGURE 11—*Canadaspis* cf. *perfecta* (Walcott, 1912), KUMIP 314077 (part), Wheeler Formation, Drum Mountains, Millard County, Utah (see text for additional locality information). Left-lateral view of nearly complete specimen; scale bar equals 1 cm.

with *Waptia* (Hou and Bergström, 1997). On the basis of additional material Chen (2004) assigned the species to *Waptia*.

WAPTIA cf. FIELDENSIS Walcott, 1912
 Figure 12

Material examined/locality.—KUMIP 314044 (Fig. 12.1, 12.2), a part and partial counterpart of the posterior end of the abdomen preserved in oblique aspect; KUMIP 314038 (Fig. 12.3), an incomplete part and counterpart preserved in lateral aspect. Both specimens are from Cataract Canyon.

Description/discussion.—KUMIP 314044 (Fig. 12.1, 12.2) is incompletely preserved, showing part of the last two segments of the abdomen, and the telson and caudal furca. The caudal rami overlap but are clearly divided into three segments. The morphology of the specimen is consistent with its identification as *W. fieldensis* Walcott, 1912 (see Walcott, 1931; Størmer, 1944; Conway Morris et al., 1982). KUMIP 314038 (Fig. 12.3) is poorly preserved. It shows some superficial resemblance to *Canadaspis* but the proportions of the eyes, the body segments that extend beyond the carapace, and the carapace itself are more similar to *Waptia* than *Canadaspis*.

Order PROTOCARIDIDA Simonetta and Delle Cave, 1975
 Genus BRANCHIOCARIIS Briggs, 1976
 BRANCHIOCARIIS PRETIOSA? (Resser, 1929)
 Figure 13

Branchiocaris pretiosa (Resser). BRIGGS, 1976 (see for more extensive synonymy); BRIGGS AND ROBISON, 1984, p. 6, figs. 5–9; ROBISON, 1991, p. 97, fig. 7.8.

Material examined/localities.—KUMIP 204792–204797 from Sponge Gully. UU 06011.06 (Fig. 13.1–13.3), a well preserved specimen from Phyllocarid Flats. The taxon also occurs in the Wheeler Formation, Drum Mountains and questionably in the Spence Shale, Langston Formation and the Bloomington Formation in the Wellsville Mountains (see Robison and Richards, 1981; Briggs and Robison, 1984).

Description/discussion.—Specimen UU 06011.06 (Fig. 13.1–13.3) shows the bivalved carapace preserved in near parallel aspect, the valves folded beneath themselves. Structures projecting a short distance anteriorly from beneath the valves may represent appendages; the preservation does not reveal any details.

The trunk projects posteriorly beyond the carapace. It appears to be preserved in lateral aspect, with the appendages on the right side evident, indicating that the carapace and body have been rotated one relative to the other. About 14 somites are evident

