Paleontological Contributions

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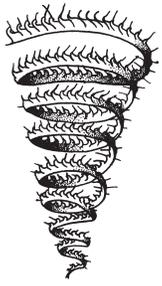
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DEDICATION

To Lloyd, Metta, and Val Gunther, extraordinary fossil collectors, for exceptional contributions to paleontology. They received the Paleontological Society's first Strimple Award in 1984 for outstanding achievement in paleontology by amateurs. Several fossils described here are products of their continued commitment to advancing knowledge of Earth's ancient life. We mourn the passing of Metta Gunther as we celebrate the life of Lloyd Gunther, who at age 94 continues to donate fossils for use in science and education.

Paleontological Contributions

SYSTEMATICS, PALEOBIOLOGY, AND TAPHONOMY OF SOME EXCEPTIONALLY PRESERVED TRILOBITES FROM CAMBRIAN LAGERSTÄTTEN OF UTAH

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ABSTRACT

Mid-Cambrian biotas of the Spence, Wheeler, Marjum, and Weeks formations in Utah are exceptionally diverse. Continued collecting has produced additional trilobites here assigned to one new genus, *Meniscopsia,* and 25 new species. The new species, all known from complete or nearly complete dorsal exoskeletons, are *Amecephalus jamisoni, Athabaskia gladei, Bolaspidella jarrardi, Bolaspidella reesae, Burlingia halgedahlae, Coosella kieri, Ehmaniella whitei, Glossopleura campbelli, Glossopleura yatesi, Ithycephalus stricklandi, Kootenia randolphi, Kootenia youngorum, Meniscopsia beebei, Menomonia sahratiani, Modocia comforti, Modocia kohli, Modocia whiteleyi, Norwoodia boninoi, Olenoides skabelundi, Olenoides vali, Polypleuraspis cooperi, Ptychoparella lloydi, Ptychoparella mettae, Zacanthoides liddelli,* and *Zacanthoides marshalli.* Descriptions of two other species, *Triadaspis bigeneris* and *Zacanthoides typicalis,* are expanded to include new information from complete dorsal exoskeletons. The ventral cephalic presence of a functional rostral-hypostomal suture in the corynexochoid *Zacanthoides marshalli* further demonstrates that a fused rostral-hypostomal plate is not a unique defining character of the order Corynexochida, adding to evidence that the Corynexochida may be a polyphyletic taxon. The ventral cephalic presence of a median suture, associated with a rostellum in *Norwoodia boninoi,* order Ptychopariida, is further evidence for a polyphyletic origin of the median suture, previously cited as a unique apomorphic character defining the order Asaphida, which needs revision. The presence of a mineralized alimentary tract and digestive glands in some specimens of *Meniscopsia beebei* and *Coosella kieri* suggests that the gut was fluid filled at the time of burial and that the species were predaceous. Collapsed glabellas are interpreted as further evidence of fluid-filled gut tracts in some of the new species. Many of the articulated trilobites preserved in mid-Cambrian Lagerstätten of Utah were probably buried under rapidly deposited sediment clouds on a storm-prone marine shelf. Occasionally, trilobite clusters were buried. Encrustation of fully articulated individuals with calcitic cone-in-cone deposits in the Wheeler and Marjum formations is a likely consequence of concretionary-type growth within a biofilm shortly after death.

Keywords: Agnostida, Asaphida, Corynexochida, Ptychopariida, taxonomy, biofilm

INTRODUCTION

Diverse biotas occur in Konservat-Lagerstätten deposits of the Spence, Wheeler, Marjum, and Weeks formations in Utah (Robison, 1991a). These deposits previously have been assigned a Middle Cambrian age (Lincolnian Series, Delamaran to Marjuman stages of Laurentian regional usage; see review by Babcock, Robison, and Peng, 2011). Work toward a uniform global chronostratigraphic scale by the International Subcommission on Cambrian Stratigraphy (Peng and others, 2004; Babcock and others, 2005; Peng and Babcock, 2008; Babcock, Robison, and Peng, 2011) is resulting in new terminology and definitions. In the new global chronostratigraphic scheme, ages of these Utah formations all fall within provisional Series/Epoch 3 (Fig. 1). Continued collecting from these formations has produced numerous trilobites representing incompletely known or new taxa described here (Figs. 2–30).

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Global chronostratigraphic units			Agnostoid biostratigraphy Open-shelf Laurentia	Polymerid trilobite biostratigraphy Open shelf	Restricted shelf	Some lithostratigraphic units in Utah	
Cambrian System	Series 3 (provisional)	Guzhangian Stage	*Proagnostus bulbus* Zone	*Cedaria* Zone		Lower Orr Formation	
						Weeks Formation	Trippe and Lamb formations
			Lejopyge laevigata Zone	*Bolaspidella* Zone	*Eldoradia* Zone		
		Drumian Stage	*Ptychagnostus punctuosus* Zone			**Marjum Formation**	Pierson Cove Formation
			Ptychagnostus atavus Zone			**Wheeler Formation**	Eye of Needle Formation
		Stage 5 (provisional)	*Ptychagnostus gibbus* Zone	*Oryctocephalus* Zone	*Ehmaniella* Zone	Swasey, Whirlwind, and Dome formations	
			Ptychagnostus praecurrens Zone		*Glossopleura* Zone	**Spence Shale**	Chisholm Formation
					Albertella Zone		Howell and Pioche formations
					Plagiura-Poliella Zone		

Figure 1. Relationships of stratigraphic units mentioned in this paper. For lithologic content, geographic relationships, and thickness of each formation, refer to Hintze (1988) and Hintze and Davis (2003).

Because of significant differences in ecologic and geographic distributions, separate zonal schemes have commonly been used for the polymerid and agnostoid trilobites of Laurentia (e.g., Robison, 1976; Babcock, Robison, and Peng, 2011). At times during Cambrian Epoch 3, separate biofacies with varying degrees of faunal exchange existed around the Laurentian paleocontinent (e.g., Robison, 1976; Pratt, 1992; Ludvigsen and Westrop, 1993; Babcock, 1994; Sundberg and McCollum, 2000; Babcock, Robison, and Peng, 2011). Lithofacies patterns show variable development of carbonate platform deposits, flanked landward by lagoonal muds and nearshore sands, and flanked further seaward by outer-shelf muds. The inner-shelf biofacies was likely influenced by restricted currents and tended to have sparse, low-diversity trilobite faunas dominated by endemic polymerids. Outer, open-shelf agnostoid and polymerid biofacies had greater access to the open ocean and its currents. Apart from notable oryctocephalids, most mid-Cambrian polymerid genera of the open shelf were endemic to single paleocontinents, and species commonly have only regional biostratigraphic utility. In contrast, many agnostoid species were cosmopolitan in open-marine environments, and their evolution was relatively rapid, which makes them excellent global biostratigraphic guides. Most agnostoid zones recognized in the Cambrian of Utah (Fig. 1) are also recognized intercontinentally (Geyer and Shergold, 2000; Peng and Robison, 2000; Peng and Babcock, 2008; Terfelt and others, 2008; Babcock, Robison, and Peng, 2011).

Recent efforts to produce a high-resolution trilobite zonation of Cambrian Series 2 and lower Series 3 in the southern Great Basin, especially in southern Nevada, has resulted in new zonal nomenclature (e.g., Sundberg and McCollum, 2000, 2003; Hollingsworth, 2011; Hollingsworth, Sundberg, and Foster, 2011; McCollum and McCollum, 2011; Sundberg, 2011; Webster, 2011). However, that nomenclature is not used here because the eponymous and most other guide species have yet to be reported from coeval strata in Utah.

Polymerid trilobites in the Spence Shale of northern Utah include a mixture of taxa occurring elsewhere either in the open-shelf *Oryctocephalus* Zone or the restricted-shelf *Glossopleura* Zone (e.g., Robison, 1976; Fig. 1). Polymerid trilobites from the Wheeler, Marjum, and Weeks formations in western Utah represent the open-shelf *Bolaspidella* and *Cedaria* zones (Fig. 1). All four formations accumulated in open-marine ramp and basin environments on the seaward side of broad, shallow-water carbonate platforms. Liddell, Wright, and Brett (1997) most recently reviewed the stratigraphy and depositional environments of the Spence Shale in northern Utah and southern Idaho. Hintze and Robison (1975) reviewed regional stratigraphic

relationships of the younger Wheeler, Marjum, and Weeks formations in western Utah. Brady and Koepnik (1979), Rees (1986), Beebe (1990), Elrick and Snider (2002), Gaines and Droser (2003, 2005), Babcock and others (2004, 2007), Howley, Rees, and Jiang (2006), Elrick and Hinnov (2007), Brett and others (2009), Halgedahl and others (2009), and Howley and Jiang (2010) have provided more detailed information about the stratigraphy and depositional environments of the three younger formations. Babcock, Robison, and Peng (2011) reviewed stratigraphic relationships in the Great Basin and elsewhere across the Laurentian paleocontinent, including historical changes in age interpretation. Other associated formations (Fig. 1) include sediment mostly deposited on shallow carbonate platforms or in inner-shelf, siliciclastic-dominated sedimentary environments, probably with more restricted water flow and more variable salinity.

In the southeastern Drum Mountains, the boundary between the Wheeler Formation and overlying Pierson Cove Formation has usually been placed at one of two horizons. An intervening, shale-bearing, lithologic unit thins toward the northwest from a maximum thickness of about 35 m, and its outcrop extends about 7 km. The unit is significant because it contains an exceptionally preserved biota in a Konservat-Lagerstätte that includes some of the new trilobites described here. As mapped by Dommer (1980) and followed by some (e.g., Gunther and Gunther, 1981; Hintze and Oviatt, 1993; Brett and others, 2009; Halgedahl and others, 2009), the Wheeler–Pierson Cove boundary was placed at the lower horizon. Because lithologic characters of the intervening unit are most similar to those of the Wheeler Formation in the House Range, Vorwald (1983) and others (e.g., Rees, 1986; Robison, 1991a) placed the Wheeler–Pierson Cove boundary at the higher horizon. Within the unit, Vorwald (1983) statistically distinguished four trilobite assemblages: one in a lower platy limestone and shale tongue that is dominated by *Elrathia kingii* (Meek, 1870); one in an upper platy limestone and shale tongue that is dominated by *Asaphiscus wheeleri* Meek, 1873; and associated beds of mottled and bioclastic limestone that contain mixed and transported trilobite assemblages. At least one publication (Bonino and Kier, 2009) and photo captions on several Internet sites assign trilobites from the intervening unit to the Marjum Formation, a stratigraphic name otherwise restricted to the House Range (Hintze and Davis, 2003). Here, we continue assignment of the unit and its biota to the upper Wheeler Formation, which best conforms to rules of the North American Stratigraphic Code (North American Commission on Stratigraphic Nomenclature, 2005) and recommendations of the International Stratigraphic Guide (Salvador, 1994). Its trilobite faunas are representative of the polymerid lower *Bolaspidella* Zone and the agnostoid *Ptychagnostus atavus* Zone.

Morphologic features of some illustrated trilobites were exposed by advanced preparation techniques described and illustrated by David Comfort ("Fossil preparation techniques," in Bonino and Kier, 2010, p. 452–459). If necessary, a broken part was mended using cyanoacrylate, available commercially as Crazy Glue. Most matrices were then removed using a variety of pneumatic air scribes. Finally, remnant matrices were removed with extremely fine abrasive powder propelled through a tiny nozzle by compressed air. Total preparation time for a single specimen can vary from a few minutes to more than a hundred hours.

All illustrations in this paper are new.

PALEOBIOLOGY AND TAPHONOMY

New trilobite specimens from Konservat-Lagerstätten deposits of the Spence, Wheeler, Marjum, and Weeks formations of Utah offer new or additional paleobiologic and taphonomic information, including some concerning morphologic details and circumstances of exceptional preservation. In this section, we address some general paleobiologic and taphonomic matters pertaining to the trilobites from the Utah Lagerstätten. Other comments are included in discussions of individual species.

Spines

Spinosity ranging from minor to extreme is expressed in 12 polymerid species illustrated here, as well as in the agnostoid *Triadaspis bigeneris* Öpik, 1967. The new species *Kootenia randolphi* (see Fig. 8), *K. youngorum* (Fig. 9), *Olenoides vali* (Fig. 11), *Zacanthoides liddelli* (Fig. 12), and *Z. marshalli* (Fig. 13) all show arrays of large axial spines and marginal spines. In addition, two previously described species of *Zacanthoides* Walcott, 1888, *Z. grabaui* Pack, 1906 (Fig. 2) and *Z. typicalis* (Walcott, 1886) (Fig. 14), show large axial and marginal spines. The new species *Glossopleura yatesi* (Fig. 6), *Amecephalus jamisoni* (Fig. 15), and *Norwoodia boninoi* (Figs. 27, 28.1) show large axial spines and genal spines, but other marginal spines are restricted to falcate tips on the thoracic pleurae. Smaller axial spines are evident in the new species *Ehmaniella whitei* (Fig. 16), and *Ptychoparella lloydi* (Fig. 19).

Although spines in polymerid trilobites are inferred to have had varied functions, the size, arrangement, and location on these forms imply that they functioned in part for resisting durophagous predators (see Babcock, 2003). Most of the vital organs of the nervous, circulatory, and alimentary systems were housed under the axis of the trilobite (e.g., Harrington, 1959a; Cisne, 1975, 1981; Stürmer and Bergström, 1973; Babcock and Robison, 1989; Babcock, 1993, 2003; Levi-Setti, 1993; Whittington, 1997a; Whiteley, Kloc, and Brett, 2002), and spines situated in that region would have provided some deterrence of larger durophagous predators. Thickened exoskeleton associated with the spine bases may have added structural rigidity to exoskeleton housing the axial organs. Moreover, in the case of predaceous attack, axial spines may have played another role, by deflecting the point of wounding away from vital organs. If a trilobite were to successfully escape attack, breakage of a projecting spine would have been preferable to incision through an axial ring and damage to underlying organs.

Apart from mechanical, sensory, and perhaps other functions, marginal spines probably served, in part, to deter predators from attacking the vulnerable margins of the polymerid trilobite body. The tendency for marginal spines to be most highly developed on the pygidium and mid- to posterior thorax (Figs. 2, 8–14) is consistent with observations that those areas were subject to greater rates of sublethal attack than other areas of the trilobite body (Babcock and Robison, 1989; Babcock, 1993, 2003). Attacks on marginal areas evidently yielded lower mortality rates than attacks on the axial region, and breakage of marginal spines by predators, as opposed to damage to the axial region, would have been more readily survivable for the trilobite prey.

Three specimens show healed injuries on marginal areas and help to demonstrate the relative survivability of injuries to the margin

Figure 2. *Zacanthoides grabaui* Pack, 1906, with an indentation on the anterior glabella above the underlying, slightly displaced hypostome, indicating the likely presence of either a functional hypostomal suture or a natant hypostomal condition. Ends of the left pleurae of thoracic segments 7 and 8 show evidence of a healed injury. The specimen, 40 mm long excluding spines, is from 47 m above the base of the Spence Shale in Miners Hollow, Wellsville Mountain (photo courtesy of David Comfort).

of the exoskeleton. In a specimen of *Zacanthoides grabaui* (Fig. 2), the distal areas of two spines on the left posterior thorax have been broken and healed. Breakage of multiple spines in this manner has been considered evidence of sublethal predaceous attack (Conway Morris and Jenkins, 1985; Babcock and Robison, 1989; Babcock, 1993). An individual of *Ithycephalus stricklandi* (Fig. 17.2) shows an asymmetrical, healed, V-shaped injury to the left librigena. As this injury is extensive, and on an area unlikely to have been accidently broken, it, too, is interpreted as the result of sublethal attack. The holotype of *Olenoides vali* (Fig. 11.1) shows a large, asymmetrical, W-shaped injury to the right genal area and conterminant margin of the anterior thorax, loss of the genal spine, and distinct evidence of wound healing, including growth of a small anomalous spine at the anterolateral margin of the cephalon.

The agnostoid *T. bigeneris* is of small size, and, because of this, it seems unlikely that marginal spines played much role in predator deterrence. Other sensory and swimming- or buoyancy-related functions are possibilities. Few healed injuries or other damage is known in agnostoids (Jago, 1974; Babcock, 1993, 2003), and healed spinal

injuries are virtually unknown. The reasons for this are speculative and untested. Major differences in size and ecology between agnostoids and most polymerids render direct comparisons uncertain.

The new polymerid species described here add substantially to the record of mid-Cambrian (Epoch 3) trilobites known to be spinose. In addition, three new examples of inferred sublethal predation scars are illustrated (Figs. 2, 11.1, 17.2). Together, these lines of evidence provide support for the hypothesis that ecologic escalation was already underway in predator-prey systems as early as the Cambrian Period (Vermeij, 1995; Babcock, 2003), and they provide further evidence that escalation between durophagous predators and their trilobite prey began early in the evolutionary history of trilobites.

Macrocephaly

Two new species, *Modocia kohli* (Fig. 22) and *Norwoodia boninoi* (Figs. 27, 28.1), show large cephala with unusually elongate, stout genal spines, and comparatively small thoracopyga. Here, we use the term macrocephaly to denote a species-level characteristic, and we do not use it in the medical sense of a malformation confined to an individual. In *N. boninoi*, enlargement of the cephalic region compared to the thoracopygon is extreme, whereas in *M. kohli*, enlargement is less pronounced but obvious in comparison to related species of *Modocia* (Figs. 21, 23).

In both *Modocia kohli* and *Norwoodia boninoi*, which are inferred to have been nektobenthic, the general exoskeletal morphology invites comparison with xiphosuran arachnomorphs. As in extant *Limulus* (Eldredge, 1970; Vosatka, 1970), the large head shield, with broad genal areas and spines, may have promoted rapid digging into sediment for concealment, aided in search for prey, or aided in righting behavior. In *N. boninoi*, the large medial spines extending from the occipital ring and the fourth thoracic segment also may have helped right an animal that was overturned.

Internal Anatomy, Exuviation, and Early Taphonomic History

Internal anatomy of trilobites is rarely preserved. A specimen of *Coosella kieri* n. sp. (Fig. 18.5) and two specimens of *Meniscopsia beebei* n. gen., n. sp. (Figs. 29.2–29.3) show a dark central feature that we interpret to be an early diagenetic filling of the alimentary tract and paired laterally projecting digestive glands (foregut and midgut glands), with one pair per segment, as in some modern chelicerate arthropods (see Butterfield, 2002; Babcock, 2003). Two specimens (Figs. 18.5, 29.3) show what appears to be an outline of the stomach within the cephalon. In both specimens, the organs are preserved by a mineral different from that of the exoskeleton and matrix, and both are mud-free and sclerite-free. The hypostome is partly exposed in both specimens, and in each specimen, the calcitic plate appears to be preserved beneath the secondarily mineral-lined stomach cavity. Although not analyzed chemically, the black color and vitreous luster of the alimentary fill is consistent with preservation by means of calcium phosphate (apatite).

Mineralized alimentary tracts in *Meniscopsia beebei* suggest that they were fluid filled at the time of burial. If this interpretation is correct, we infer that these trilobites were predaceous, perhaps feeding in a manner similar to living chelicerates (see Butterfield, 2002; Babcock, 2003; English and Babcock, 2007). Lack of sediment in the alimentary tract rules out sediment-deposit-feeding as

a food-gathering mode, and sediment was not introduced into the tract after death.

Exoskeletal and alimentary tract preservations help to constrain the decay interval of the *Coosella kieri* and *Meniscopsia beebei* specimens showing internal anatomy. Outstretched posture implies that exoskeletons settled to the seafloor or were reoriented by currents following the time of muscle relaxation and prior to the time when sclerites disarticulated through decay along the arthrodial membranes. Experimental work on modern *Limulus polyphemus* (Linnaeus, 1758) by Babcock and Chang (1997) and Babcock, Merriam, and West (2000) suggests that this interval begins a few hours after death and lasts three or four weeks.

Early diagenetic mineralization of axial structures is inferred to have begun quickly after death, probably as a result of the precipitation of a mineral coating over nonbiomineralized tissues, mediated by the activity of autolithifying microbes (compare Briggs and Kear, 1993a, 1993b, 1994; Borkow and Babcock, 2003; Babcock and Peel, 2007; English and Babcock, 2007). Similar to most specimens of *Buenellus higginsi* Blaker, 1988, from North Greenland showing preserved alimentary tracts (Babcock and Peel, 2007), the guts of *Coosella kieri* and *Meniscopsia beebei* specimens must have been coated by secondary minerals before significant disarticulation of the appendages occurred. Babcock and Chang (1997) and Babcock, Merriam, and West (2000) observed in *Limulus* that the internal soft parts decay within 7 days in aerobic marine water. After about 7 days, the book gills begin detaching, and appendages begin detaching after about 10 days. Using this information as a guide, we conclude that precipitation of a mineral coating leading to preservation of the internal soft parts in these fossil taxa probably began within about a week of death.

Indirect evidence that the stomach cavities of some illustrated trilobites were fluid filled at the time of burial, rather than filled with sediment or any other solid matter, including skeletal parts, is provided by crushed or collapsed glabellas. Collapse of exoskeleton along the axial lobe may have occurred in some molts, but it seems more likely to have occurred preferentially in specimens having differential sediment infill to the ventral side of an exoskeleton. In most cases, this implies that a specimen lacked the ventral integument at burial. This condition would have been more common in corpses than in molts. In molts, the area under the glabella is likely to have become sediment filled, similar to other areas on the ventral side of the exoskeleton. Crushing of the glabellar area is also evidence that the stomach cavities of some specimens were not significantly strengthened by secondary mineral fill early in the postmortem history of the fossils (compare Babcock, 2003; Babcock and Peel, 2007; English and Babcock, 2007).

Crushed glabellas are illustrated on specimens of *Athabaskia gladei* (Figs. 4.1–4.1), *Glossopleura campbelli* (Figs. 5.1–5.2), *Kootenia randolphi* (Figs. 8.1–8.2), *K. youngorum* (Figs. 9.1–9.4), *Olenoides vali* (Fig. 11.1), *Zacanthoides liddelli* (Figs. 12.1, 12.3), *Z. marshalli* (Fig. 13.1), *Coosella kieri* (Figs. 18.3–18.4), *Modocia comforti* (Figs. 21.1–21.2), *M. whiteleyi* (Figs. 23.2–23.4), and *Norwoodia boninoi* (Fig. 27.2). Crushed glabellas on outstretched, articulated trilobites have been illustrated previously, without comment, in a number of lower Paleozoic trilobites. In a richly pictorial volume on trilobites (Levi-Setti, 1993), crushed glabellas similar to those illustrated here are evident on complete exoskeletons of Cambrian forms identified as

Asaphiscus, *Eccaparadoxides*, *Elrathia*, *Hemirhodon*, *Modocia*, *Olenellus*, *Olenoides*, and *Paradoxides*, and in Ordovician forms identified as *Dikelocephalina*, *Ogyginus*, and *Pseudogygites.* In another extensively pictorial volume (Whiteley, Kloc, and Brett, 2002), crushed glabellas are present on complete exoskeletons of Ordovician forms identified as *Achatella*, *Calyptaulax*, and *Ceraurus.*

If the stomachs of these trilobites were fluid filled at burial and later crushed under the weight of overlying sediment layers, these specimens can be inferred to have been corpses rather than molts. Reinforcing this interpretation is the observation that none of the specimens with crushed glabellas, neither the ones illustrated here nor those illustrated by Levi-Setti (1993) and Whiteley, Kloc, and Brett (2002), has detached librigenae. Although trilobites evidently had various exuviation strategies (Henningsmoen, 1975; McNamara and Rudkin, 1984; Speyer, 1985; Speyer and Brett, 1985; McNamara, 1986; Whittington, 1997b; Whiteley, Kloc, and Brett, 2002), many Cambrian and Ordovician species lost their librigenae during molting (e.g., McNamara and Rudkin, 1984; McNamara, 1986; Speyer, 1990b; Brandt, 1993; Karim and Westrop, 2002; Gaines and Droser, 2003; Gutiérrez-Marco and others, 2009). Specimens of *Ptychoparella mettae* (Figs. 20.1–20.3) show variation in the appearance of molts, but exuviation in this species appears to involve rupture at the facial sutures, followed by displacement or loss of the librigenae, and possible displacement of the cranidium. Also reinforcing the interpretation that crushed glabellas are predominantly preserved in carcasses rather than molts is the observation that specimens showing this taphonomic condition commonly show hypostomes in place or nearly so (Webster and Hughes, 1999; Webster, Gaines, and Hughes, 2008) when slabs are prepared or advantageously split.

Trilobite Clusters and Event Deposition

Two slabs containing multiple trilobite exoskeletons, one from the Spence Shale (Fig. 12.3) and the other from the Weeks Formation (Fig. 28.1), show size-sorted and bidirectionally arranged fossils, suggesting sediment smothering under storm or similar conditions. Trilobites on the Weeks slab (Fig. 28.1) are mostly complete, fully outstretched exoskeletons and, with about four exceptions, all are oriented dorsal up, as prepared. The original stratigraphic-up direction is not known. *Norwoodia boninoi* specimens on the slab are preserved in various enrolled states, ranging from tucking of the pygidium ventrally to full, loose enrollment of the thoracopygon. The Spence slab (Fig. 12.3) shows five specimens of *Zacanthoides liddelli* that are outstretched, loosely enrolled, or partly disarticulated. Collection and deposition of exoskeletons in currents presumably followed periods of decay ranging from post-exuviation or post-*rigor mortis* (hours after death) to pre-exoskeletal disarticulation (probably less than four weeks after death, as suggested by experiments on comparative modern marine arthropods; Briggs and Kear, 1994; Babcock and Chang, 1997; Babcock, Merriam, and West, 2000; Deng, Hua, and Hui, 2010). The less common disarticulated specimens probably had experienced periods of decay and disarticulation exceeding one month.

Robison (1991a), Liddell, Wright, and Brett (1997), and Brett and others (2009) provided sedimentologic and biostratinomic evidence of episodic storm burial (sediment smothering) of assemblages along certain bedding planes in the Spence and Wheeler formations. Although exceptionally preserved remains in the Weeks Formation

were not included in those studies, the same lines of evidence (e.g., articulated, mostly convex in the same direction, bidirectionally arranged, trilobite exoskeletons; Figs. 28.1–28.2) can be used to infer rapid, episodic burial of trilobite clusters at the bases of tempestite sequences. The buried specimens must have been molts, corpses, or weakened living animals at the time of burial, as otherwise the trilobites would have been capable of burrowing through thin deposits of overlying sediment and escaping burial. Other examples of clustered trilobites have been reported from the Paleozoic, many of which have been attributed to episodic burial beneath storm-generated clouds of suspended sediment (Speyer and Brett, 1985; Brett, Speyer, and Baird, 1986; Speyer, 1990a; Karim and Westrop, 2002; Hunda, Hughes, and Flessa, 2006; Webster, Gaines, and Hughes, 2008).

The trilobite cluster on the slab from the Spence Shale is monospecific (*Zacanthoides liddelli*; Fig. 12.3). Of the five specimens, one is outstretched, two are loosely enrolled, one is a molt assemblage, and another is a separated cephalon with the librigenae attached. Speyer and Brett (1985), Speyer (1990a), and Karim and Westrop (2003) discussed some monospecific molt clusters of trilobites as so-called snapshots illustrating aspects of gregarious behavior among conspecifics, in particular simultaneous, precopulatory ecdysis. Specimens of *Z. liddelli* on the Spence Shale slab are consistent with this interpretation. Notably, one specimen (Fig. 12.3, upper) appears to be a molt assemblage, and a pair of librigenae is exposed on the slab just behind the group of sclerites. If the librigenae belong to this individual, sediment smothering of this cluster must have occurred with little, if any, associated current transportation. Minor current reorientation is suggested by the bidirectional alignment of remains on the slab (Fig. 12.4). One specimen on the slab (Fig. 12.3, lower left) has a crushed glabella and, as discussed above, may represent a corpse. Loose enrollment of two specimens on the slab could have been caused by flexure of post-*rigor mortis* exoskeletons in the presence of currents or may represent an exuviation posture (compare Speyer and Brett, 1985; Speyer, 1990a, 1990b).

The cluster of trilobites on the slab from the Weeks Formation is polyspecific (Fig. 28.1) but overwhelmingly dominated by one species, *Norwoodia boninoi*. More than 35 dorsal exoskeletons are completely articulated and outstretched; about four are overturned; and at least two are separated cephala. All of the *N. boninoi* specimens appear to be holaspids; at least 27 are greater than 10 mm in length, and 8 are less than 10 mm in length. The next most common species on the slab is *Menomonia sahratiani*, which is represented by 7 large holaspids (greater than 10 mm) and 9 smaller specimens, all of which are articulated and outstretched. An articulated, outstretched holaspid of *Coosella kieri* (15 mm in length) and some articulated outstretched agnostoids are also present. The outstretching of these specimens is inferred to have followed *rigor mortis* as soft tissues and membranes relaxed. A predominant bidirectional orientation of exoskeletons (Fig. 28.2) suggests some current orientation of remains during transport to the burial site. The relatively large aggregation of conspecifics, especially of *N. boninoi* and *M. sahratiani*, suggests gregarious, possibly precopulatory, behavior in these species, and final association of the exoskeletons by weak currents.

Calcite Encrustation

The upper Wheeler Formation of the House Range is famous for its abundance of articulated exoskeletons of *Elrathia kingii* (Meek, 1870), *Asaphiscus wheeleri* Meek, 1873, and *Bolaspidella housensis* (Walcott, 1886), commonly having encrustations of cone-in-cone calcite, usually on the ventral surface, allowing them to be easily separated from calcareous shale matrix (Bright, 1959; Robison, 1964; Levi-Setti, 1975, 1993; Hintze and Robison, 1987; Gaines and Droser, 2003). Lesser numbers of other similarly preserved Wheeler trilobites have been described (Robison, 1971), and similarly preserved specimens of new species are described here, the latter being *Ehmaniella whitei* (Fig. 16), *Modocia kohli* (Fig. 22), and *Ptychoparella lloydi* (Fig. 19.1) from the Wheeler Formation, and *Bolaspidella jarrardi* (Figs. 24.1, 24.3–24.4) from the lower Marjum Formation. All of these skeletal encrustations are interpreted to have resulted from very early, microbially mediated precipitation of calcium carbonate in a biofilm halo (compare Borkow and Babcock, 2003; Deng, Hua, and Hui, 2010) around both decaying trilobite tissues and exoskeletal parts.

Malformations

Five illustrated specimens show malformations of the exoskeleton. Three are healed injuries inferred to be predation scars because they are extensive and have shapes and locations more consistent with predaceous attack than accidental injury (compare Conway Morris and Jenkins, 1985; Owen, 1985; Babcock and Robison, 1989; Babcock, 1993, 2003). In the illustrated *Zacanthoides grabaui* (Fig. 2), the distal ends of two marginal spines on the left side of the thorax have been removed and healed. A large, V-shaped, healed injury is present on the left genal area of a specimen of *Ithycephalus stricklandi* (Fig. 17.2). A large, asymmetrical W-shaped healed injury, associated with a deformed margin and an anomalous spine, are present on the right genal area and anterior thorax of a specimen of *Olenoides vali* (Fig. 11.1).

The left genal spine of a paratype of *Olenoides vali* (Figs. 11.3–11.4) is abnormally elongate and slightly enlarged compared to the right genal spine, and it is misshaped, appearing slightly twisted. The left genal spine reaches to the seventh thoracic segment, whereas the right genal spine reaches to the sixth thoracic segment. Unilateral damage to the genal spine suggests a teratologic (due to a genetic abnormality) condition or, more likely, an injury. Marginal spines are one of the areas of the trilobite body most likely to have been damaged during withdrawal from the exoskeleton during molting (Owen, 1985; Babcock and Robison, 1989; Babcock, 1993). If this is the case, irregularity of the spine would have resulted from wound healing during the soft shell stage, with enlargement of the damaged area being attributable to compensatory hypertrophy (Babcock, 1993).

Some posterior thoracic segments in the largest observed specimen of *Menomonia sahratiani* (Fig. 26.5) are malformed. At two places along the axis, small incomplete axial rings have been inserted, and their presence has caused distortion of the axis, including lateral expansion of the axial outline. It is uncertain whether these malformations are teratological or the result of a healed injury.

HIGH-LEVEL CLASSIFICATION OF TRILOBITES

Harrington (1959b, p. 145) opened the chapter on trilobite classification in the first edition of Part O of the *Treatise on Invertebrate Paleontology* by stating that "a wholly satisfactory, natural classification

of trilobites is beyond possibility at the present moment," a statement reiterated by Fortey (1997, p. 290) in the revision of *Treatise* Part O. Harrington explained that homeomorphy resulting from parallel or convergent evolution is a significant contributing factor. Additional evidence of such homeomorphy, presented here, is relevant to the orders Corynexochida and Asaphida as defined by Fortey.

A fused rostral-hypostomal plate (conterminous hypostomal condition) has been cited as a cardinal character uniting the Corynexochida (e.g., Fortey, 1990, 1997). However, Hopkins and Webster (2009) subsequently documented an ontogenetic change from a fused rostral-hypostomal plate to a functional hypostomal suture in the Cambrian Epoch 2 corynexochoid *Zacanthopsis palmeri* Hopkins and Webster, 2009. Ventral holaspid morphology of the new Epoch 3 corynexochoid species *Zacanthoides marshalli* (see Fig. 13.2) shows that it, too, had a functional rostral-hypostomal suture, further demonstrating that a conterminous hypostomal condition does not unite all Corynexochida. This is consistent with interpretation of the Corynexochida as a polyphyletic taxon. An alternative possibility is that most zacanthoidid species are plesiomorphic with a fused rostral-hypostomal plate. As a related observation, we suggest that *Zacanthoides grabaui* (Fig. 2), a common Utah species with an elongated preglabellar field, likely had either a functional hypostomal suture or a natant hypostomal condition.

In defining the ptychparioid suborder Asaphina, Fortey and Chatterton (1988) concluded that most evidence favored a monophyletic origin for a median suture on the ventral cephalon, which they regarded to be a cardinal apomorphic character. For averred lack of "compelling morphological evidence," they rejected the previously inferred origin of a median suture within the family Pterocephaliidae by gradual reduction and loss of a rostrum (Palmer, 1960, 1965; Robison, 1964), and they excluded *Aphelaspis* and other rostrum-bearing taxa from the family. Fortey (1997, p. 300–301) subsequently elevated the Asaphina to order rank, Asaphida, and grouped a restricted family Pterocephaliidae with inferred primitive asaphoids in the superfamily Anomocaroidea. In further comment on the median suture, Fortey (1997) noted that it might have arisen by reduction and eventual loss of the rostral plate. He further noted that those trilobites having a small, triangular rostral remnant, a rostellum, probably show an intermediate grade of organization. Park and Choi (2009, 2010, 2011) recently demonstrated that a ventral median suture developed independently and in different fashions at least three times during the history of Cambrian trilobites, thus indicating the need for significant revision of the order Asaphida. Concurrently, Bonino and Kier (2009, fig. 21.c; 2010, fig. 24.b) illustrated the presence of a ventral median suture and associated rostellum in a new species, *Norwoodia boninoi* (see Figs. 27, 28.1), belonging to the family Norwoodiidae. Fortey (1997, p. 302) and several other authors have assigned norwoodiids without question to the order Ptychopariida. We here cite the presence of a median suture in *N. boninoi* as further evidence for the polyphyletic origin of the median suture, which Fortey and Chatterton (1988) said would be necessary to disprove their classification. We also reiterate the likely independent origin of a median suture within the family Pterocephaliidae, as defined and well documented by Palmer (1960, 1965) and Pratt (1992), and we favor retention of the family in the order Ptychopariida.

LOCALITIES

Most trilobites described here are from one or more of the following localities. Numbers correspond to those in an unpublished locality file assembled over many years by one of us (R. A. R.). Precise locality information is not available for some specimens or photos provided by various collectors.

114—Estimated 100 m below top of Wheeler Formation on east side near crest of north-trending ridge, about 700 m south of water trough below Swasey Spring (informally referred to as Swasey Spring locality), sec. 24 (unsurveyed), T. 16. S., R. 13 W., east side of central House Range.

115—Upper 30 m of Wheeler Formation at its type locality in Wheeler Amphitheater, SE¼ sec. 2, T. 17 S., R. 13 W., House Range.

116—Upper 30 m of Wheeler Formation on southern flank of Antelope Mountain, SE¼SE¼NE¼ sec. 35 (unsurveyed), T. 17 S., R. 13 W., House Range.

122—Uppermost few meters of Spence Shale on ridge between North Fork and South Fork of High Creek, T. 14 N., R. 2 E., Bear River Range, Cache County, Utah.

347—Estimated 60 m above base of Marjum Formation, in dry stream bed (informally referred to as Sponge Gully), NW¼SE¼SE¼ sec. 4 (unsurveyed), T. 18 S., R. 13 W., about 4.7 km east-northeast of Marjum Pass, House Range.

391—Estimated 100 m above base of Marjum Formation, south of road near base of Marjum cliffs, SW¼NE¼ sec. 17 (unsurveyed), T. 18 S., R. 13 W., about 3.2 km east of Marjum Pass, House Range.

520—About 60 m above base of Wheeler Formation, top of low east-facing escarpment, NW¼NW¼SE¼ sec. 21, T. 15 S., R. 10 W., Drum Mountains.

716—Estimated 100–200 m above base of Marjum Formation, ledges along south side of dry wash (informally referred to as Red Wash), SW¼NW¼ sec. 24 (unsurveyed), T. 17 S., R. 13 W, about 4.0 km south of Wheeler Amphitheater, House Range.

719—About 40 m below the top of the Wheeler Formation, NE¼NW¼ sec. 20, T. 15 S, R. 10 W., Drum Mountains.

794—Upper Wheeler Formation, outcrop on north side of gully, a few meters west of road between Marjum Pass and Wheeler Amphitheater (informally referred to as Mockingbird Gulch), NE¼NE¼SW¼ sec. 4, T. 18 S, R. 13 W., House Range.

811—About 190 m above the base of the Marjum Formation, near base of steep slope and cliffs (informally referred to as White Hill quarry), SW¼NE¼ sec. 17, T. 18 S, R. 13 W., House Range.

824—Upper Weeks Formation previously exposed on hillside north of road in North Canyon (Weeks Canyon of C. D. Walcott), SE¼NW¼ sec. 29, T. 18 S, R. 13 W., House Range. This is the same as locality 30n of Walcott (1912, p. 191), and it is the type locality for several taxa. Much rock at this locality was recently removed by commercial quarrying for flagstone.

SYSTEMATIC PALEONTOLOGY

Name-bearing type specimens are deposited with collections of the University of Utah Department of Geology and Geophysics (UU), Salt Lake City, Utah; the University of Kansas Museum of Invertebrate Paleontology (KUMIP), Lawrence, Kansas; the U. S. National Museum of Natural History, Smithsonian Institution

(USNM), Washington, D.C.; and the Back to the Past Museum (BPM), which is housed in the Azul Sensatori Hotel near Cancun, Mexico. The last museum contains the large trilobite collection of Carlo Kier (Bonino and Kier, 2009, 2010). Other specimens are in private collections cited in text that follows.

Specimens photographed by the authors and illustrated in grayscale were coated with either ammonium chloride or magnesium oxide. Specimens photographed by others are uncoated and illustrated in color.

Some specimens illustrated herein are held in private collections. These specimens reveal additional morphological information that the authors consider to be of important scientific value. Hence, while it is not the usual custom to illustrate in scientific journals material not held in publicly accessible institutions, in this instance, the illustrations are being made available in order to increase knowledge of these taxa. All name-bearing type material is held in public repositories in accord with rules of the International Code of Zoological Nomenclature (1999).

Order AGNOSTIDA Salter, 1864

Mounting evidence (e.g., Walossek and Müller, 1990; Bergström and Hou, 2005; Stein, Waloszek, and Maas, 2005; Haug, Maas, and Waloszek, 2010; Stein and Selden, 2011) suggests that agnostoids have close phylogenetic affinities with crustaceanomorph arthropods. The relationship of agnostoids to polymerid trilobites is in contention, as trilobites are commonly considered to have affinities with arachnomorph arthropods (e.g., Fortey and Owens, 1997). However, some recent evidence suggests that polymerid trilobites share a more recent common ancestry with crustaceans than with chelicerates (Scholtz and Edgecombe, 2006). Cotton and Fortey (2005) provided phylogenetic justification for retention of agnostoids in the class Trilobita, and pending resolution of this phyletic conundrum, we provisionally treat the agnostoids as trilobites. Following Peng and Robison (2000), we exclude condylopygoids and eodiscoids from the order Agnostida.

Family CLAVAGNOSTIDAE Howell, 1937
Genus TRIADASPIS Öpik, 1967

Type species.—*Triadaspis bigeneris* Öpik, 1967, p. 125–126.

Emended diagnosis.—Clavagnostids having median preglabellar furrow, glabellar F3, and fulcral cephalic spines. Pygidium weakly zonate, with auxiliary furrow transversely short and anterior border ridge entire; axis divided longitudinally by full-length intranotular furrows; ring furrows weak; posteroaxis long and ogival, with deep transverse sulcus; rear margin having three spines. Border furrows all narrow.

Discussion.—*Triadaspis* Öpik, 1967, was erected on three poorly preserved pygidia of the type species, *T. bigeneris* Öpik, 1967, from Australia, of which only one was illustrated. Based on many additional, better preserved, and more complete specimens of *T. bigeneris* from the Weeks Formation of Utah, the diagnosis of *Triadaspis* is here significantly revised and expanded. *Triadaspis bigeneris* is the only named species of *Triadaspis*.

The presence of a glabellar F3 and a median preglabellar furrow characterize the cephalon of *Triadaspis*. A transversely reduced anteroglabella and presence of a weak and carinate glabellar node indicate its clavagnostid affinities. It further resembles most clavagnostids in having an angular posterior glabella and fulcral spines.

The pygidium of *Triadaspis* has a unique combination of characters, but some of these differ from the description by Öpik (1967, p. 125–126). An intranotular region is outlined by paired notular furrows along the entire length of the axis but is deeply divided by a sagittally wide transverse sulcus on the posteroaxis. The anterior part of the intranotular region is hemicylindrical and well defined. Because the agnostoid transverse sulcus does not necessarily correspond to a segmental boundary (Robison, 1988, p. 32; Peng and Robison, 2000, p. 10), the pygidial axis of *Triadaspis* is not necessarily "quadrilobate" as described by Öpik. Also, the median tubercle does not extend over "three axial annulations," but terminates at the approximate level of F2. The rear termination of the tubercle is indicated by an abrupt, steplike change in lateral profile and is well forward of the transverse sulcus. Laterally convex notular furrows, which weaken rearward, bound the intranotular region behind the transverse sulcus. Öpik (1967, p. 125) noted that *Triadaspis* has a "*Clavagnostus*-like pair of pits at the end of its third axial annulation." These pits (fossae) are at confluences of the transverse sulcus and paired notular furrows.

Triadaspis is known from Australia, Canada, and the United States, where it ranges from the upper *Lejopyge laevigata* Zone to the upper *Proagnostus bulbus* Zone. It was first reported from the *Erediaspis eretes* Zone of Australia (Öpik, 1967), which approximates the position of the *P. bulbus* Zone.

TRIADASPIS BIGENERIS Öpik, 1967
Figures 3, 28

Oedorhachis? *ulrichi* Resser. Robison, 1960, p. 13, pl. 1,*9.*
Triadaspis bigeneris Öpik, 1967, p. 125–126, pl. 54,*6;* Shergold and Laurie, 1997, fig. 235.4.

Emended diagnosis.—Cephalon subcircular to subquadrate. Genae smooth; bisected by narrow, median preglabellar furrow that may weaken anteriorly. Glabella divided by narrow, shallow F3; anteroglabella narrower than posteroglabella, rounded to slightly angular in front; posteroglabella slightly tapers rearward, with angular termination; median node weak, carinate, and slightly forward of posteroglabellar midpoint. Basal lobes simple, moderate in size. Fulcral spines short and slender.

Pygidium subpentagonal. Axis long, narrowly abutting border furrow; longitudinally divided by paired, long, shallow, notular furrows; ring furrows weak to effaced. Median tubercle broad, coalescing anteriorly with hemicylindrical intranotular region, terminating posteriorly near level of F2. Posteroaxis ogival, moderately broad, and divided by deep transverse sulcus about one-third distance from front; intranotular region centrally expanded behind transverse sulcus. Rear border weakly zonate; auxiliary furrow transversely short and triangular; anterior border ridge entire and differentially elevated; margin having three spines, median one being smaller.