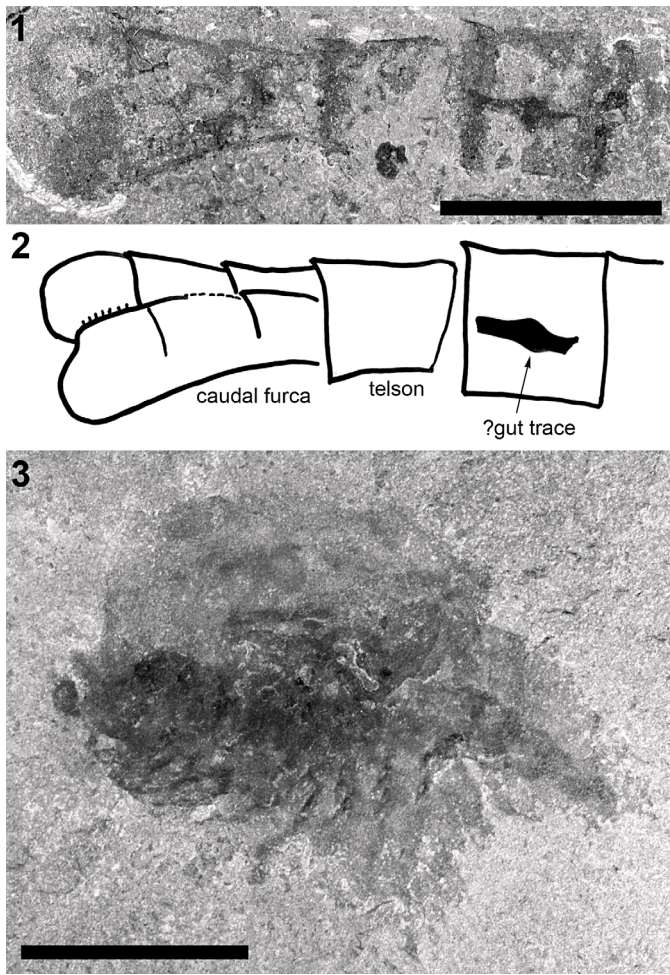


FIGURE 12—*Waptia* cf. *fieldensis*, Walcott, 1912, Spence Shale Member, Langston Formation, Cataract Canyon, Wellsville Mountains, Box Elder County, Utah. 1, KUMIP 314044 (part), oblique view of abdomen, telson, and caudal furca of incomplete specimen; scale bar equals 1 cm. 2, camera lucida drawing of KUMIP 314044. 3, KUMIP 314038 (part), left-lateral view of anterior of incomplete specimen; scale bar equals 1 cm.

beyond the carapace, and extrapolation anteriorly indicates that there were more than 40 in total. The trunk terminates in a rounded telson with a ventral process. The telson differs from that in *B. pretiosa* from the Burgess Shale (Briggs, 1976) in the presence of posterodorsal spines on the telson itself and a series of posteriorly directed spines on the dorsal surface of the telson process. These features suggest this Utah specimen may represent a new species, but given the lack of other differences, here we assign it to *B. pretiosa*? pending the discovery of additional specimens revealing more of the morphology. The specimen is 77 mm long.

The genus has also been reported from the Lower Cambrian of China as *Branchiocaris? yunnanensis* Hou, 1987 but only the valves are known (see Hou et al., 2004).

Subphylum UNCERTAIN
Class UNCERTAIN
Genus ISOXYS Walcott, 1890

Discussion.—*Isoxys* was considered comprehensively by Williams et al. (1996) and Vannier and Chen (2000) but its phylogenetic position remains uncertain.

ISOXYS sp.
Figure 14

Material examined/locality.—KUMIP 312404 (Fig. 14.1, 14.2), complete left valve from Miners Hollow.

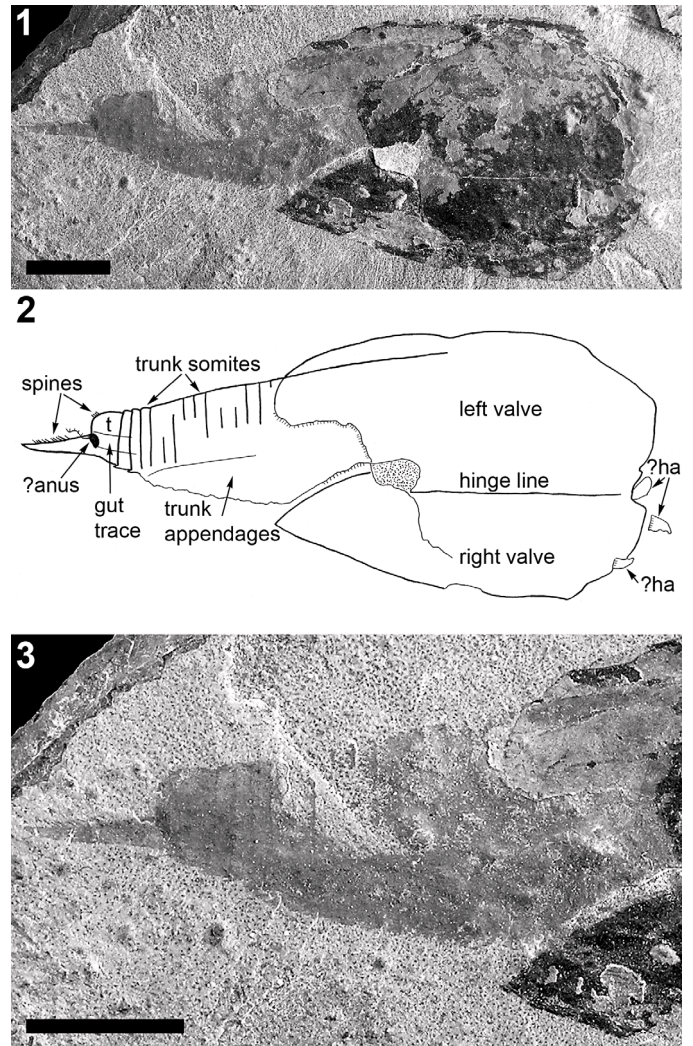


FIGURE 13—*Branchiocaris pretiosa*? (Resser, 1929), UU 06011.06, Wheeler Formation, site F4, Drum Mountains, Millard County, Utah. 1, near parallel view of complete specimen; scale bar equals 1 cm. 2, camera lucida drawing. Abbreviations: a, anus; ha, head appendage; and t, telson. 3, detail of abdomen; scale bar equals 1 cm.