Discussion.—*Triadaspis bigeneris* is the only named species of *Triadaspis*. In general axial form and number of marginal spines, it resembles *Utagnostus trispinulus* Robison, 1964, a likely sister taxon, but not an immediate phyletic source. *T. bigeneris* has several inferred apomorphies, including a pygidial border that is weakly zonate rather than simplimarginate. The posteroglabella tapers forward in early holaspides of *U. trispinulus* and became nearly parallel sided in late holaspides. During the holaspid ontogeny of *T. bigeneris*, the glabellar M3 became laterally swollen, causing the posteroglabella to change from nearly parallel sided to tapered rearward. The pygidial
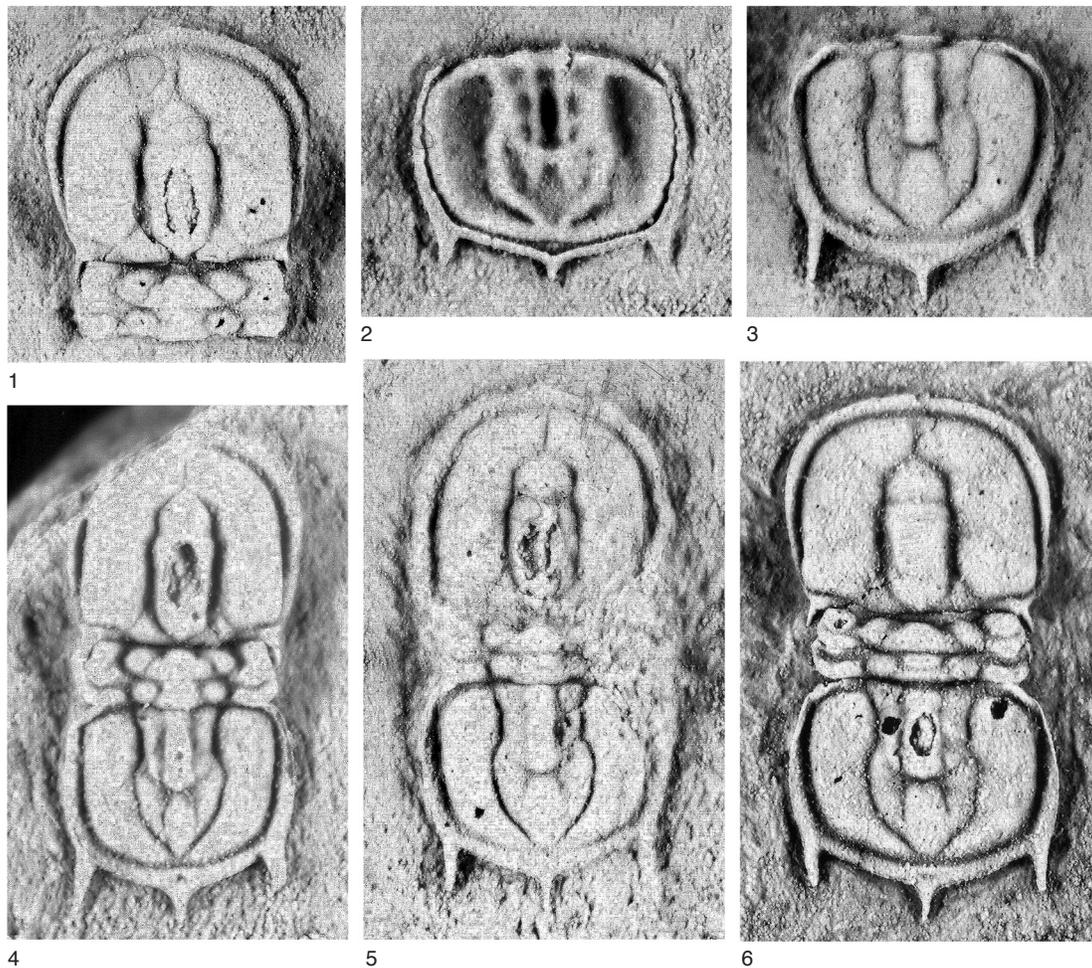
Figure 3. *Triadaspis bigeneris* Öpik, 1967, all specimens are silicified in calcareous shale of the upper Weeks Formation, House Range; all from locality 824. *1*, Cephalon and thorax, UU 10051.01, length 3.5 mm; *2*, ventral surface of pygidium showing doublure, UU 10051.02, length 2.5 mm; *3*, pygidium showing deep transverse sulcus on posteroaxis, UU 10051.03, length 3.0 mm; *4*, smaller exoskeleton, UU 10051.04, length 4.5 mm, donated by Marc Behrendt; *5*, exoskeleton, UU 10051.05, length 6.0 mm; *6*, exoskeleton, KUMIP 204387, length 6.0 mm.

axis of *T. bigeneris* differs from that of *U. trispinulus* by the presence of long notular furrows, presence of a deep transverse sulcus on the posteroaxis, and a larger and more carinate median tubercle. *T. bigeneris* also has a median preglabellar furrow, which is absent in *U. trispinulus*, and its five marginal spines are somewhat larger. Because the maximum holaspid size of *U. trispinulus* is distinctly smaller than that of *T. bigeneris*, some of their differences may be peramorphic (hypermorphic).

Occurrence.—*Triadaspis bigeneris* is known from Australia (Queensland), Canada (British Columbia), and the United States (Utah). Many specimens are in collections made by Robison from the middle and upper Weeks Formation in the House Range. Other specimens from the upper Weeks Formation (locality 824) are in KUMIP collections (204403, 204415–20420), Brigham Young University collections (Robison, 1960, p. 13; as reassigned), and U. S. National Museum of Natural History collections. Michael Cuggy (personal communication, 2001) collected specimens of *T. bigeneris* from the Sullivan Formation in Yoho National Park, British Columbia. The species ranges from the upper *Lejopyge laevigata* Zone to the upper *Proagnostus bulbus* Zone.

Order CORYNEXOCHIDA Kobayashi, 1935

Whittington (2009) briefly reviewed the suborder Corynexochina, which includes all Cambrian corynexochoids, and concluded that families of the suborder are inadequately discriminated one from another. As ordinal-level taxonomy is beyond the scope of this paper, we continue to use established family names pending publication of better alternatives.

Family DOLICHOMETOPIDAE Walcott, 1916b
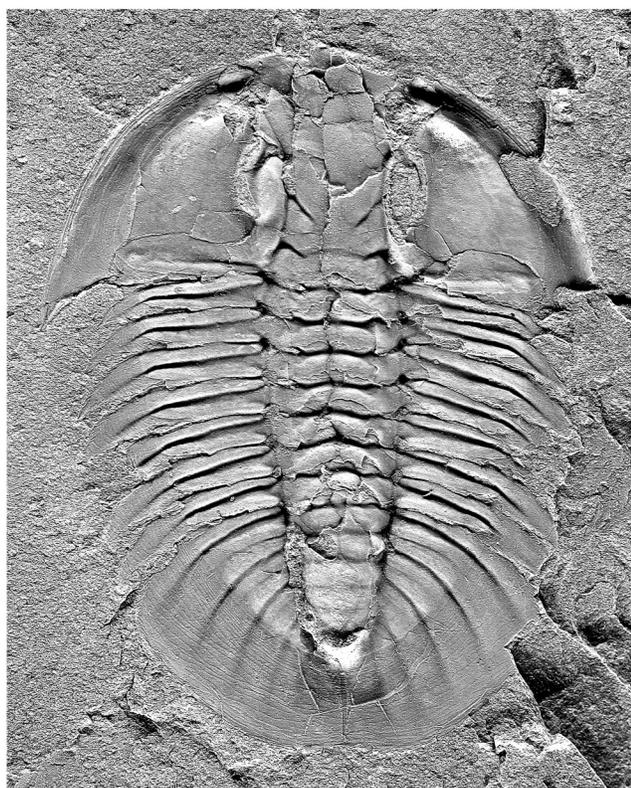## Genus ATHABASKIA Raymond, 1928

Type species.—*Athabaskia ostheimeri* Raymond, 1928, p. 311. The generic diagnosis by Palmer (1954, p. 66) is followed.

ATHABASKIA GLADEI new species
Figure 4

Diagnosis.—*Athabaskia* with relatively wide exoskeleton. Cephalon and pygidium about equal in length. Genal spines short, tips opposite thoracic axial ring 2 or 3. Thorax containing seven segments. Pygidium having small, convex, triangular, pleural fields and wide, weakly concave border; medial rear margin weakly indented. Pleural

Figure 4. *Athabaskia gladei* new species, Spence Shale, Miners Hollow, Wellsville Mountain. *1*, Holotype exoskeleton, UU 10051.06, length 67 mm, donated by Glade and Val Gunther; *2*, paratype exoskeleton in Lloyd Gunther collection, length 62 mm (photo courtesy of Thomas Whiteley).

furrows of pygidium weak, terminating near inner margin of border; interpleural furrows prominent, extending across much of border. Pygidial axis containing five rings and terminal piece, length about two-thirds that of pygidium.

Etymology.—After Glade Gunther, for promoting knowledge of Cambrian biotas.

Types.—Holotype exoskeleton, UU 10051.06 (Fig. 4.1); paratype exoskeleton in Lloyd Gunther collection (Fig. 4.2), and its external mold is UU 10051.07.

Discussion.—*Athabaskia gladei* is characterized by a wide exoskeleton, short genal spines, wide pygidial border, pleural and interpleural furrows of markedly different lengths on the pygidium, and a weak medial indentation of the rear pygidial margin. It is partly coeval with *A. bithus* (Walcott, 1916b) and *A. wasatchensis* (Resser, 1939), both of which have a narrower exoskeleton, 8 rather than 7 thoracic segments, and a narrower pygidial border that usually lacks medial indentation. *A. bithus* has short genal spines like those of *A. gladei*, but pygidial pleural and interpleural furrows are about equal in depth and length. *A. wasatchensis* has genal spines of moderate length, tips opposite axial ring 4 or 5 of thorax, and its pygidial interpleural furrows are weaker than those of *A. gladei*.

Occurrence.—*Athabaskia gladei* is known from the *Glossopleura* Zone in the Spence Shale at Wellsville Mountain. Although its stratigraphic range partly overlaps those of *A. bithus* and *A. wasatchensis*, the species are rarely found in association.

Genus GLOSSOPLEURA Poulsen, 1927

Type species.—*Dolichometopus boccar* Walcott, 1916b, p. 363.

Glossopleura warrants taxonomic revision that is beyond the scope of this paper. It includes more than 50 named species from North America, Greenland, and the Precordillera terrane of Argentina, most being based on disarticulated cranidia and pygidia. We follow the generic diagnosis of Palmer (1954, p. 67), with minor emendation by Babcock (1994, p. 94).

GLOSSOPLEURA CAMPBELLI new species
Figure 5

Glossopleura sp. Gunther and Gunther, 1981, p. 37, pl. 23.
Glossopleura similaris. Bonino and Kier, 2009, tavola 26.e.
Glossopleura n. sp. Bonino and Kier, 2010, pls. 8.9, 40.e.

Diagnosis.—*Glossopleura* having a broad axis. Cephalon semicircular with short genal spines, shallow border and occipital furrows, and narrow border. Glabella expands slightly toward anterior. Thorax containing eight segments, each with short, falcate, pleural tips and narrow ventral doublures. Pygidium slightly shorter than cephalon, with long pygidial axis, unusually large pleural fields, and unusually narrow border. Boundary between pleural field and border ill defined by change in slope. Pygidial doublure approximately same width as overlying border.

Etymology.—After Douglas P. Campbell, for advancing knowledge of the Spence Shale and its fauna (Campbell, 1974).
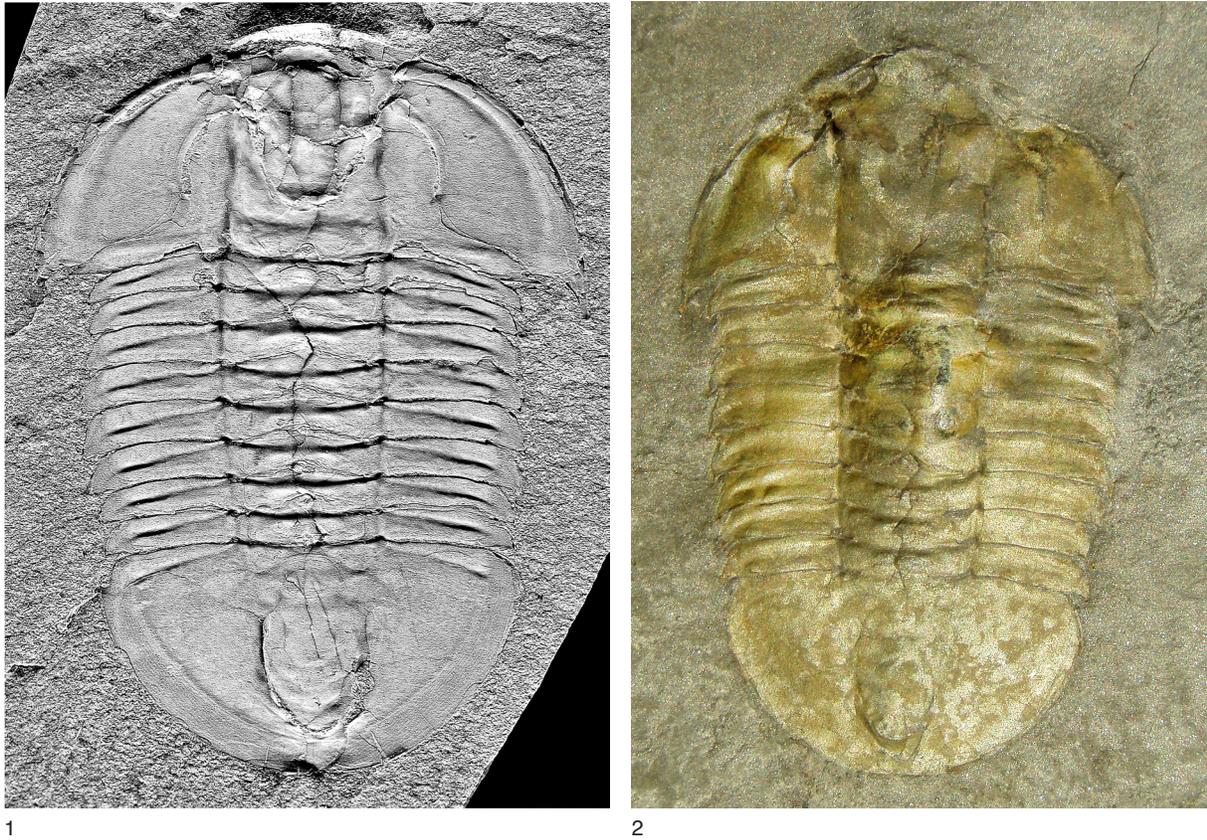
Figure 5. *Glossopleura campbelli* new species, upper Spence Shale, Antimony Canyon, Wellsville Mountain. *1*, Holotype, mostly internal mold, UU 10051.08, length 67 mm, donated by Val Gunther; *2*, paratype exoskeleton, BPM 1003, length 66 mm (photo courtesy of Enrico Bonino).

Types.—Holotype, UU 10051.08 (Fig. 5.1), and paratype, BPM 1003 (Fig. 5.2).

Discussion.—*Glossopleura campbelli* differs from all other species of *Glossopleura* by the combination of its broad axis, short genal spines, and unusually large pleural areas and narrow border on the pygidium. It resembles *G. similaris* Resser (1939) in having a narrow border on the pygidium. However, the pygidial length of *G. campbelli* is shorter relative to width, and its axial and pleural segmentation is more effaced. Species of *Glossopleura* can show either wide or narrow limits of variation in pygidial outline and width of the pygidial border (Babcock, 1994; Sundberg, 2005). Available specimens of *G. campbelli* show minor variation in these characters, and much of it can be attributed to differences in compaction (compare the convex exoskeleton in Fig. 5.2 with the compacted exoskeleton in Fig. 5.1).

Occurrence.—The type specimens are from the *Glossopleura* Zone of the upper Spence Shale at Wellsville Mountain.

GLOSSOPLEURA YATESI new species
Figure 6

Diagnosis.—*Glossopleura* having moderately wide exoskeleton and eight thoracic segments. Cephalon broad, with moderately long genal spines. Glabella moderately expanded anteriorly, lateral furrows shallow and ill defined. Occipital furrow wide (sag.) and shallow, occipital ring smooth and weakly defined. Palpebral lobes slender, long, and weakly curved. Thorax having medial spines on segments 2 to 8, with spine length greatly increasing on posterior segments; pleural tips of thoracic segments long and falcate. Pygidium having weak alate outline resulting from medial indentation of rear margin; maximum width about twice as great as length. Furrows on dorsal surface of pygidium mostly effaced, and axis is defined mainly by change in slope of dorsal surface. Pygidial axis relatively short, length being about two-thirds that of pygidium, having up to four rings and a terminal piece defined by weak furrows.

Etymology.—After Kent Yates, who has generously permitted the collection of Spence Shale fossils from his land on Wellsville Mountain.

Types.—Holotype exoskeleton, UU 10051.09 (Fig. 6.1), and paratype exoskeleton, UU 10051.10 (Figs. 6.2–6.3).

Discussion.—*Glossopleura yatesi* differs from all named species of *Glossopleura* by a unique combination of skeletal characters. The most distinctive of these are the presence of axial spines on the thorax that significantly increase in length toward the rear, long and falcate pleural tips on the thoracic segments, a relatively short pygidial axis, and a prominent medial indentation of the rear pygidial margin. Search of relevant literature discovered no named species of *Glossopleura* having an indentation of the rear pygidial margin, although Campbell, in an unpublished M.S. thesis (1974), illustrated a disarticulated pygidium from about 38 m above the base of the Spence Shale on the ridge south of Antimony Canyon, Wellsville Mountain, which
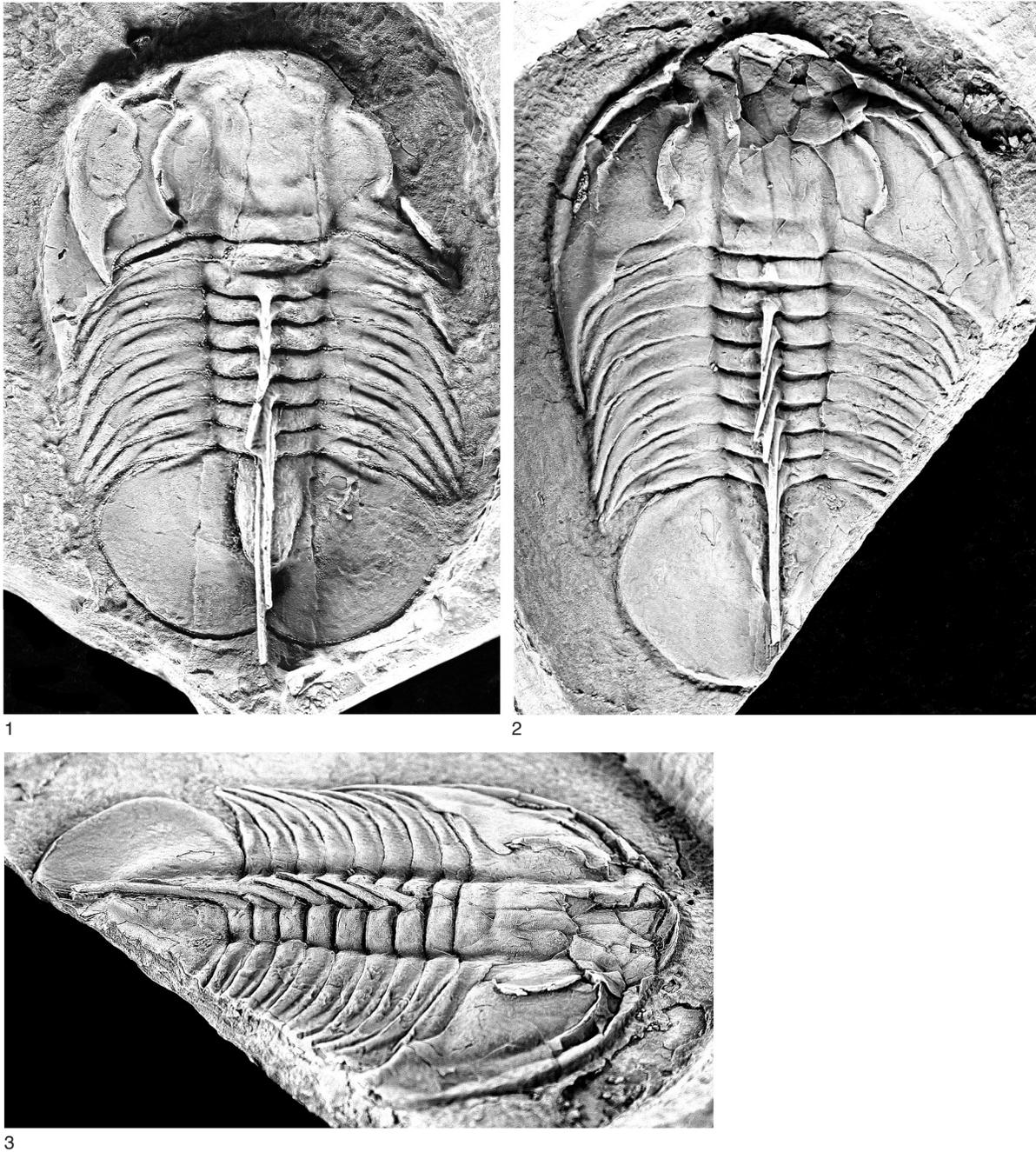
Figure 6. *Glossopleura yatesi* new species, about 34 m above the base of the Spence Shale in Miners Hollow, Wellsville Mountain; the specimens were collected, prepared, and donated by Paul Jamison. *1*, Holotype exoskeleton lacking right librigena, UU 10051.09, length 57 mm; inverted smaller librigena of another trilobite is superimposed on the left side of the cephalon; *2–3*, paratype incomplete exoskeleton in dorsal and oblique views, UU 10051.10, length 82 mm.

likely is conspecific with *G. yatesi*. Two specimens of an unnamed species of *Glossopleura* from the Arrojos Formation in Sonora, Mexico (Lochman, 1952, pl. 31,*13–14*), may have a very weak indentation of the pygidial margin, but the specimens differ from *G. yatesi* by having a longer pygidial axis, likely a narrower doublure, and medial nodes on the rear 5 or 6 axial rings of the thorax.

Occurrence.—Available specimens are from the *Glossopleura* Zone, about 34 m above the base of the Spence Shale, near the top of parasequence 3 of Liddell, Wright, and Brett (1997) in Miners Hollow, Wellsville Mountain.

Genus POLYPLEURASPIS Poulsen, 1927

Type species.—*Polypleuraspis solitaria* Poulsen, 1927, p. 270.

Emended diagnosis.—Exoskeleton long and slender; length of cephalon and thorax about equal, length of pygidium ranging from about equal to about 50 percent greater than that of cephalon or thorax. Axial lobe
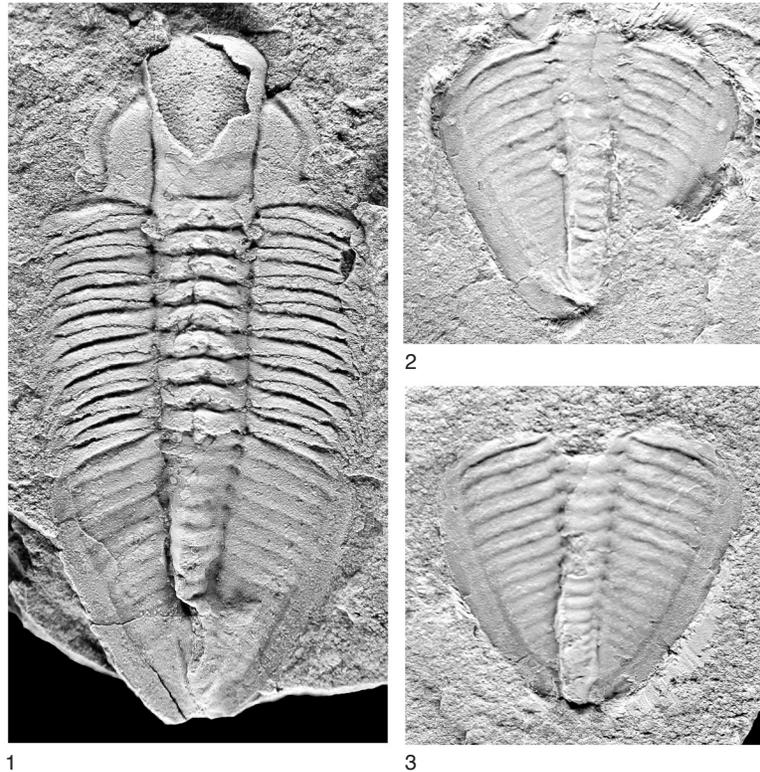
Figure 7. *Polypleuraspis cooperi* new species, middle part of the Spence Shale at Wellsville Mountain. *1*, Holotype exoskeleton lacking librigenae, UU 10051.11, length 34 mm, Hansen Canyon, donated by Jacob Skabelund; *2*, large paratype pygidium, UU 10051.12, length 27 mm, Antimony Canyon, donated by Val Gunther; *3,* smaller paratype pygidium, UU 10051.13, length 17 mm, Antimony Canyon, donated by Val Gunther.

strongly convex. Glabella long and narrow, expanding forward, reaching anterior cranidial margin. Occipital furrow and as many as four pairs of shallow glabellar furrows may be visible. Palpebral lobes narrow, length about half that of glabella. Posterior fixigenae laterally wide and exsagittally slender, possibly varying to narrowly triangular. Librigenae wide with narrow borders and genal spine of moderate length. Thorax of 7 or 8 segments; pleurae each terminating in slender, rearward-curving spine. Pygidium of near equal length and width. Pygidial axis weakly tapered, nearly reaching posterior pygidial margin, number of rings ranging from about 8 to 15. Pleural lobes sloping downward with pleural furrows similar in number to interring furrows in axis. Pygidial border narrow and concave, about half as wide as underlying doublure.

Discussion.—The generic diagnosis by Rasetti (1951, p. 175–176) is expanded to accommodate variation in characters of specimens from Utah.

Poulsen (1927) originally described *Polypleuraspis* from a single pygidium collected from the *Glossopleura* Zone in North Greenland. Although Rasetti (1951) reported large numbers of disarticulated specimens from some beds in the *Glossopleura* Zone of British Columbia, the genus is rare in the *Glossopleura* Zone of Utah. A single cranidium and a single tiny pygidium from the Chisholm Formation of the Drum Mountains in western Utah were previously identified as *Polypleuraspis* sp. (Oldroyd, 1973), and a single small pygidium from the Spence Shale of Wellsville Mountain in northern Utah was identified as *Polypleuraspis* sp. (Campbell, 1974). Three additional specimens from the Spence Shale, together with the Campbell specimen, are here assigned to a new species.

POLYPLEURASPIS COOPERI new species
Figure 7

Diagnosis.—*Polypleuraspis* having 8 thoracic segments and 14 or 15 pygidial segments. Posterior fixigenae laterally wide and exsagittally slender.

Etymology.—After Jason Cooper, an avid collector of Cambrian trilobites.

Types.—Holotype exoskeleton with missing librigenae, UU 10051.11 (Fig. 7.1); paratype pygidia, UU 10051.12 and 10051.13 (Figs. 7.2–7.3).

Discussion.—*Polypleuraspis cooperi* differs from *P. insignis* Rasetti (1951), the only species of the genus previously known from a complete dorsal exoskeleton, by having 8 rather than 7 thoracic segments, and 14 or 15 rather than 8 to 10 pygidial segments. Comparing pygidia of similar size, those of *P. cooperi* have at least 4 more segments than do those of *P. insignis*, indicating that the difference is likely genetic rather than ontogenetic. Rasetti (1951) described the posterior fixigene of *P. insignis* as being small and narrowly triangular, but those illustrated appear to be either broken or partly covered. If they are actually short and triangular, they differ significantly from those of *P. cooperi*.

Polypleuraspis cooperi differs from *P. solitaria* Poulsen, 1927, the type species of the genus, known from a single pygidium, which has only 10 segments. The pygidium of *P. solitaria*, collected from Greenland, also was reported to have axial nodes or spines, which are not present on the two North American species.

Occurrence.—About 100 m above the base of the Spence Shale, *Glossopleura* Zone, in Antimony and Hansen canyons, Wellsville Mountain.

Family DORYPYGIDAE Kobayashi, 1935
Genus KOOTENIA Walcott, 1888

Type species.—*Bathyuriscus (Kootenia) dawsoni* Walcott, 1889, p. 446.

Discussion.—The generic diagnosis by Palmer (1968, p. 47) is mostly followed, but the observed number of pygidial border spines ranges from one to seven pairs. The thorax characteristically contains seven segments.

More than 125 species of *Kootenia* have been named worldwide. These are mostly based on disarticulated sclerites showing unusual variation in spine morphology. How much of this variation may be intraspecific is difficult to evaluate. Also, the paucity of skeletal details for most species of *Kootenia* hinders taxonomic comparisons with the complete dorsal exoskeletons described here.

Some species of *Kootenia* superficially resemble species of *Dorypyge*, a genus reviewed by Zhang and Jell (1987) and Peng, Babcock, and Lin (2004). As noted by Zhang and Jell (1987) and Sundberg (1994), *Dorypyge* is distinguished from *Kootenia* and *Olenoides* by slight contraction in glabellar width between fossulae in the axial furrow, and it has different segmentation of the pygidium. Also, the dorsal exoskeleton of *Dorypyge* is commonly thick and pustulated, whereas that of *Kootenia* is thinner and commonly smooth or weakly granulated. We agree with Zhang and Jell (1987) that Utah specimens assigned to *Dorypyge* by Gunther and Gunther (1981) should be reassigned to *Kootenia*. These are described below under the new name *Kootenia youngorum*. Also, *Dorypyge swasii* Sundberg (1994) is reassigned here to *Kootenia*, as is a single pygidium from Alaska (Palmer, 1968). Both forms have morphologies more consistent with *Kootenia* than *Dorypyge*. Although *Dorypyge* is widespread in mid-Cambrian strata of Gondwana, Siberia, Baltica, and Avalonia, evidence for its occurrence in Laurentia is equivocal. This is consistent with evidence for geographic isolation of Laurentia during the Cambrian (Robison, 1991b).

KOOTENIA RANDOLPHI new species
Figure 8

Kootenia sp. Gunther and Gunther, 1981, p. 43, pl. 29.
Dorypyge swasii. Bonino and Kier, 2009, tavola 34.b.
Kootenia n. sp. Bonino and Kier, 2009, tavola 34.d; 2010, pl. 53.d.

Diagnosis.—*Kootenia* having ovate exoskeletal outline. Glabella slightly expanding forward, indenting narrow anterior cranidial border. Occipital ring with short median spine. Genal spines short to moderately long, with tips opposite thoracic axial ring 2 to 4. Thoracic axial rings each having median spine slightly shorter than that of occipital ring. Paired pleural spines of thorax and pygidium gradually increase in length rearward. Pygidial axis containing four rings and terminal piece, border having four pairs of marginal spines. Spaces between pygidial spines progressively widen rearward.

Etymology.—After Robert L. Randolph, for initial study of trilobites from the Swasey Formation in the Drum Mountains (Randolph, 1973).

Holotype.—Exoskeleton, BPM 1004 (Fig. 8.1).

Discussion.—*Kootenia randolphi* resembles *K. youngorum* n. sp. but differs by having 4 rather than 5 pairs of marginal spines on the pygidium. Also, the spacing and patterns of spine elongation differ. *Kootenia randolphi* is the only species of *Kootenia* known to have four pairs of marginal spines on the pygidium so far described from the Wheeler Formation or its lateral equivalents in the Great Basin.

Occurrence.—Locally common in the upper 30 m of the Wheeler Formation of the Drum Mountains, as used here, where it occurs in the lower *Bolaspidella* Zone. Some authors have referred these strata to the Pierson Cove Formation.

KOOTENIA YOUNGORUM new species
Figure 9

Dorypyge sp. Gunther and Gunther, 1981, p. 31, pl. 17.
?*Kootenia* sp. Gunther and Gunther, 1981, p. 42, pl. 28.
?*Dorypyge* cf. *D. olenekensis* Lazarenko. Palmer, 1968, p. 47, pl. 4,25.

Diagnosis.—*Kootenia* having broad glabella that widens slightly toward anterior. Genal spines moderately long, tips opposite thoracic axial ring 4 or 5. Occipital and thoracic rings each having a prominent medial spine, with spine lengths similar, except for notable increase on thoracic rings 6 and 7. Axial and pleural regions of thorax about equal in width, pleurae each terminating in short spine. Pygidium semicircular with prominent axis extending almost to rear margin. Pygidial axis containing four rings and terminal piece, ring furrows weakening rearward. Pleural furrows of pygidium becoming narrower and shallower toward rear. Pygidial margin having five pairs of spines; anterior three pairs short and about equal in length; fourth pair long and slender, length similar to that of pygidial axis; posterior, fifth pair very short.

Etymology.—After members of the Malcolm Young family, who for many years have generously permitted the collection of Spence Shale fossils from their land in Miners Hollow, Wellsville Mountain.

Types.—Holotype exoskeleton, UU 10051.14 (Fig. 9.1), and paratype exoskeleton, UU 10051.15 (Fig. 9.2).

Discussion.—*Kootenia youngorum* is most similar to *K. swasii* (Sundberg, 1994) but differs in pygidial spine morphology. The length of spine pairs 1 to 3 is about equal, and pair 4 is much longer in *K. youngorum*, whereas the length of spine pairs 1 to 4 regularly increases rearward in *K. swasii*. *Kootenia youngorum* differs from *K. randolphi* n. sp. by having 5 rather than 4 pairs of more evenly spaced pygidial spines and differs in the lengths of the spines. *Kootenia randolphi* does not show elongation of the terminal pair of spines, as shown in *K. youngorum*.

One paratype specimen of *Kootenia youngorum* demonstrates the prominent set of medial spines on the occipital and axial rings (Figs. 9.3–9.4). Beginning with the occipital ring, these mostly have a braided appearance of right-left curvature. In lateral view, the spines appear to have been slightly bent downward, which indicates that the braided appearance is a taphonomic artifact. A comparable pattern of downward and lateral flexure of axial spines is illustrated in other trilobites, *Amecephalus jamisoni* n. sp. (see Figs. 15.1–15.2) and *Glossopleura yatesi* n. sp. (Figs. 6.2–6.3), but in these examples, the spines are bent predominantly to one side. Some spines in both species are broken at the base, but the extent of flexure suggests that they had become somewhat flexible at some point in the taphonomic
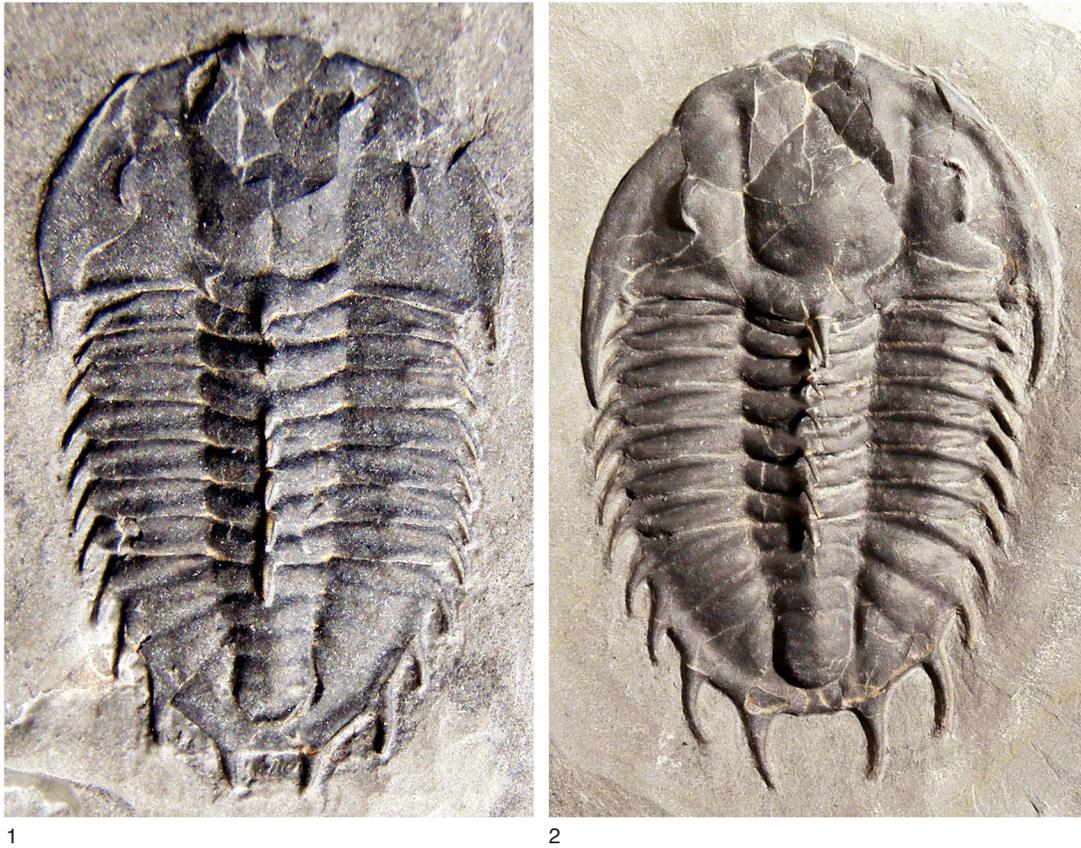
Figure 8. *Kootenia randolphi* new species, upper Wheeler Formation, Drum Mountains; *1*, holotype exoskeleton, BPM 1004, length 33 mm (photo courtesy of Carlo Kier); *2*, exoskeleton, length 47 mm (photo courtesy of David Comfort).

process. How such spines on a calcified exoskeleton became flexible is not known.

Occurrence.—Uppermost part of parasequence 3 of Liddell, Wright, and Brett (1997) in the upper Spence Shale, *Glossopleura* Zone, Wellsville Mountain. The species also is questionably represented by a single pygidium stated to be from lower Middle Cambrian strata in east-central Alaska (Palmer, 1968).

Genus OLENOIDES Meek, 1877

Type species.—*Paradoxides*? *nevadensis* Meek, 1870, p. 62. The generic diagnosis by Robison (1964, p. 537) is followed.

OLENOIDES SKABELUNDI new species
Figure 10

Olenoides sp. Robison, 1960, p. 23–24, pl. 2,*14.*
Olenoides sp. Bonino and Kier, 2009, tavola 46; 2010, pl. 69.

Diagnosis.—*Olenoides* lacking axial nodes and spines. Glabella expanding anteriorly with front bulging beyond anterior margin. Genal spines moderately long, tips opposite second or third axial ring. Paired marginal spines on each thoracic and pygidial segment short and similar in length. Pygidium having six pairs of marginal spines. Pygidial axis with five rings and terminal piece. Dorsal skeletal surface mostly covered with dense pustules that weaken rearward.

Etymology.—After Jacob Skabelund, who collected the holotype and two paratypes illustrated here.

Types.—Holotype pygidium, UU 10051.17 (Fig. 10.2); paratype cephalon and thorax, UU 10051.18 (Fig. 10.1); and paratype exoskeleton, partly reconstructed, BPM 1006 (Fig. 10.3).

Discussion.—*Olenoides skabelundi* is the largest trilobite known from the Weeks Formation, reaching at least 185 mm in length. It is most similar to *O. marjumensis* Resser, 1942, but differs by having greater anterior expansion of the glabella, abundant surface pustules, and the absence of either a medial node or spine on the occipital ring and each thoracic ring.

Olenoides skabelundi has an unusual morphology that readily distinguishes it from all other dorypygid species. Although retaining characters typical of *Olenoides* and other dorypygids, some are exaggerated or reduced to result in an exoskeleton that appears weakly convergent with that of paradoxidid and centropleurid trilobites. The exoskeleton is unusually large and elongate rather than ovoid, as observed in most dorypygids. The axial region is convex, with the glabella expanded upward and forward, bulging beyond the anterior cephalic margin, whereas the pleural areas are flattened and somewhat reduced laterally. Marginal spines are elongate but not unusually extended. Axial spines are absent, which is rare in dorypygids, and the marginal spines are short and stout, resembling the falcate marginal spines of paradoxidids and centropleurids. The pygidium is larger and broader than in most dorypygids.
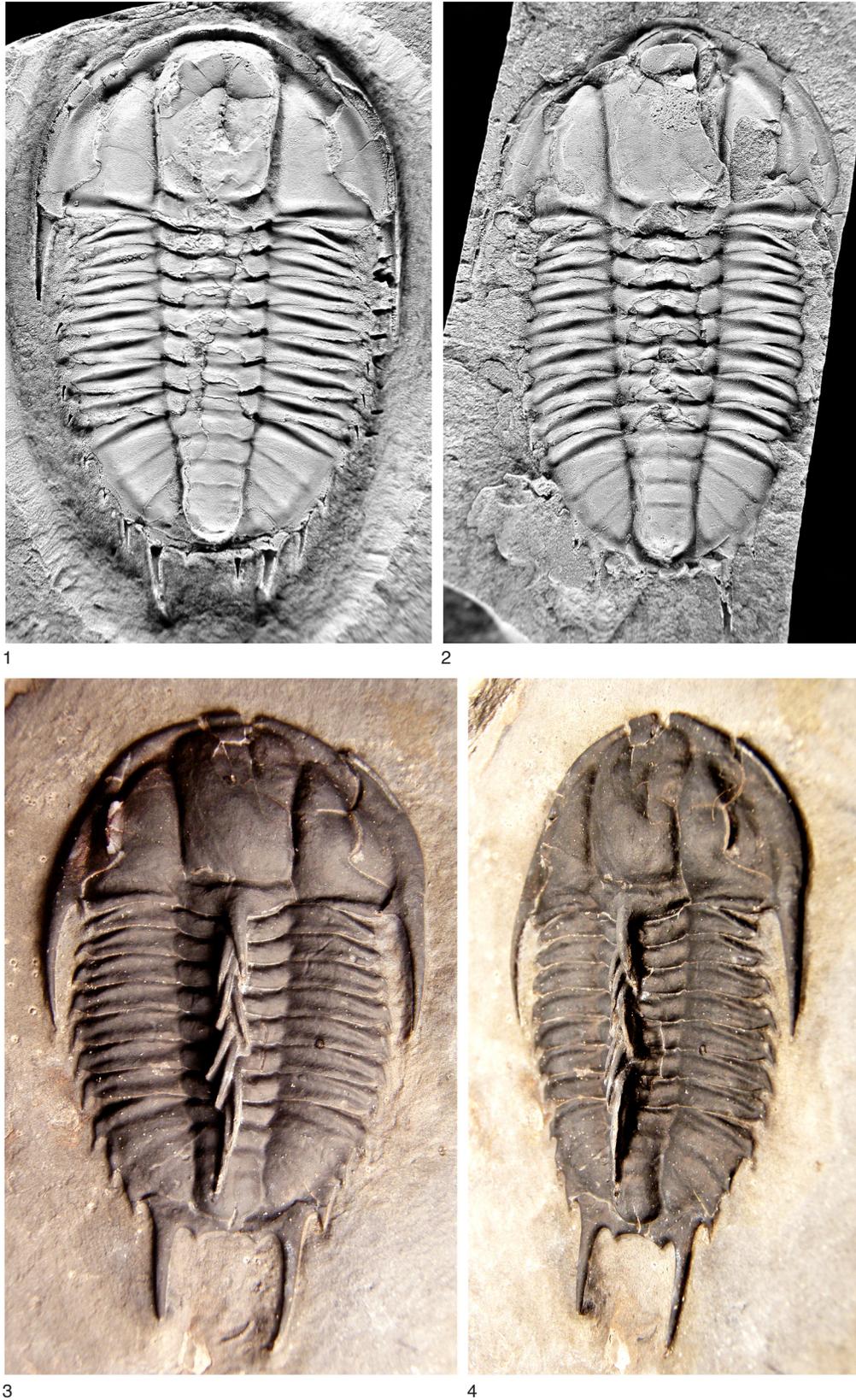
Figure 9. *Kootenia youngorum* new species, upper Spence Shale at Wellsville Mountain. *1*, Holotype, mostly an internal mold with minor skeletal remnants, UU 10051.14, length without spines 50 mm, Antimony Canyon, donated by Val Gunther and prepared by Paul Jamison; *2*, paratype exoskeleton with dorsal spines broken away, UU 10051.15, length without spines 41 mm, donated by Val Gunther; *3–4*, exoskeleton in dorsal and oblique views showing details of spine morphology, length without spines 38 mm, from about 35 m above the base of the Spence Shale in Miners Hollow (specimen prepared and photographed by Paul Jamison).

Figure 10. *Olenoides skabelundi* new species, upper Weeks Formation, House Range, collected by Jacob Skabelund. *1*, Paratype fragment of cephalon and thorax, UU 10051.18, sagittal length 109 mm; *2*, holotype pygidium, UU 10051.17, length 60 mm; *3*, paratype exoskeleton with left side of cephalon mostly reconstructed with parts from two other specimens, BPM 1006, length 119 mm (photo courtesy of Enrico Bonino).