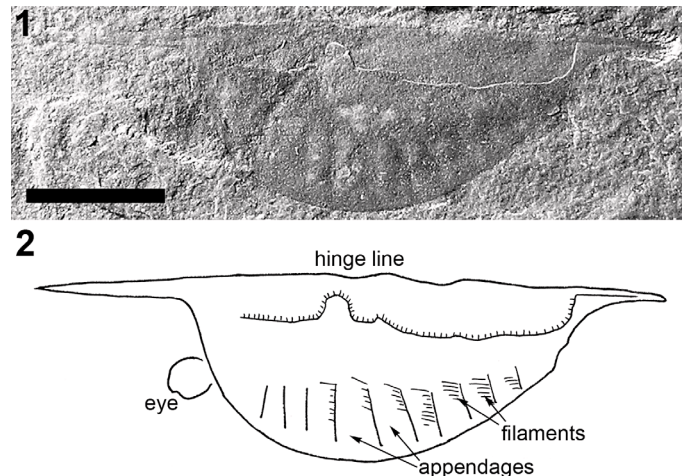


FIGURE 14—*Isoxys* sp. Walcott, 1890, KUMIP 312404, Spence Shale Member, Langston Formation, Miners Hollow, Wellsville Mountains, Box Elder County, Utah; scale bar equals 5 mm.

Description/discussion.—The example investigated preserves the eye, thus removing any uncertainty about the orientation of the valve. The anterior spine is longer than the posterior, and the anterior margin of the valve makes a higher angle with the hinge line than does the posterior. The large eye projects beyond the margin of the valve; it is stalked and roughly spherical. Nine raised lozenge shaped structures in the ventral half of the specimen reveal evidence of transverse filaments when the contrast is enhanced under water. These are inferred to represent the homonomous series of limbs with large exopodites described in *Isoxys auritus* (Shu et al., 1995; Vannier and Chen, 2000).

The outline of the carapace valve most closely resembles that of *I. communis* Glaessner, 1979 from the Early Cambrian Emu Bay Shale, South Australia, although the anterior spine is relatively longer in *Isoxys* sp. from the Spence Shale described here (the orientation of *I. communis* is uncertain: Williams et al., 1996, fig. 7). The specimen from the Spence also resembles *I. acutangulus* (Walcott, 1908) from the Burgess Shale in the overall outline of the valve, though the anterior cardinal spine is relatively longer. The taxonomy of specimens of *Isoxys* is difficult to determine on the basis of valve shape as the outline varies with orientation to bedding and the true spine length may not be preserved (Williams et al., 1996, p. 953).

The soft parts are similar to those described in *I. auritus* Jiang in Luo et al., 1982 by Vannier and Chen (2000), including the position of the eye and the exopodite setae. There is evidence of only nine pairs of limbs whereas Vannier and Chen (2000) identified more than fourteen in *I. curvirostratus*, but it is likely that they are incompletely preserved in the Spence Shale specimen.

ACKNOWLEDGMENTS

The KUMIP specimens were collected by the Gunther family and also Phil Reese, Barry Richards, Carl Walker, and Arvid Aase, who generously donated them to KU for study. Dick Robison kindly allowed us to study these specimens. The UU specimens were collected and donated to UU by SLH and RDJ. This project is funded by NSF EAR-0518547 to BSL, DEGB, M. L. Droser, and R. R. Gaines. Part of this research was conducted while BSL was on sabbatical leave at the Peabody Museum of Natural History and the Department of Geology and Geophysics of Yale University. He acknowledges funding from the Division of Invertebrate Paleontology, Peabody Museum of Natural History, from the ECOSAVE Center of the Yale Institute for Biospheric Studies, and also from a Self Faculty Award, NSF EAR-0518976, and NASA Astrobiology NNG04GM41G. Doug Erwin and Jann Thomson facilitated access to the Walcott Collection at the National Museum of Natural History, Washington D.C. Jean-Bernard Caron and Diego Garcia-Bellido drew our attention to the new specimen of *Leaenchoilia protogonia* and J.-B.C. kindly arranged a loan of that specimen from the Royal Ontario Museum. We are grateful to them and to Des Collins and Greg Edgecombe for scientific discussions. Comments on the manuscript were provided by Greg Edgecombe and Bob Gaines.

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ACCEPTED 4 APRIL 2007