Fortey (1985) discussed characteristics of trilobites adaptive for, or associated with, a pelagic or nektonic lifestyle, and the characters of *O. skabelundi* are consistent with many of them. Small eyes and lack of terrace lines are not expected on a large pelagic trilobite. Small eyes, however, are a feature of other inferred pelagic forms (Fortey, 1985). Unusually coarse pustulation, which is present on the dorsal surface of *O. skabelundi*, perhaps served the same function as dorsal terrace lines on other pelagic or nektonic species, including providing lift by helping to create vertical vortices in water flow over the dorsal surface. The pleural areas of *O. skabelundi* are reduced compared to most other dorypygids, but not strongly reduced as in the inferred pelagic or nektonic forms *Irvingella* (Fortey, 1985), *Centropleura* (Babcock, 1994; Rushton, 2011),

or *Luhops* (Rushton, 2011). At present, the known geographic distribution of this species is limited to western Utah, whereas many trilobites inferred to have been pelagic or nektonic have intercontinental distributions (e.g., Fortey, 1985; Babcock, 1994; Rushton, 2011). Dorypygids, as a family, are intercontinentally distributed, but individual species tend to show strong regional endemism (e.g., Zhang and Jell, 1987; Peng, Babcock, and Lin, 2004).

Occurrence.—*Olenoides skabelundi* is generally rare in the upper Weeks Formation of the House Range. Its presence in the *Cedaria* Zone may be as high as any known for the genus. Other rare *Olenoides* have been reported from that zone in Quebec (Rasetti, 1946) and Tennessee (Rasetti, 1965).

OLENOIDES VALI new species
Figure 11

Olenoides rooksi Bonino and Kier, 2009 (*nom. nud.*), tavola 36.c, 36.d.
Olenoides trispinosus Bonino and Kier, 2009 (not *O. trispinosus* Rasetti, 1946), tavola 38.b.
Olenoides n. sp. Bonino and Kier, 2010, pls. 56.b–56.d.

Diagnosis.—*Olenoides* with weak anterior expansion of glabella. Posterior cephalic border having tiny intergenal spines, with posterior cephalic margins between intergenal and genal spines deflected forward. Genal spines long, terminating approximately opposite front of pygidium. Occipital spine exceptionally long, arching strongly upward and rearward, terminating just in front of thoracic-pygidial boundary. Medial thoracic spines projecting upward with minor rear curvature and with length progressively increasing rearward from short to quite long beneath arching occipital spine; medial spine on eighth thoracic segment approximately same length as pygidial axis. Paired marginal spines on thorax and pygidium progressively increase in length rearward, with length of posterior pygidial pair similar to that of genal spines. Pygidium having three pairs of marginal spines and axis with four rings and terminal piece.

Etymology.—After Val G. Gunther, for his many contributions to knowledge of Cambrian fossils (e.g., Gunther and Gunther, 1981).

Holotype.—Exoskeleton, UU 10051.18 (Fig. 11.1).

Discussion.—*Olenoides vali* n. sp. and *O. trispinosus* Rasetti (1946) are the only species of *Olenoides* known to have three pairs of marginal spines on the pygidium. However, the pygidial spines of *O. vali* markedly increase in length toward the rear, whereas those of *O. trispinosus* decrease in length toward the rear. Also, the pygidial axis of *O. vali* has four rings and a terminal piece, whereas *O. trispinosus* has five rings and a terminal piece. *Olenoides vali* further differs from all other species of *Olenoides* by exceptional elongation of the occipital spine and greater rearward elongation of medial spines on the thorax.

White (1973), in an unpublished thesis, described a poorly preserved exoskeleton and a few small, disarticulated sclerites, here assigned to *Olenoides trispinosus*. Comparison of specimens known to the present authors shows a minor ontogenetic increase in lateral expansion of the anterior glabella. In some specimens, that expansion was further increased by taphonomic compression.

Olenoides rooksi Bonino and Kier (2009) is an unavailable name because it fails to meet criteria of Article 13 of the International Code of Zoological Nomenclature.

Occurrence.—*Olenoides vali* has an observed stratigraphic range through approximately the upper 110 m of the Wheeler Formation in the Drum Mountains, as defined herein. Some collectors have referred specimens from the upper part of this interval to either the Marjum or Pierson Cove formations.

Family ZACANTHOIDIDAE Swinnerton, 1915
Genus ZACANTHOIDES Walcott, 1888

Type species.—*Zacanthoides romingeri* Resser, 1942, *nom. nov. pro Embolimus spinosa* Rominger, 1888, *non Ogygia*? *spinosa* Walcott, 1884; subsequent designation, Resser, 1942, p. 56.

The generic diagnosis by Palmer (1954, p. 69) is followed.

Many species of *Zacanthoides* are based on disarticulated sclerites. Two new species of *Zacanthoides* are described from entire dorsal exoskeletons having distinctive spinal morphology. Lack of similar information for most species of *Zacanthoides* precludes adequate morphologic comparisons.

ZACANTHOIDES LIDDELLI new species
Figure 12

Zacanthoides typicalis Bonino and Kier, 2009, tavola 29.c.
Zacanthoides n. sp. Bonino and Kier, 2010, pl. 43.c.

Diagnosis.—*Zacanthoides* with moderately wide exoskeleton. Glabella weakly tapering forward. Anterior border and preglabellar field about equal in sagittal width. Genal spines well advanced, long and rather slender, curving outward and backward, tips opposite thoracic axial ring 5 or 6. Intergenal spines moderately long and slender. Thoracic pleurae with falcate tips, lengthening rearward to maximum at about segment 6 and then shortening slightly. Occipital and thoracic rings each with short medial spine, except for long and slender spine, about half as long as exoskeleton without spine, on thoracic ring eight. Pygidium subquadrate, probably with four pairs of rear marginal spines that decrease in length toward midline.

Etymology.—After Professor W. David Liddell, Utah State University, for contributions to knowledge of Cambrian stratigraphy and depositional environments in Utah.

Holotype.—Exoskeleton, UU 10051.22 (Fig. 12.1).

Discussion.—*Zacanthoides liddelli* is primarily characterized by its spinal morphology, which includes long genal spines, moderately long intergenal spines, a long axial spine on thoracic segment 8, and short medial spines on the occipital ring and thoracic rings other than the eighth. See *Zacanthoides marshalli* for a discussion of character differences.

Occurrence.—Rare in the Spence Shale, *Glossopleura* Zone, at Wellsville Mountain and in the Bear River Range.

ZACANTHOIDES MARSHALLI new species
Figure 13

Diagnosis.—*Zacanthoides* with slender exoskeleton. Glabella weakly tapering forward. Occipital ring bearing medial node. Sagittal width of preglabellar field more than twice that of upturned anterior border. Rostrum and hypostome abut along functional rostral-hypostomal suture. Genal spines moderately advanced, stout, curving outward and backward, tips opposite thoracic axial ring 6 to 8. Intergenal spines short, weakly developed. Thoracic pleurae with falcate tips that progressively lengthen rearward. Thoracic segment 8 having large, posteriorly directed axial spine, its length about half that of exoskeleton without spine. Other thoracic segments each having medial node. Pygidium subquadrate with four pairs of rear marginal spines that decrease in length toward midline.

Etymology.—After Mark Marshall, who contributed the holotype.

Holotype.—Exoskeleton, UU 10051.20 (Fig. 13.1).

Discussion.—*Zacanthoides marshalli* is primarily characterized by its slender skeletal outline, long and stout genal spines, short intergenal spines, and no axial spines except for the long medial spine on thoracic segment 8. It differs from *Z. liddelli* by having a narrower skeletal outline, longer preglabellar field, more robust genal spines, shorter intergenal spines, absence of axial spines except that on thoracic segment 8, and shorter falcate tips on the thoracic
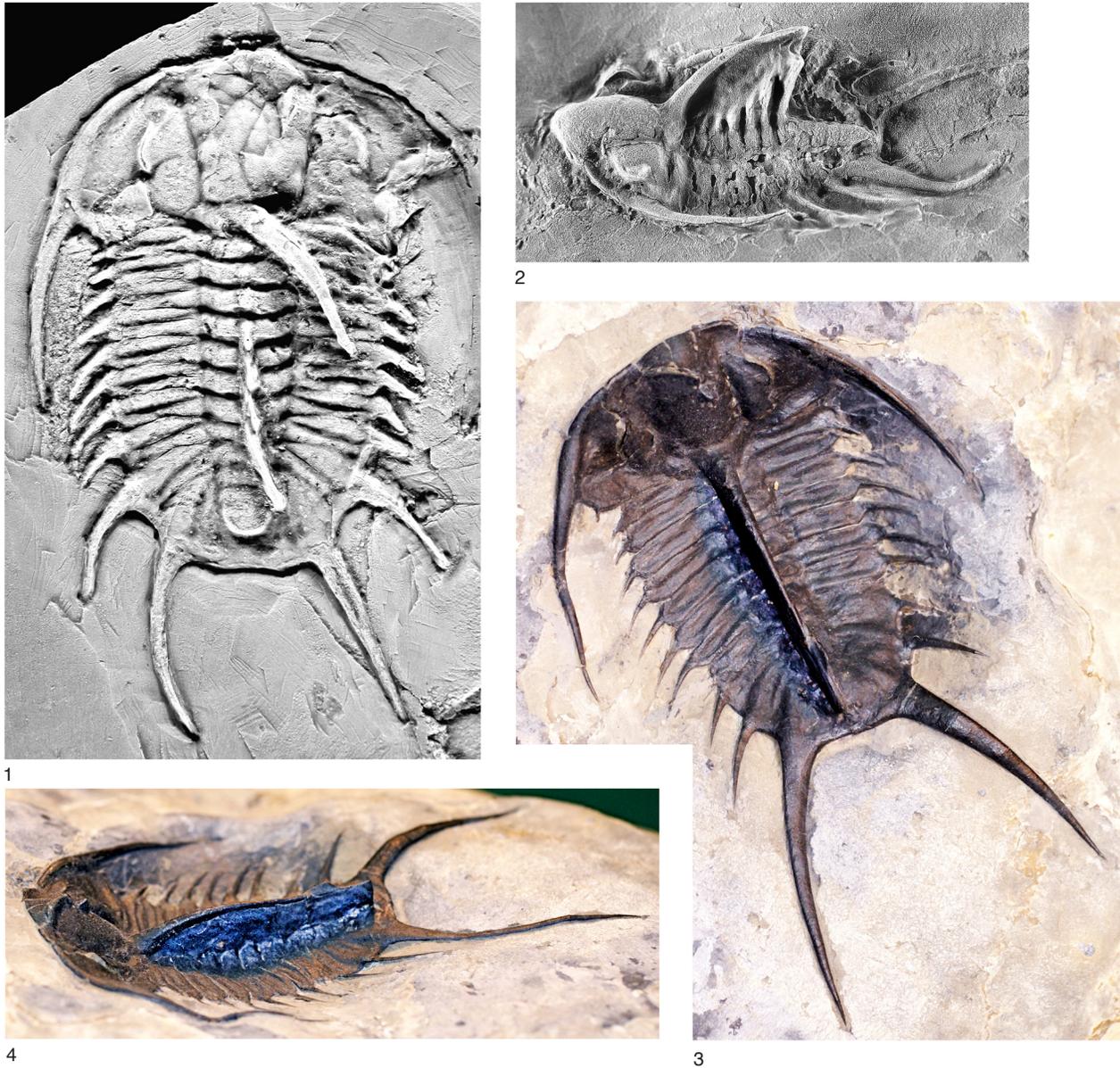
Figure 11. *Olenoides vali* new species, upper 30 m of the Wheeler Formation, Drum Mountains. *1*, Holotype exoskeleton, UU 10051.18, length including spines 72 mm; the right genal spine is missing and a healed injury to the right side of the cephalon and two anterior thoracic segments presumably resulted from a failed predatory attack, deformation of other spines likely resulted from taphonomic processes; *2*, small exoskeleton in oblique view showing medial thoracic spines rising beneath the occipital spine, length including pygidial spines 33 mm, loaned by Dustin Rooks and prepared by David Comfort; *3–4*, exoskeleton in dorsal and oblique views, having upturned cephalon, flattened axial spines, deformed left genal spine, and minor restoration, length including spines 81 mm (photos courtesy of Mark Marshall).

pleurae. It differs from *Z. typicalis* in having a narrower cephalon, longer preglabellar field, shorter intergenal spines, more advanced and shorter genal spines, and shorter tips on the thoracic pleurae.

Zacanthoides marshalli is the first species of the genus and only the second species of the order Corynexochida demonstrated to have a functional rostral-hypostomal suture (Fig. 13.2). The taxonomic significance of that character is discussed in the introductory section on High-level Classification of Trilobites (p. 6–7 herein).

Occurrence.—The species is rare in the *Glossopleura* Zone of the uppermost Spence Shale in the Wellsville and Bear River mountains.

ZACANTHOIDES TYPICALIS (Walcott, 1886)
Figure 14

Olenoides typicalis Walcott, 1886, p. 183–184, pl. 25,*2,2a*.
Zacanthoides typicalis (Walcott). Walcott, 1888, p. 165; Pack, 1906, p. 299, pl. 3,*2,2a–f;* Grabau and Shimer, 1910, p. 273, fig. 1570; Walcott, 1913, pl. 24,*2;* Shimer and Shrock, 1944,
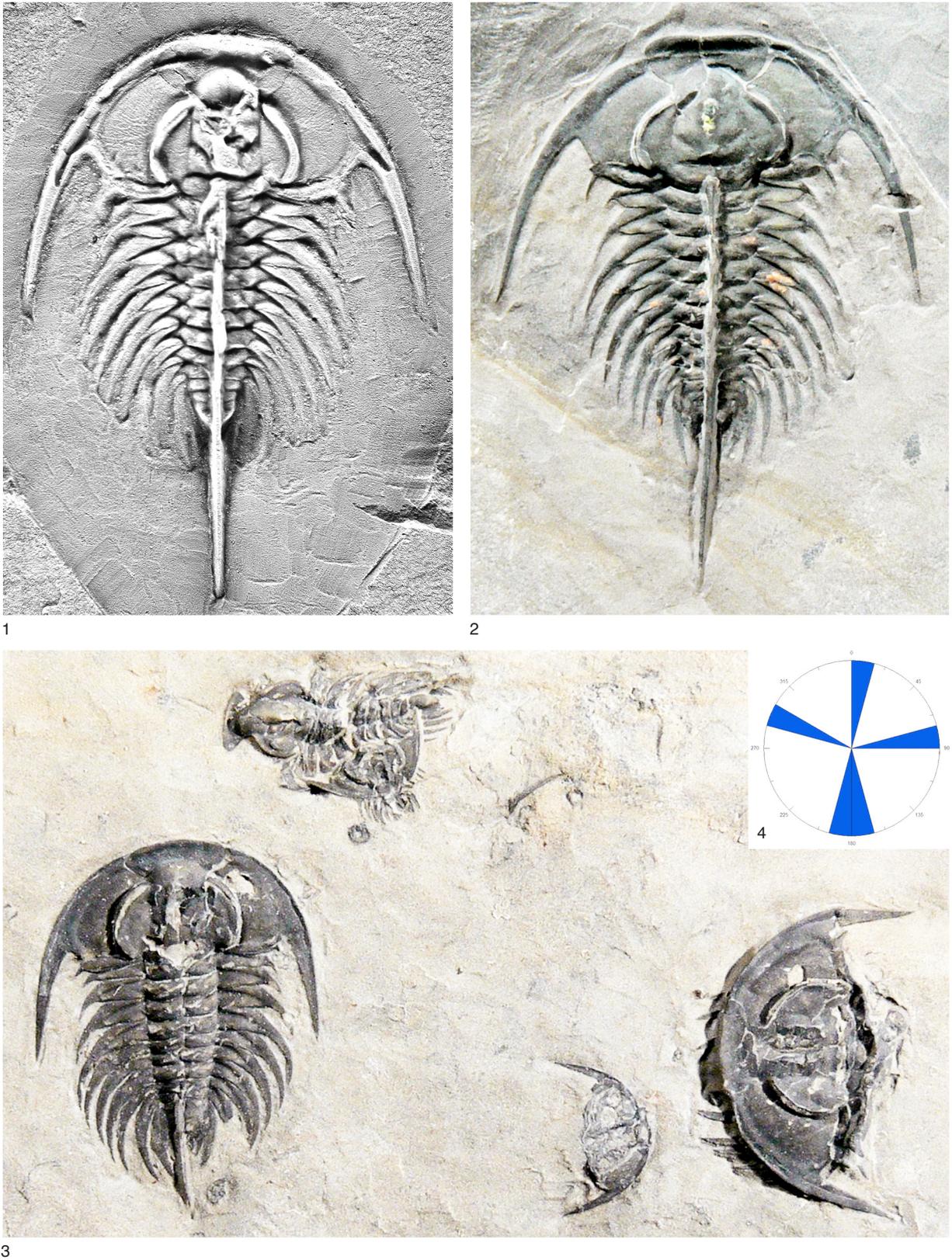
Figure 12. *Zacanthoides liddelli* new species, Spence Shale. *1*, Holotype exoskeleton, Wellsville Mountain, length including axial spine 30 mm, UU 10051.22, donated by Val Gunther; *2*, dorsal exoskeleton, Wellsville Mountain, BPM 1007, length including axial spine 37 mm, photo courtesy of David Comfort; *3*, smaller specimens including an outstretched dorsal exoskeleton (lower left, length 18 mm), a molt assemblage with superimposed enrolled exoskeleton (upper), an enrolled exoskeleton (lower right), and a separated cephalon retaining the librigenae (lower center), Bear River Range (cycle 3 of Liddell, Wright, & Brett, 1997), photo courtesy of Jacob Skabelund; *4*, rose diagram showing orientations of trilobite exoskeletons on slab in view *3*. Specimens (n = 5) were measured along mean axial direction with the cephalon pointing forward and plotted in 15° classes.

Figure 13. *Zacanthoides marshalli* new species, uppermost Spence Shale. *1*, Holotype exoskeleton in dorsal view with the anterior glabella indented and broken above the slightly displaced and partly exposed hypostome, UU 10051.20, length without spines 18 mm, from the top of parasequence 8 of Liddell, Wright, and Brett (1997) in Antimony Canyon, Wellsville Mountain, donated by Mark Marshall; *2*, exoskeleton in ventral view showing hypostome (*h*) disconnected from rostral plate (*rp*) and resting on ventral glabellar surface, providing evidence of a functional rostral-hypostomal suture, UU 10051.21, length without spines 22 mm, locality 122 in the Bear River Range (specimen collected and prepared by Paul Jamison).

p. 619, pl. 257,*20–22;* Palmer, 1954, p. 70–71, pl. 15,*9;* Levi-Setti, 1975, pls. 66–67; Levi-Setti, 1993, pls. 73–74; Bonino and Kier, 2009, tavola, 1.1; 2010, pl. 4.1.

not *Zacanthoides typicalis* Bonino and Kier, 2009, tavola 29.c (=*Z. liddelli* n. sp.).

Emended diagnosis.—*Zacanthoides* with relatively large cephalon. Glabella parallel sided to weakly tapering forward. Preglabellar field and upturned anterior cranidial border about equal in sagittal width. Genal spines barely advanced, unusually thick and long, may extend as far rearward as do spines of pygidium. Intergenal spines slender and moderately long. Thoracic pleurae with falcate tips that progressively lengthen rearward. Thoracic segment 8 having large, long axial spine that extends well beyond terminal spines of pygidium. Other thoracic rings having medial axial node or incipient spine. Pygidium subrectangular with long outer pair of rear marginal spines and shorter inner marginal spines.

Discussion.—Nearly entire dorsal exoskeletons of *Zacanthoides typicalis* are illustrated, and based on these specimens, the species diagnoses of Walcott (1886, p. 183) and Palmer (1954, p. 70–71) are emended to include additional morphological information. The species is characterized by exceptionally long, robust, and barely advanced genal spines and an unusually long axial spine on thoracic segment 8. These characters alone distinguish it from all other named species in the genus.

Occurrence.—Chisholm Shale near Pioche, Nevada, and upper Spence Shale at Wellsville Mountain, both localities in the *Glossopleura* Zone.

Order PTYCHOPARIIDA Swinnerton, 1915
Family ALOKISTOCARIDAE Resser, 1939

Remarks.—From phylogenetic analysis of species of *Alokistocare* and similar Laurentian taxa, Sundberg (1999) restricted the family Alokistocaridae to species occurring in the Topazan Stage (*sensu* Sundberg, 2005; or lower part of the Marjuman Stage, *sensu* Palmer, 1998b) as used in Laurentia. The base of the Topazan Stage coincides with the base of the *Ehmaniella* Zone. The Topazan Stage corresponds to the upper part of provisional Stage 5 of the developing global chronostratigraphy (Babcock and others, 2005; Peng and Babcock, 2008; Babcock, Robison, and Peng, 2011). Closely similar species from the subjacent Delamaran Stage (of Laurentian usage), including the *Glossopleura* Zone, were assigned by Sundberg to *Amecephalus*, which he excluded from the Alokistocaridae and left unassigned at the family level. In summarizing generic differences, Sundberg and McCollum (2000) subsequently stated that "*Amecephalus* differs from *Alokistocare* in having a poorly developed occipital ring and furrow, strap-like posterior area of the fixigena, and a pygidium with poorly defined anterior pleural bands that do not project from the border
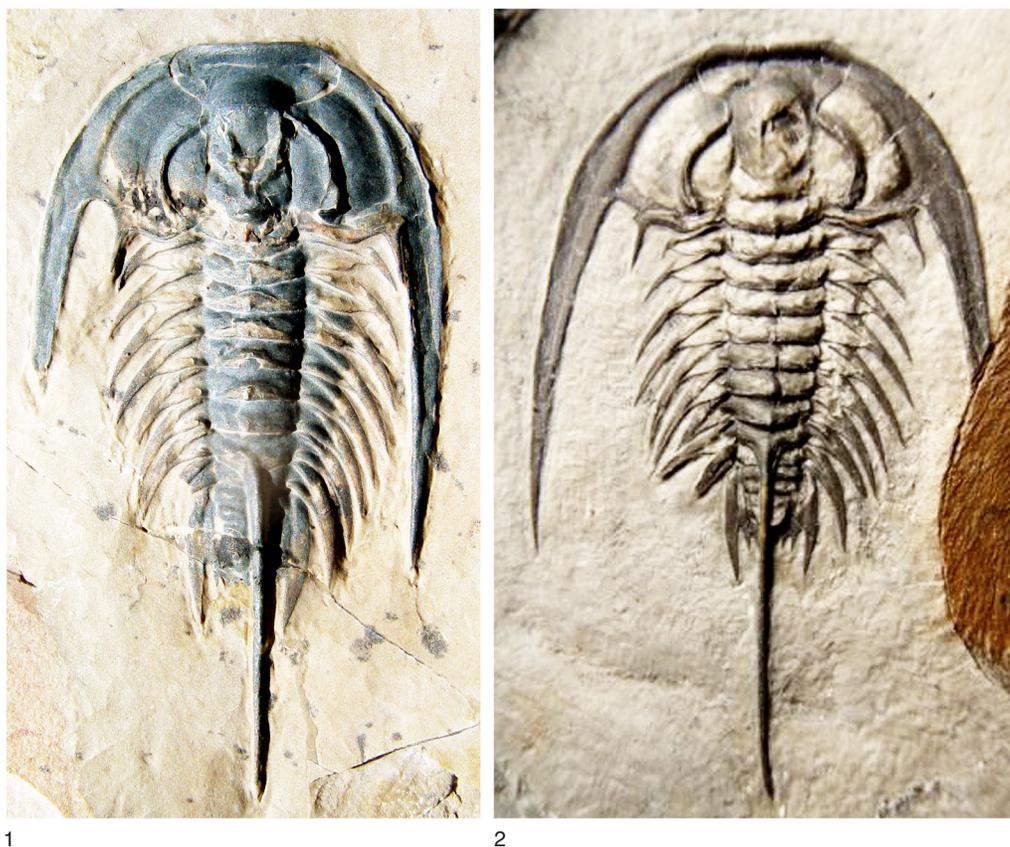
Figure 14. *Zacanthoides typicalis* (Walcott, 1886); *1*, topotype exoskeleton, Chisholm Formation near Half Moon mine, Pioche District, Nevada, length including medial spine 46 mm (photo courtesy of Carlo Kier); *2*, exoskeleton, 47 m above the base of the Spence Shale in Miners Hollow, Wellsville Mountain, length including medial spine 45 mm (prepared and photographed by Paul Jamison).

area . . . .” Comparing examples of *Amecephalus arrojosensis* (Sundberg and McCollum, 2000, figs. 5.1–5.13) with those of *Alokistocare subcoronatum* (Sundberg, 1999, figs. 5.1–5.7 and 6.1–6.14), we interpret the generic differences cited by Sundberg to be relatively minor. Greater effacement of dorsal furrows on the pygidium of *A. arrojosensis* is notable, but that difference is one of degree and not presence or absence. We regard additional generic differences listed by Sundberg (1999, p. 1131) to be taxonomically minor. Other differences between *A. arrojosensis* and *A. subcoronatum*, such as those in the anterior margin of the pygidium, and outline and length of the pygidial axis, are treated as being of species-level rather than genus-level significance. Alternatively, we interpret the species assigned by Sundberg (1999, fig. 3) to *Amecephalus*, *Alokistocare*, and *Altiocculus* to likely represent parts of a monophyletic lineage. Whether those species are assigned to a single genus (*Alokistocare* having priority) or to three genera, in our opinion, is arbitrary. Pending further phyletic analysis, we here assign a new species from the *Glossopleura* Zone of the Spence Shale to *Amecephalus*. In addition, we follow Jell and Adrain (2003) in assigning *Amecephalus* to the family Alokistocaridae.

Genus AMECEPHALUS Walcott, 1924

Type species.—*Ptychoparia piochensis* Walcott, 1886, p. 201.

The diagnosis of *Amecephalus* by Sundberg and McCollum (2000) is expanded here to include specimens having axial spines. Variation in the presence or absence of axial spines is common in other trilobite genera, including *Bolaspidella*, *Ehmaniella*, *Glossopleura*, *Olenoides*, and *Ptychoparella,* represented in this study.

AMECEPHALUS JAMISONI new species
Figure 15

Diagnosis.—*Amecephalus* with long, prominent medial spines on occipital ring and thoracic segments 4 to 12, and variably present on thoracic segments 1 to 3. Glabella moderately tapered, S1 and S2 well developed, S3 and S4 weak. Anterior branches of facial suture strongly divergent. Genal spines moderately long. Thorax having as many as 17 segments, with falcate pleural tips progressively lengthening rearward on anterior thorax and progressively shortening rearward on posterior thorax. Pygidium micropygous, alate with posterior median notch.

Etymology.—After Paul Jamison, who collected and prepared the holotype. He also collected and generously donated other specimens used in this study.

Types.—Holotype, UU 10051.60 (Figs. 15.1–15.2).

Discussion.—*Amecephalus jamisoni* differs from all described species of *Amecephalus* by the presence of an occipital spine and a medial axial spine on most thoracic segments. Its pygidium is known from an unnamed Spence Shale specimen illustrated on the Internet (Marshall, 2011).
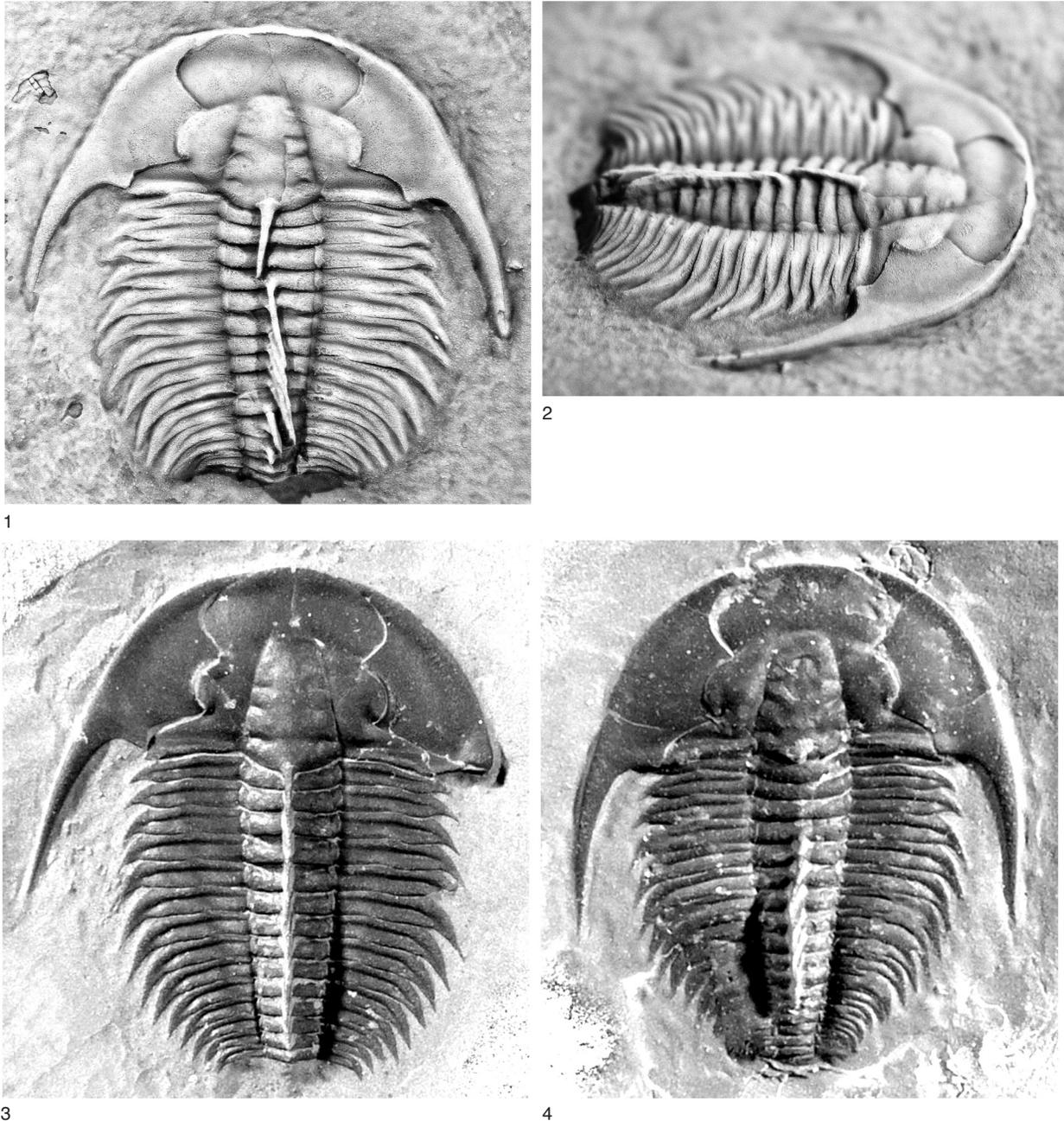
Figure 15. *Amecephalus jamisoni* new species, 35 m above the base of the Spence Shale in Miners Hollow, Wellsville Mountain. *1–2,* Holotype with its posterior thorax and pygidium likely enrolled or folded beneath the visible part of its exoskeleton, in dorsal (*1*) and oblique (*2*) views, UU 10051.60, length 22 mm, specimen prepared by Paul Jamison and obtained from James Cook; *3,* exoskeleton showing medial axial spines on each thoracic segment (photo courtesy of David Comfort); *4,* exoskeleton showing medial axial spines on thoracic segments 4 to 12, and an incipient spine on the third axial ring (photo courtesy of David Comfort).

Most known specimens of *A. jamisoni* are preserved with the micropygous pygidium and some segments of the posterior thorax projecting downward into the matrix, or tucked under the dorsal surface (see especially Figs. 15.1–15.2). This manner of preservation is interpreted as taphonomic in origin and related to loose flopping of the pygidium as the specimen was carried in a current prior to burial.

Occurrence.—*Amecephalus jamisoni* is rare in the middle part of the Spence Shale at Wellsville Mountain.

Genus EHMANIELLA Resser, 1937

Type species.—*Crepicephalus (Loganellus) quadrans* Hall and Whitfield, 1877, p. 238.

The generic diagnosis by Sundberg (1994, p. 53–54) is followed.

EHMANIELLA WHITEI new species
Figure 16

Diagnosis.—*Ehmaniella* having broadly ovate exoskeletal outline. Glabella moderately tapered, lateral furrows weak. Occipital ring with
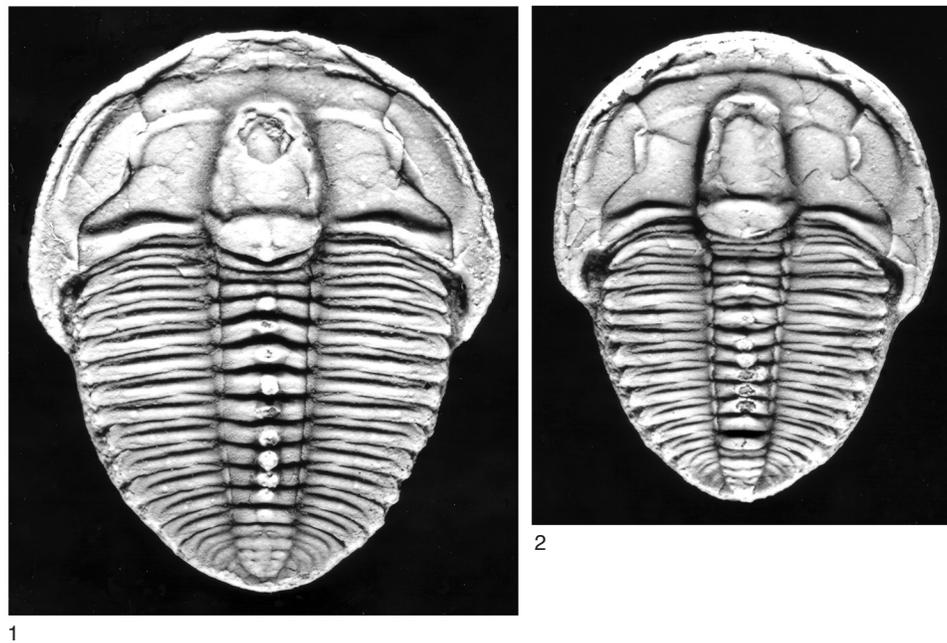
Figure 16. *Ehmaniella whitei* new species, preserved with calcite cone-in-cone encrustation on the ventral surface, Wheeler Formation, locality 114, House Range, specimens donated by Lloyd and Metta Gunther. *1*, Holotype exoskeleton, UU 10051.23, length 12 mm; *2*, paratype exoskeleton, UU 10051.24, length 10 mm.

incipient spine on rear margin. Eye ridges prominent, distally merging into palpebral lobes. Genal spine broad based, distally curving inward, almost reaching tip of thoracic segment 5. Cephalic surface having sparse, scattered granules. Thorax containing 13 segments; axial ring of segments 4 to 13 having medial spine. Pygidium small, alate, axis containing 4 rings and terminal piece.

Etymology.—After William W. White, for advancing knowledge of the Wheeler Formation and its fauna in the Drum Mountains (White, 1973).

Types.—Holotype exoskeleton, UU 10051.23 (Fig. 16.1); paratype, UU 10051.24 (Fig. 16.2).

Discussion.—*Ehmaniella whitei* most closely resembles *E. fronsplanata* Sundberg (1994), which may be a sister species. *Ehmaniella whitei* differs from all species of *Ehmaniella* by the presence of axial spines on the thorax. It further differs from *E. fronsplanata* by the presence of an incipient spine rather than a weak node on the occipital ring, and the genal spines are curved rather than straight. *Ehmaniella fronsplanata* occurs in the upper Whirlwind and lower Swasey formations and coeval strata in the eastern Great Basin, about midway through the *Ehmaniella* Zone.

Occurrence.—*Ehmaniella whitei* is rare at locality 114 in the middle part of the Wheeler Formation, House Range. Its presence in the lower *Bolaspidella* Zone is the highest stratigraphic occurrence reported for *Ehmaniella*. Associated trilobites at the locality, including abundant and diverse agnostoids, are part of a typical open-shelf biota.

Family ASAPHISCIDAE Raymond, 1924
Genus ITHYCEPHALUS Resser, 1938

Type species.—*Ithycephalus typicalis* Resser, 1938, p. 82.

Emended diagnosis.—Exoskeleton isopygous. Cephalon semicircular with narrow and shallow axial furrow, narrow anterior border, and no preglabellar field. Glabella wide, unfurrowed, and nearly rectangular with very weak lateral constriction midway along anterior half. Palpebral area of fixigenae narrow. Eyes slightly anterior from glabellar midpoint, length about one-fourth that of glabella. Posterior section of facial suture reaching cephalic margin inside acute genal angle, which has no spine. Hypostome wide anteriorly, attaching at hypostomal suture to rostral plate of similar width (tr.). Thorax having seven segments with shallow pleural furrows. Pygidium large, semicircular, with mostly effaced furrows; axis tapers slightly to rounded terminus, length about three-fourths that of pygidium.

Discussion.—Resser (1938) erected *Ithycephalus* for three tiny cranidia of *I. typicalis*, which are probably immature. The type cranidia are from the lowermost bed of the Nolichucky Formation (*Cedaria* Zone) in Tennessee, and Rasetti (1965) illustrated an additional cranidium from the uppermost bed of the underlying Maryville Limestone. Resser's (1938, p. 82) brief generic diagnosis is emended to include information from two new, larger, nearly entire exoskeletons from the upper Weeks Formation (*Cedaria* Zone) in Utah. The Utah cranidia mainly differ from the smaller Tennessee cranidia by having a narrower palpebral area of the fixigena, slightly more posterior eyes, and an occipital ring of more uniform length. Such differences commonly developed during trilobite ontogenies (compare Fig. 19) and have questionable taxonomic significance. Thus, the few described characters of *I. typicalis* are regarded to be inadequate for taxonomic comparison at the species level, and the more complete Utah specimens are assigned to a new species, *I. stricklandi*.

Newly revealed characters of *Ithycephalus* suggest a likely affinity with *Blountia*, from which it mainly differs in anterior shape of the glabella, absence of a preglabellar field, and greater effacement of dorsal furrows. The glabella of *Blountia* tapers forward and has a
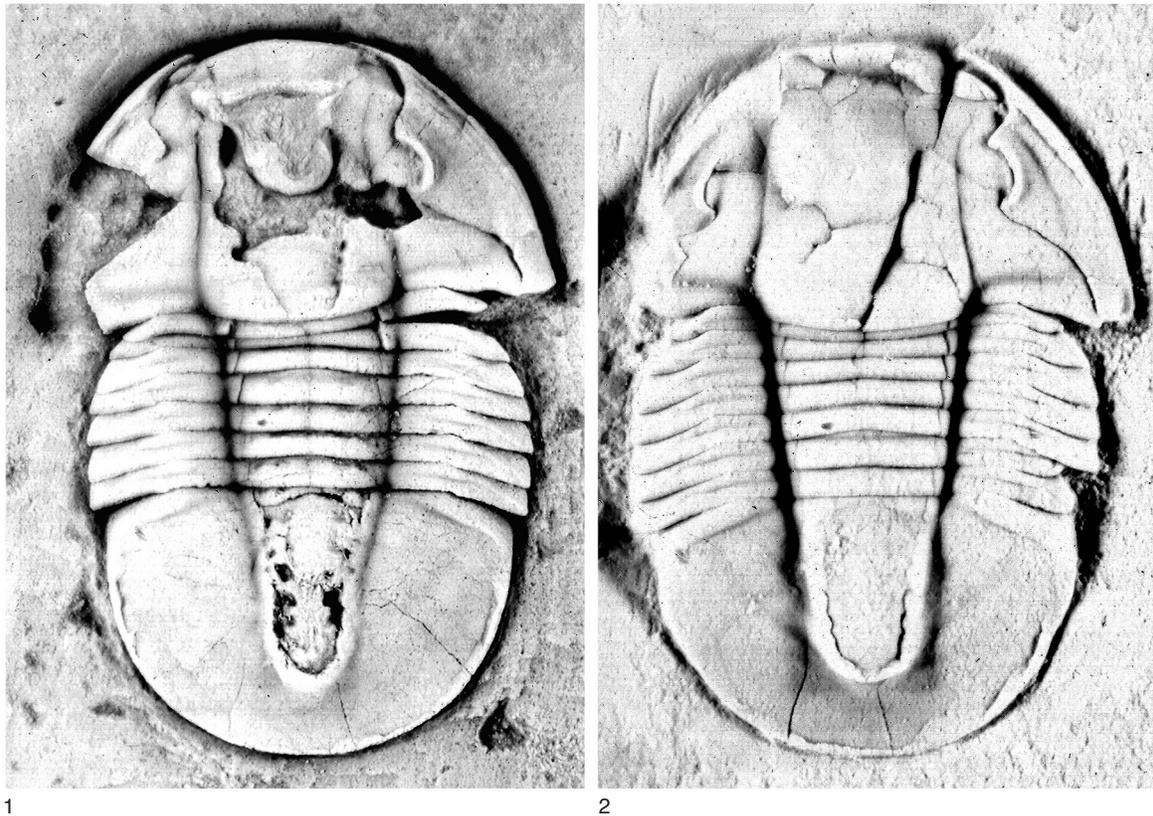
1   2

Figure 17. *Ithycephalus stricklandi* new species, upper Weeks Formation, House Range. *1*, Holotype, UU 10051.25, length 20 mm, locality 824; some of the anterior glabella is broken away, partly exposing the underlying rostral plate and hypostome, which are slightly displaced along the hypostomal suture; *2*, dorsal exoskeleton in the collection of Robert Schacht, which was kindly loaned for study and photography, length 17 mm, with healed injuries to the left librigena and the right side of thoracic segments 6 and 7.

well-rounded front, whereas the glabella of *Ithycephalus* is less tapered and more bluntly terminated. Presence of a short preglabellar field indicates that *Blountia* may have a natant hypostome, a holaspid character of most ptychoparioids. In comparison, *Ithycephalus* has a conterminant hypostome, a likely secondary condition derived by neoteny.

Ithycephalus resembles some Cambrian corynexochoid trilobites in having an elongate glabella, a reduced number of thoracic segments, and a large pygidium. Because these are also juvenile characters of trilobites, their presence in *Ithycephalus* is just as likely the result of neotenous convergence as close genetic affinity. Most Cambrian corynexochoids differ from *Ithycephalus* by the absence of a hypostomal suture and fusion of rostral and hypostomal plates.

ITHYCEPHALUS STRICKLANDI new species
Figure 17

Diagnosis.—*Ithycephalus* with a shallow occipital furrow and an occipital ring of near uniform length.

Etymology.—After Douglas K. Strickland, for contributions to knowledge of the Weeks Formation and its biota. Numerous fossils collected by Strickland from the Weeks Formation and coeval strata of the Great Basin are housed in the University of Kansas Museum of Invertebrate Paleontology.

Holotype.—Exoskeleton, UU 10051.25 (Fig. 17.1).

Discussion.—The occipital furrow of *Ithycephalus stricklandi* is shallower than that of *I. typicalis,* and its occipital ring is not medially expanded. Growth series are needed to evaluate the possibility that these differences intergrade during ontogeny.

Occurrence.—*Ithycephalus stricklandi* is rare in the upper Weeks Formation, *Cedaria* Zone, at locality 824 in North Canyon, House Range.

Family CREPICEPHALIDAE Kobayashi, 1935
Genus COOSELLA Lochman, 1936

Type species.—*Coosella prolifica* Lochman, 1936, p. 39. The generic diagnosis by Palmer (1955, p. 728) is followed.

COOSELLA KIERI new species
Figures 18, 28

Coosella sp. Type 1 Bonino and Kier, 2009, tavola 1.4, 7.9, 40.d.
Coosella sp. Type 2 Bonino and Kier, 2009, fig. 171.g; tavola 5.7, 40.c.
Maryvillia arion. Bonino and Kier, 2009, tavola 42.c.
Coosella sp. Bonino and Kier, 2010, pls. 4.4, 8.7, 62.c,d.
Coosella n. sp. Bonino and Kier, 2010, pl. 63.a.

Diagnosis.—*Coosella* with very short, angular, genal spines. Cephalon semicircular, border nearly uniform in width and well defined by narrow border furrow. Glabella moderately tapered and strongly rounded at front. Thorax containing 11 or 12 segments;
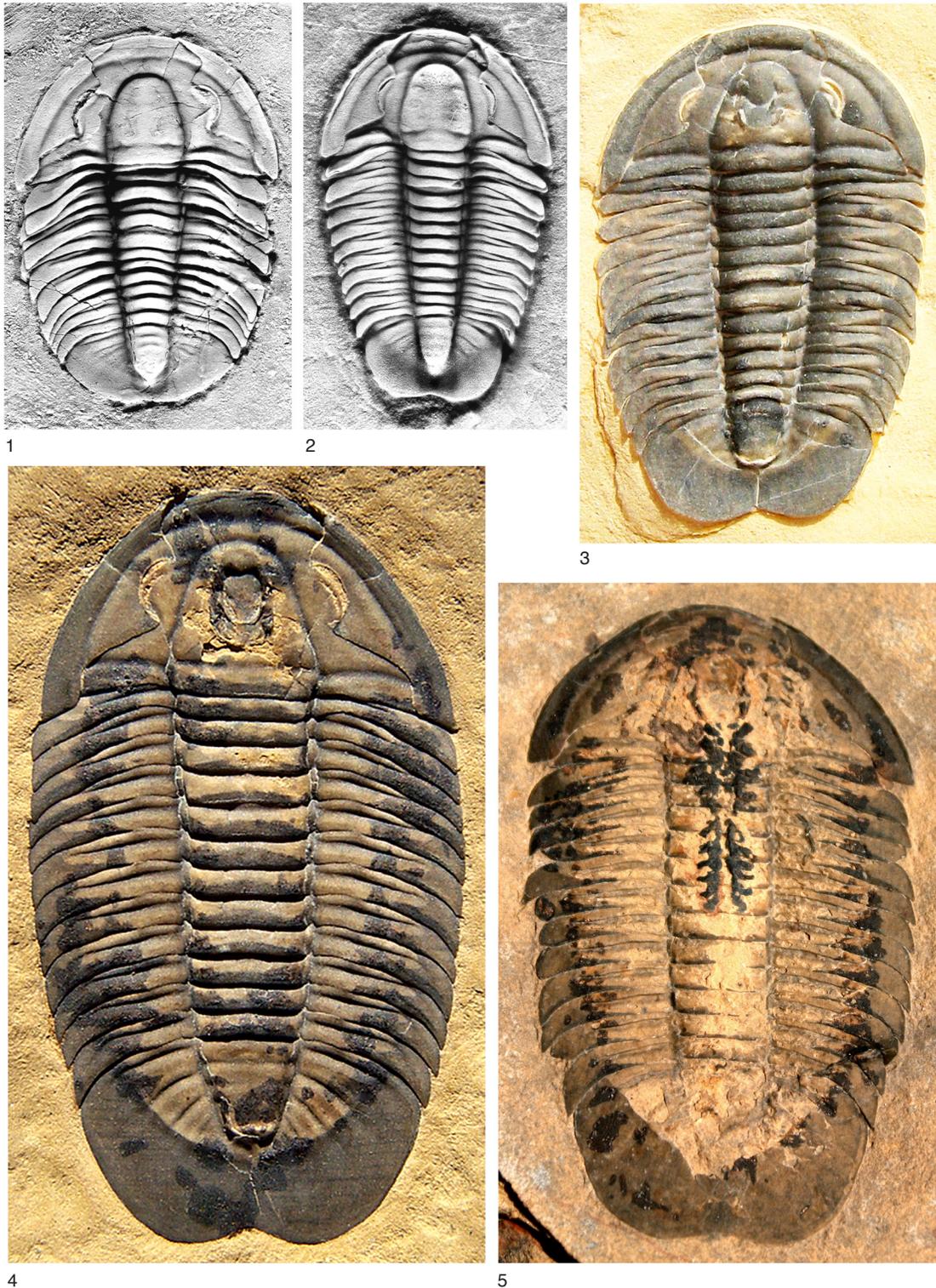
Figure 18. *Coosella kieri* new species, upper Weeks Formation, North Canyon, House Range. *1*, Paratype exoskeleton, BPM 1015, length 27 mm; *2*, paratype exoskeleton, BPM 1016, length 22 mm; *3*, paratype exoskeleton, BPM 1017, length 25 mm (photo courtesy of Enrico Bonino); *4*, holotype exoskeleton, glabella crushed and partly broken away, exposing the hypostome, UU 10051.26, length 39 mm (photo courtesy of Quintin Sahratian); *5*, dorsal exoskeleton with exposed dark filling of anterior alimentary canal and short, laterally projecting stubs of digestive diverticula, BPM 1008, length 45 mm (photo courtesy of Enrico Bonino).

pleural furrows narrow, moderately deep; lateral tips acutely angular. Pygidium with prominent median indentation of rear margin. Pygidial axis moderately tapered with bluntly rounded terminus, length about half that of pygidium, ring furrows weaken rearward. Pygidial border wide, ill defined, and mostly unfurrowed. Pygidial length, relative to cephalic length, increased during holaspid ontogeny from less than 65 percent to more than 130 percent.

Etymology.—After Carlo Kier, for promoting knowledge of trilobites (Bonino and Kier, 2009, 2010).

Types.—Holotype, UU 10051.26 (Fig. 18.4); paratypes, BPM 1015–1017 (Figs. 18.1–18.3), BPM 1008 (Fig. 18.5), and BPM 1011 (Fig. 28.1).

Discussion.—Although more than 20 species of *Coosella* have been described, they are mostly known from disarticulated cranidia and pygidia. Comparable characters of *Coosella kieri*, known from many complete dorsal exoskeletons, do not appear to match closely those of any named species.

An incomplete alimentary tract, preserved by a black mineral, presumably apatite, is present in one specimen of *C. kieri* (Fig. 18.5). Visible are the rim of the stomach cavity overlying the hypostome and a narrow gut lining flanked by bilateral midgut glands in the axial portion of the anterior thorax.

Occurrence.—Upper Weeks Formation, *Cedaria* Zone, locality 824 in North Canyon, House Range.

Family LONCHOCEPHALIDAE Hupé, 1955
Genus PTYCHOPARELLA Poulsen, 1927

Type species.—*Ptychoparella brevicauda* Poulsen, 1927, p. 280, by original designation.

Emended diagnosis.—Micropygous lonchocephalids with opisthoparian or gonatoparian facial suture. Anterior sections of facial suture weakly convergent to weakly divergent. Anterior border and preglabellar field commonly about equal in sagittal length. Glabella rectangular to moderately tapered anteriorly; L1 may have slight lateral inflation. Lateral glabellar furrows variable in depth to effaced; S1 curves obliquely rearward and may be weakly bifurcate, S2 oblique rearward, S3 transverse or slightly oblique forward. Palpebral lobes of small to moderate size, usually opposite or slightly forward from glabellar midpoint. Thorax containing 13 to 20 segments. Pygidium alate with 1 to 4 rings, width generally between 2 and 3 times length. Dorsal skeletal surface may have fine, dense granulation.

Discussion.—Based on further taxonomic review, the diagnosis of *Ptychoparella* by Blaker and Peel (1997, p. 124) is slightly expanded here. We concur with them in regarding *Syspacephalus* Resser, 1936, *Elrathina* Resser, 1937, and *Eoptychoparia* Rasetti, 1955, to be subjective junior synonyms of *Ptychoparella*.

Variable characters of *Ptychoparella* include glabellar form, depth of lateral glabellar furrows, presence or absence of genal and axial spines, and number of thoracic segments. Opisthoparian and gonatoparian species are about equally common, and these conditions directly correlate with the presence or absence of genal spines. Opisthoparian species generally have a weakly tapered glabella and deeper lateral furrows, whereas gonatoparian species commonly have a rectangular glabella and weaker or effaced lateral furrows. The number of thoracic segments generally increased during generic phylogeny, and axial spines appeared only late in generic phylogeny.

Ptychoparella is here assigned to the Lonchocephalidae. It is the oldest genus presently included in the family. As in other lonchocephalids, the glabella of *Ptychoparella* commonly varies from parallel sided to moderately tapered, and the pattern of lateral glabellar furrows is similar. The S1 furrows invariably curve inward and backward, are variably bifurcating, and almost isolate basal lobes. The pygidium, although small, is alate, as is usual for lonchocephalids.

Ptychoparella is common and widespread in open-marine deposits of Laurentia. Biostratigraphers earlier recognized a mid-Middle Cambrian *Bathyuriscus-Elrathina* [=*Ptychoparella*] Biozone in North America. However, the occurrence of both *Bathyuriscus* and *Ptychoparella* has proved to be environmentally controlled, and both genera now are known to have much longer stratigraphic ranges. *Ptychoparella* presently has an observed stratigraphic range from the upper *Olenellus* Zone as traditionally defined (provisional Stage 4) through the lower *Bolaspidella* Zone (Drumian Stage).

PTYCHOPARELLA LLOYDI new species
Figure 19

Diagnosis.—*Ptychoparella* with opisthoparian facial suture, anterior branches slightly convergent. Rostral plate transversely wide, sagittally narrow. Cranidium having broad, low anterior arch. Glabella rectangular to slightly tapered, without lateral furrows, but homologous muscle scars may be defined by absence of surface granulation. Occipital ring with central node. Anterior border and preglabellar field of cranidium about equal in sagittal width. Genal spines short. Thorax having 17 to 19 segments; axial rings on segments 3 to 12 or 13 having median spinule or short spine; most pleurae having spinal tip. Pygidium micropygous, width approximately 2.5 to 3.5 the length, with posterior arch and medially indented rear margin; axis showing one weakly defined ring and long terminal piece. Exoskeletal surface finely granulose, except in furrows and on muscle scars.

Etymology.—After Lloyd Gunther, for extraordinary contributions to knowledge of Cambrian biotas.

Holotype.—Exoskeleton with missing right librigena, UU 10051.27 (Fig. 19.1).

Discussion.—*Ptychoparella lloydi* is the only species of *Ptychoparella* known to have a median spine on some axial rings of the thorax. In characters of the glabella and frontal area, it closely resembles specimens previously assigned to *P. parallela* (Rasetti, 1951, p. 222–223, pl. 33,*19–22*). However, many complete specimens of *P. cordillerae* (Rominger, 1888) in collections of the U.S. National Museum of Natural History show a range of variation that encompasses all described characters of *P. parallela*. Thus, *P. parallela* may be a junior synonym of *P. cordillerae*, but this cannot be verified because the librigena of *P. parallela* is not known. *P. cordillerae* lacks genal spines, whereas *P. lloydi* has genal spines.

Ptychoparella lloydi differs from *P. wheelera* (Sundberg, 1994, p. 109–111, figs. 70.1–70.5) by its shorter preglabellar field, a node rather than a spine on the occipital ring, and longer genal spines. *P. wheelera* occurs near the Swasey-Wheeler boundary in the House Range and coeval strata in eastern Nevada.

Cranidia of *Ptychoparella lloydi* also resemble cranidia from Newfoundland that were assigned by Young and Ludvigsen (1989, p. 24, pl. 9,*8–13*) to *Elrathina parallela*. Cranidia and librigenae of *P. lloydi* also resemble some from North Greenland assigned by
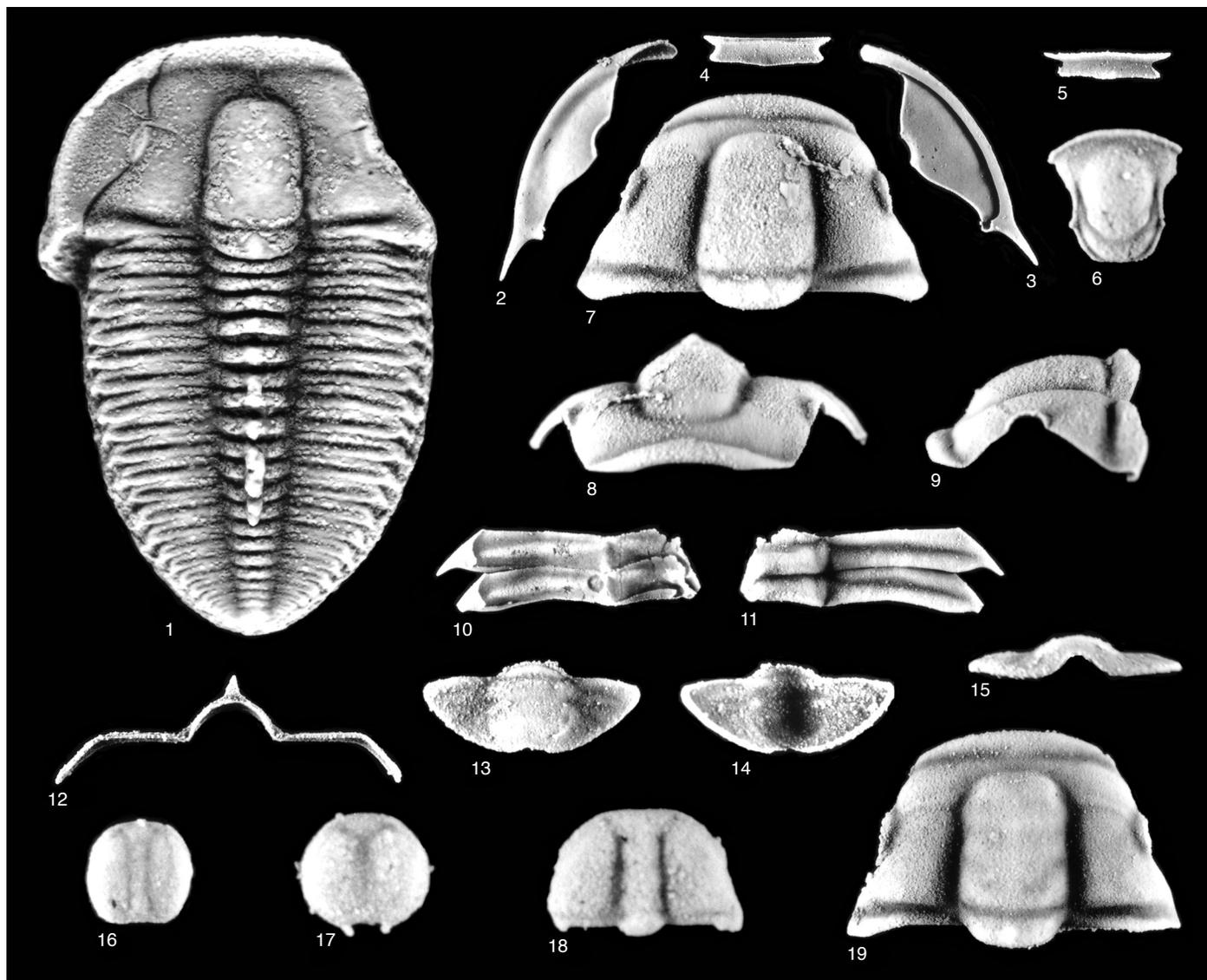
Figure 19. *Ptychoparella lloydi* new species, Wheeler Formation. *1*, Holotype lacking right librigena, locality 116, House Range, UU 10051.27, length 11 mm, donated by Lloyd and Metta Gunther; *2–19*, disarticulated and silicified sclerites from locality 520, Drum Mountains; *2–3*, left librigena in dorsal and internal views, UU 10051.28, length 7 mm including genal spine; *4–5*, rostral plate in external and internal views, UU 10051.29, length 0.5 mm; *6*, hypostome in external view, UU 10051.30, length 1.5 mm; *7–9*, cranidium in dorsal, front, and left lateral views with view *8* showing low anterior arch, UU 10051.31, length 4.5 mm; *10–11*, parts of two thoracic segments in ventral and dorsal views, UU 10051.33, width 4.5 mm; *12*, thoracic segment with medial spine, in posterior view, UU 10051.34, width 7 mm; *13–15*, pygidium in dorsal, ventral, and posterior views, with view *15* showing well-developed posterior arch, UU 10051.35, length 1.5 mm; *16*, early protaspid, UU 10051.36, 0.5 mm; *17*, late protaspid, UU 10051.37, 0.5 mm; *18*, early meraspid cranidium, UU 10051.38, 0.6 mm; and *19*, holaspid cranidium in dorsal view, UU 10051.32, length 4 mm.

Babcock (1994, p. 110, figs. 26.1–26.4) to *Syspacephalus* sp. 1. These all represent *Ptychoparella,* and all are from about the same biostratigraphic level. However, without knowledge of other exoskeletal parts, the specific assignment of each is problematic.

Ptychoparella lloydi is known in part from silicified specimens that reveal an ontogenetic series from the protaspid stage (Figs. 19.16–19.17) through the meraspid stage (Fig. 19.18) into the holaspid period (Figs. 19.1–19.15). The earliest known protaspid (Fig. 19.16) is highly convex, nearly smooth except for indentation of the axis, and nearly circular in outline except for a slight indentation posteriorly. A late protaspid (Fig. 19.17) shows a pair of short

marginal spines flanking the posteroaxis. The spine pair is apparently lost in the meraspid period.

Occurrence.—*Ptychoparella lloydi* ranges through much of the Wheeler Formation, lower *Bolaspidella* Zone, in western Utah. It is rare to abundant from 46 to 88 m above the base of the Wheeler Formation in the Drum Mountains and is especially common from 58 to 63 m above the base of the formation at Stratotype Ridge, where the GSSP (Global boundary Stratotype Section and Point) of the Drumian Stage is present at 62 m in section (Babcock and others, 2007). The holotype is from locality 116 in the upper Wheeler Formation, House Range.

PTYCHOPARELLA METTAE new species
Figure 20

Elrathina sp. Gunther and Gunther, 1981, p. 34, pl. 20.

Diagnosis.—*Ptychoparella* with opisthoparian facial suture, anterior branches moderately convergent. Rostral plate transversely wide, sagittally narrow. Glabella slightly tapered anteriorly with three pairs of prominent lateral furrows that progressively lengthen and deepen rearward. Occipital ring having weak medial node on anterior margin. Preglabellar field sagittally wider than anterior border. Genal spines short. Thorax containing 19 or 20 segments without medial nodes or spines. Pygidium micropygous, alate with posterior arch and weak medial indentation of rear margin; axial segmentation nearly effaced.

Etymology.—After Metta Gunther, for her many contributions to knowledge of Cambrian biotas.

Types.—Holotype exoskeleton UU 10051.43 (Fig. 20.1); paratypes UU 10051.44 and 10051.45 (Figs. 20.2–20.3). These and 12 additional paratypes (UU 10051.61–10051.72), all collected and donated by Metta and Lloyd Gunther, are reposited at the University of Utah.

Discussion.—*Ptychoparella mettae* most closely resembles *P. spencei* (Resser, 1939) from the Spence Shale but has 2 or 3 more thoracic segments. It differs from the coeval *P. lloydi* by having a more tapered glabella, well-developed lateral glabellar furrows, and an absence of spines on axial rings of the thorax.

Available specimens of *Ptychoparella mettae* illustrate variability in the exuviation style in this species. Three specimens (Figs. 20.1–20.3) are inferred molts. In one specimen, the librigenae have been shed and lost (Fig. 20.3). In another specimen, the librigenae have been shed but displaced below the articulating edges of the cranidium, and the cranidium has been displaced slightly backward (Fig. 20.1). In the third molted specimen, the cranidium has been shed and lost, but the librigenae and rostral plate are still present and displaced (Fig. 20.2).

Occurrence.—Rare in the upper Wheeler Formation, lower *Bolaspidella* Zone, at locality 794 in the House Range.

Family MARJUMIIDAE Kobayashi, 1935

Discussion.—The Marjumiidae includes many named species of rather ordinary ptychoparioids for which it is difficult to write a clearly definitive family diagnosis. The most recent attempt at a diagnosis is that by Robison (1988, p. 71), which Melzak and Westrop (1994, p. 975) claimed to have no obvious synapomorphic characters. However, Melzak and Westrop continued to use the family name but presented no alternative diagnosis. Pending publication of a better family diagnosis, that by Robison (1988) is followed.

Pratt (1992) and Melzak and Westrop (1994) discussed some taxonomic problems within the Marjumiidae. They concluded that differences between *Modocia*, previously defined as lacking pygidial spines, and *Marjumia*, previously defined as having pygidial spines, are artificial. Melzak and Westrop (1994) further regarded *Modocia* to be a junior synonym of *Marjumia*, and in support, cited two species having a single pair of incipient spines on the anterior pygidium. Alternatively, marjumiids with developing spines are here interpreted to be transitional morphotypes between *Modocia* and *Marjumia*, and the generic assignment of such morphs is deemed to be arbitrary. Full development of paired spines on the anterior pygidium is here

regarded to be an autapomorphic character distinguishing *Marjumia* from *Modocia*. Additional pairs of spines were added in later phylogenetic stages of *Marjumia*.

We agree with Melzak and Westrop (1994) that a full cladistic analysis of marjumiid genera is needed. However, pending publication of a cogent analysis supporting the synonymy of *Modocia* and *Marjumia*, we continue to recognize *Modocia* as a valid genus.

Genus MODOCIA Walcott, 1924

Type species.—*Arionellus (Crepicephalus) oweni* Meek and Hayden, 1861, p. 436.

Emended diagnosis.—Opisthoparian or rarely gonatoparian marjumiids. Glabella moderately tapered, rounded anteriorly; muscle scars usually evident rather than lateral furrows. Preglabellar field variable in sagittal width, commonly about same width as anterior border. Occipital ring with or without medial spine. Thorax containing 12 to 14 segments, each lacking a medial spine. Pygidium semicircular to alate with broad, bluntly terminated axis, margin lacking fully developed spines.

Discussion.—The diagnosis of *Modocia* by Robison (1964, p. 550) is emended to accommodate subsequently assigned species (Robison, 1988, p. 75) and new ones added here.

Genal spines were lost repeatedly during the evolutionary history of trilobites (Fortey and Owens, 1997). As diagnosed here, *Modocia* includes species that span the range from long and robust genal spines (*M. kohli* n. sp.), to short genal spines (*M. whiteleyi* n. sp.), or no genal spines (*M. comforti* n. sp.).

MODOCIA COMFORTI new species
Figure 21

Undescribed Bonino and Kier, 2009, tavola 45.d.
Modocia n. sp. Bonino and Kier, 2010, pl. 67.d.

Diagnosis.—*Modocia* with slender exoskeleton and relatively wide axis. Cephalon having gonatoparian facial suture and no genal spines. Thorax containing 13 segments. Pygidium of moderate size for genus. Pygidial axis having 3 rings and a terminal piece.

Etymology.—After David Comfort, for his exceptional preparation of many Cambrian trilobites.

Holotype.—Exoskeleton, BPM 1009 (Fig. 21.1).

Discussion.—*Modocia comforti* differs from all other species of *Modocia* by its lack of genal spines, the presence of a corresponding gonatoparian facial suture, and a relatively wide axis. Its other characters are not unusual for the genus. *M. comforti* most closely resembles *M. brevispina* Robison (1964), which mainly differs by having incipient genal spines, a corresponding opisthoparian facial suture, and 4 rather than 3 axial rings in the pygidium.

Occurrence.—*Modocia comforti* is rare in the *Cedaria* Zone of the upper Weeks Formation, House Range.

MODOCIA KOHLI new species
Figure 22

Proaulacopleura Bonino and Kier, 2009, tavola 32.e.
Modocia n. sp. Bonino and Kier, 2010, pl. 55.f.

Diagnosis.—*Modocia* having exceptionally long and robust genal spines. Anterior sections of facial suture strongly divergent. Preglabellar field sagittally wider than anterior border. Thorax containing 13 segments. Pygidium small for the genus. Pygidial axis having 3 or 4 rings.
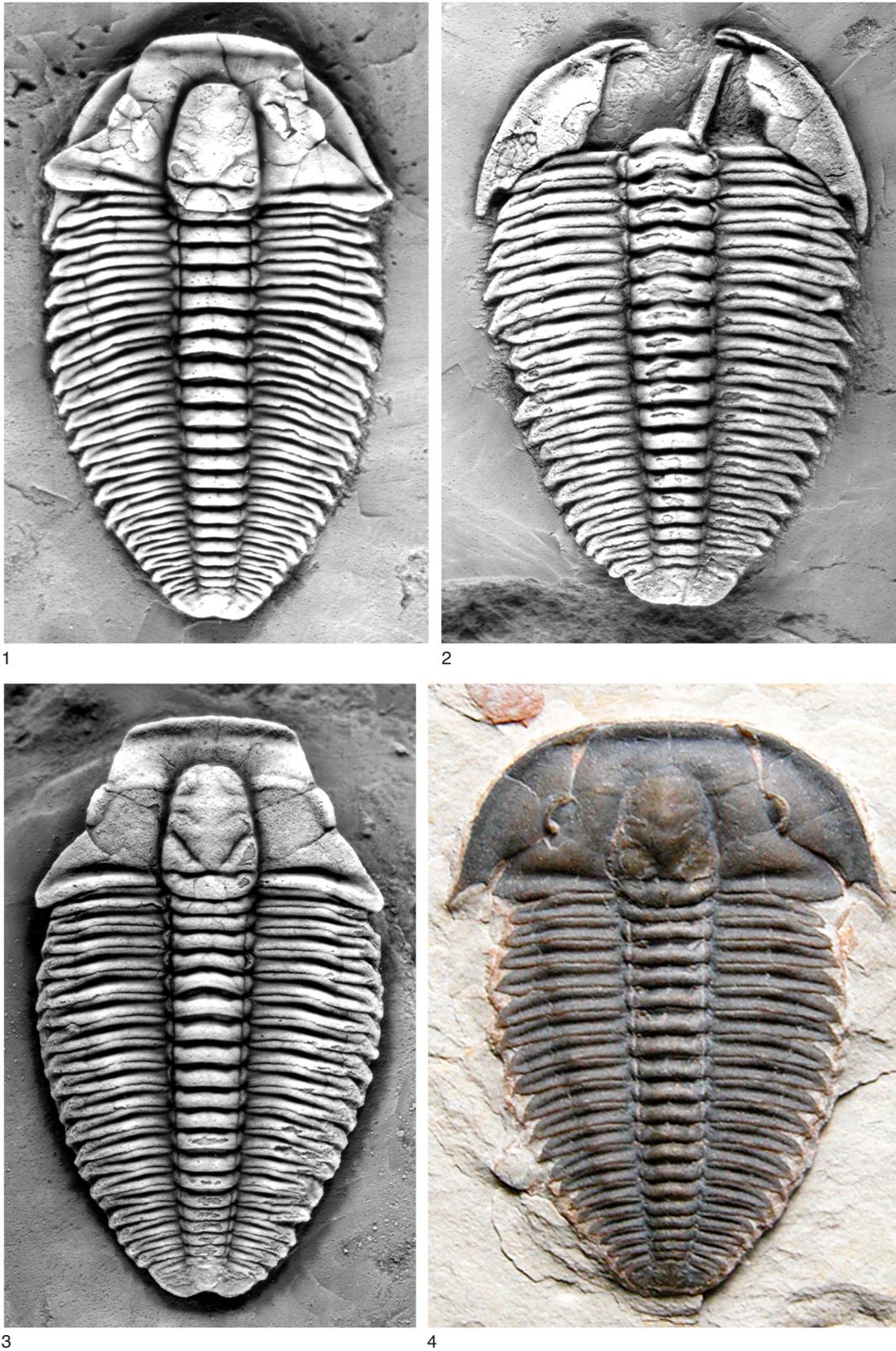
Figure 20. *Ptychoparella mettae* new species, locality 794, upper Wheeler Formation, House Range. *1*, Holotype exoskeleton, in which the librigenae have been shed but displaced below the articulating edges of the cranidium, and the cranidium has been displaced slightly backward, UU 10051.43, length 18 mm; *2*, paratype molted exoskeleton with rotated rostral plate, cranidium and hypostome are missing, UU 10051.44, length 19 mm; *3*, paratype molted exoskeleton without librigenae, UU 10051.45, length 21 mm; *4*, exoskeleton, length 15 mm (photo courtesy of Susan Halgedahl and Richard Jarrard).

Figure 21. *Modocia comforti* new species, upper Weeks Formation, North Canyon, House Range. *1*, Holotype exoskeleton, BPM 1009, length 35 mm (photo courtesy of Carlo Kier); *2*, exoskeleton (photo courtesy of David Comfort).

Etymology.—After Roy F. Kohl, who collected and donated the holotype.

Types.—Holotype, exoskeleton UU 10051.46 (Fig. 22.1). Paratypes UU 10051.47 to 10051.49 were collected and donated, one each by Lloyd Gunther, Hardy Jenkinson, and Glenn Rockers.

Discussion.—Exceptionally long and robust genal spines and strong divergence of the anterior sections of the facial suture characterize *Modocia kohli* and distinguish it from all other species of *Modocia*. *Modocia kohli* is a macrocephalic species, having the largest cephalon compared to the thoracopygon in *Modocia*, and the pygidium is one of the smallest (proportionally) known in this genus. Both of these characters also help distinguish it from most other described species. Relative length of the genal spines increased during holaspid ontogeny, increasing in the type suite from a level opposite thoracic axial ring 8 on the smallest specimen to a level opposite thoracic axial ring 12 on the largest specimen.

Occurrence.—*Modocia kohli*, a rare species, is primarily known from the middle Wheeler Formation, lower *Bolaspidella* Zone, at locality 114 in the House Range. It also has been collected from the Wheeler Formation in the Drum Mountains.

MODOCIA WHITELEYI new species
Figure 23
Weeksina sp. Robison, 1960, p. 18, pl. 1,*23.*
Modocia weekensis Bonino and Kier, 2009 (*nom. nud.*), tavola 43.c.
Modocia sp. Bonino and Kier, 2010, pl. 65.c.

Diagnosis.—*Modocia* having a short (sagittal) preglabellar field, narrow palpebral areas, short genal spines, 12 thoracic segments with angular terminations, moderate-sized pygidium with distinct medial notch, and 4 rings in the pygidial axis.

Etymology.—After Thomas E. Whiteley, for promoting knowledge of trilobites (Whiteley, Kloc, and Brett, 2002).

Types.—Holotype exoskeleton KUMIP 204402 (Fig. 23.1), and paratypes KUMIP 147797, 204390, 204466–204469, and USNM 437948.

Discussion.—*Modocia whiteleyi* differs from all other species of *Modocia* by having only 12 thoracic segments. It further differs from most *Modocia* by its short preglabellar field and narrow palpebral areas.

Specimens of this species are illustrated commonly on the Internet as either *Modocia hewlisca* or *M. weeksensis*, both of which are taxonomically invalid names (nomina nuda).

Occurrence.—*Modocia whiteleyi* is a rare to common species in the middle to upper Weeks Formation, *Cedaria* Zone, of the House Range.

Family MENOMONIIDAE Walcott, 1916a

Menomoniids are micropygous, and some are opisthoparian, whereas others are gonatoparian. Pratt (1992, p. 77) discussed additional characters and reviewed family content and taxonomic history. Family representatives from Utah demonstrate a remarkable
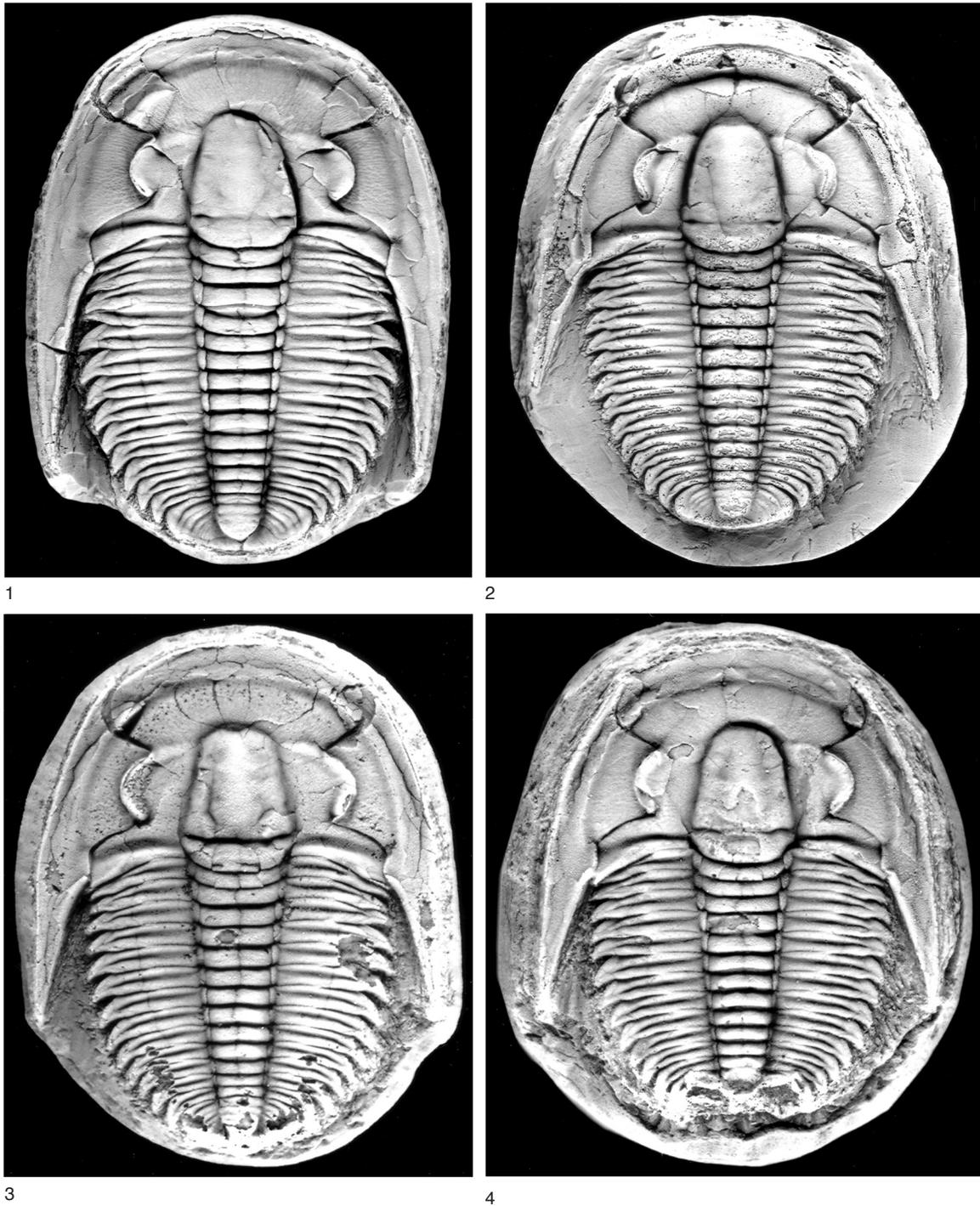
Figure 22. *Modocia kohli* new species, all preserved with calcite cone-in-cone encrustation on ventral surface, Wheeler Formation, locality 114, House Range. *1*, Holotype exoskeleton, UU 10051.46, length 25 mm; *2*, paratype exoskeleton, UU 10051.47, length 20 mm; *3*, paratype exoskeleton, UU 10051.48, length 12 mm; *4*, paratype exoskeleton, UU 10051.49, length 14 mm.
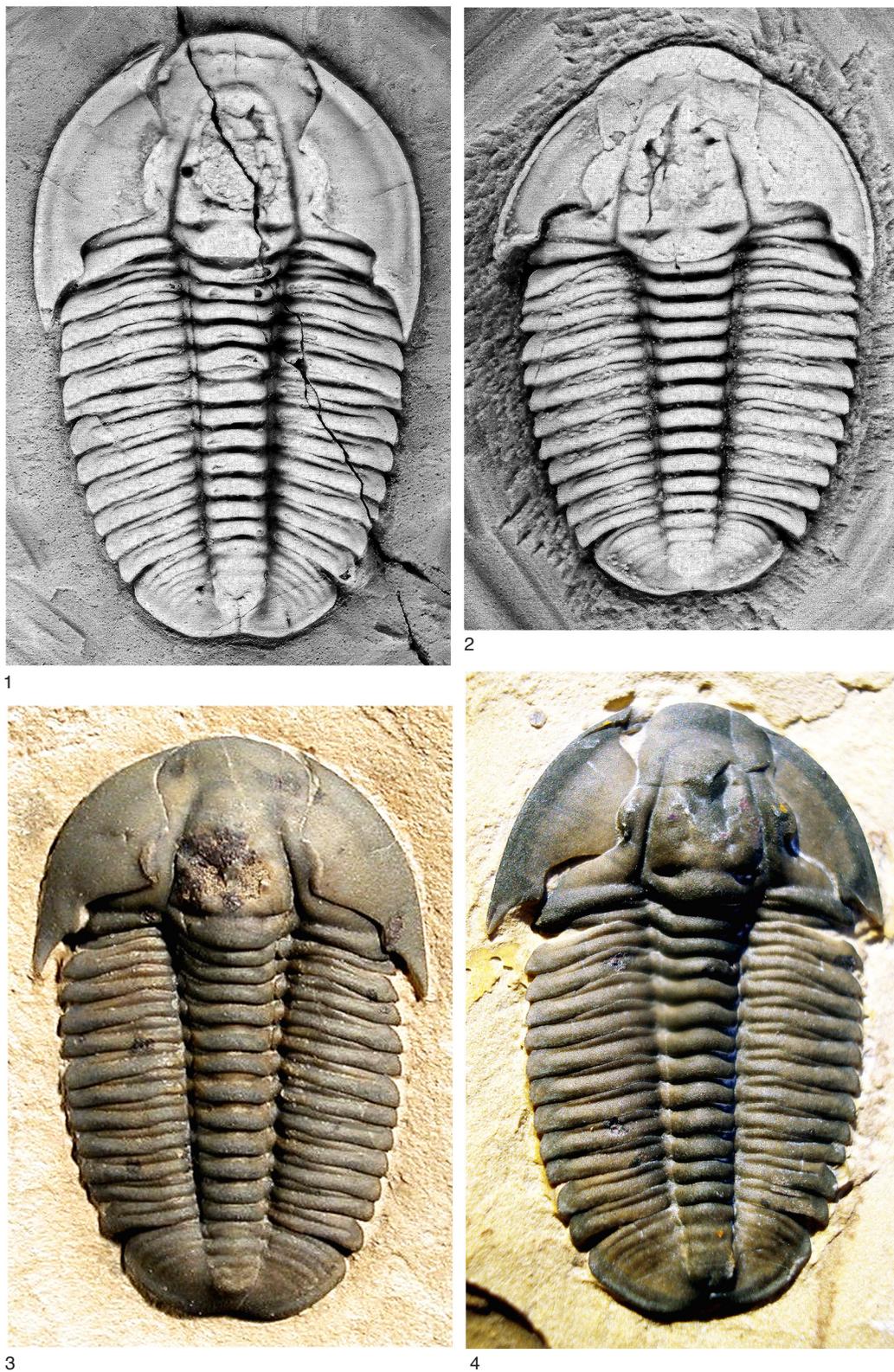
Figure 23. *Modocia whiteleyi* new species, upper Weeks Formation, locality 824 in North Canyon, House Range. *1*, Holotype exoskeleton, KUMIP 204402, length 24 mm; *2*, paratype, USNM 437948, length 14 mm; *3–4*, exoskeletons (photos courtesy of David Comfort).
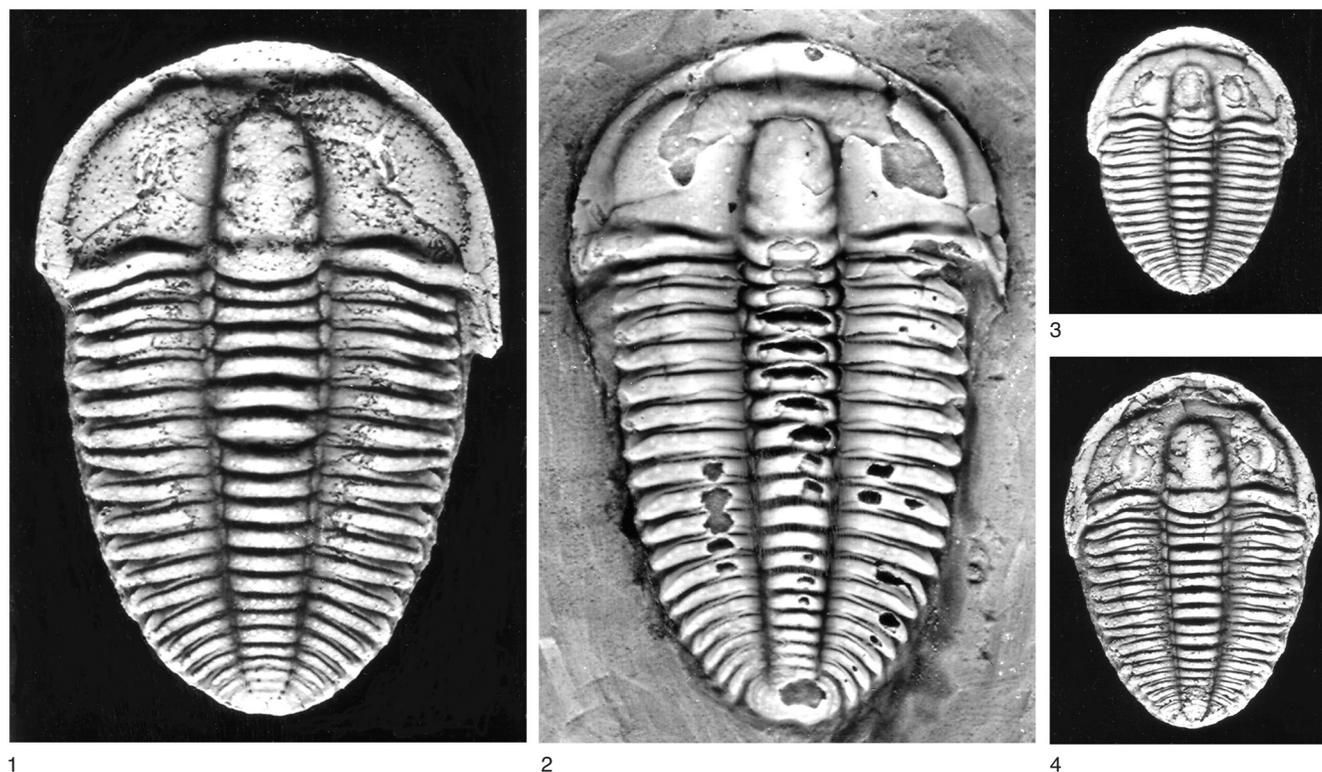
Figure 24. *Bolaspidella jarrardi* new species, Marjum Formation, House Range. *1*, Holotype exoskeleton with 18 thoracic segments and calcite cone-in-cone encrustation on the ventral surface, taphonomically flattened in argillaceous mudstone, locality 347, UU 10051.50, length 16 mm; *2*, dorsal exoskeleton with 18 thoracic segments and narrow outline, probably related to less flattening in limestone from locality 391, UU 10051.51, length 17 mm; *3*, small paratype exoskeleton with 16 thoracic segments and calcite cone-in-cone encrustation on the ventral surface, locality 347, UU 11042.01, length 8 mm; *4*, paratype exoskeleton with 16 thoracic segments and calcite cone-in-cone encrustation on the ventral surface, locality 347, UU 11042.04, length 12 mm.

increase in the number of holaspid thoracic segments, ranging from 15 (*Bolaspidella housensis*, upper Wheeler Formation) to 44 (*Menomonia sahratiani* n. sp., upper Weeks Formation), the latter number being among the most recorded in any trilobite family except the Emuellidae (Pocock, 1970; Paterson and Edgecombe, 2006) and the Olenellidae (Palmer, 1998a).

Genus BOLASPIDELLA Resser, 1937

Type species.—*Ptychoparia housensis* Walcott, 1886, p. 201.

Emended diagnosis.—Opisthoparian menomoniids with parallel-sided to moderately tapered glabella. Anterior facial sutures approximately parallel. Preglabellar area concave with upturned, convex border; preglabellar field and border commonly about equal in sagittal length. Width of palpebral area about equal to that of glabella. Palpebral lobes moderate in length and slightly elevated. Thorax containing 15 to 24 segments. Pygidium alate in outline.

Discussion.—Westrop and Ludvigsen (2000) reviewed various proposals for and against the synonymy of *Bolaspidella* and *Hysteropleura*. Although one of us (Robison, 1964, 1988) previously favored synonymy, based on phylogenetic analysis by Westrop and Ludvigsen (2000), we here accept *Hysteropleura* as a separate genus. *Bolaspidella*, as diagnosed above, mostly differs from *Hysteropleura* by its less divergent anterior facial sutures. It also usually has a less tapered glabella. Characters of the thorax and pygidium of *Hysteropleura* are not known.

Several species of *Bolaspidella* have been named from disarticulated cranidia, some retaining external surfaces and some being molds of internal surfaces with different character expressions. Entire dorsal exoskeletons now demonstrate that disarticulated cranidia may lack characters adequate to distinguish species within the genus. We regard *B. wellsvillensis* (Lochman and Denson *in* Lochman and Duncan, 1944) from the Bloomington Formation of northern Utah and *Bolaspidella contracta* Robison, 1964, from the Marjum Formation of the House Range to be examples. Therefore, we recommend that these two species names be restricted to their holotypes pending discovery of additional skeletal information. Entire exoskeletons from the Wheeler Formation previously assigned by Robison (1971) to *B. wellsvillensis* are here reassigned to a new species, *B. reesae*.

BOLASPIDELLA JARRARDI new species
Figure 24

Bolaspidella sp. Gunther and Gunther, 1981, p. 29, pl. 15; Bonino and Kier, 2009, fig. 171.c; tavola 33. a?, 33.b; 2010, pl. 19.c; pls. 57.a?, 57.c.

Diagnosis.—*Bolaspidella* without axial spines. Glabella slightly tapered. Lateral glabellar furrows variably developed, but gener-
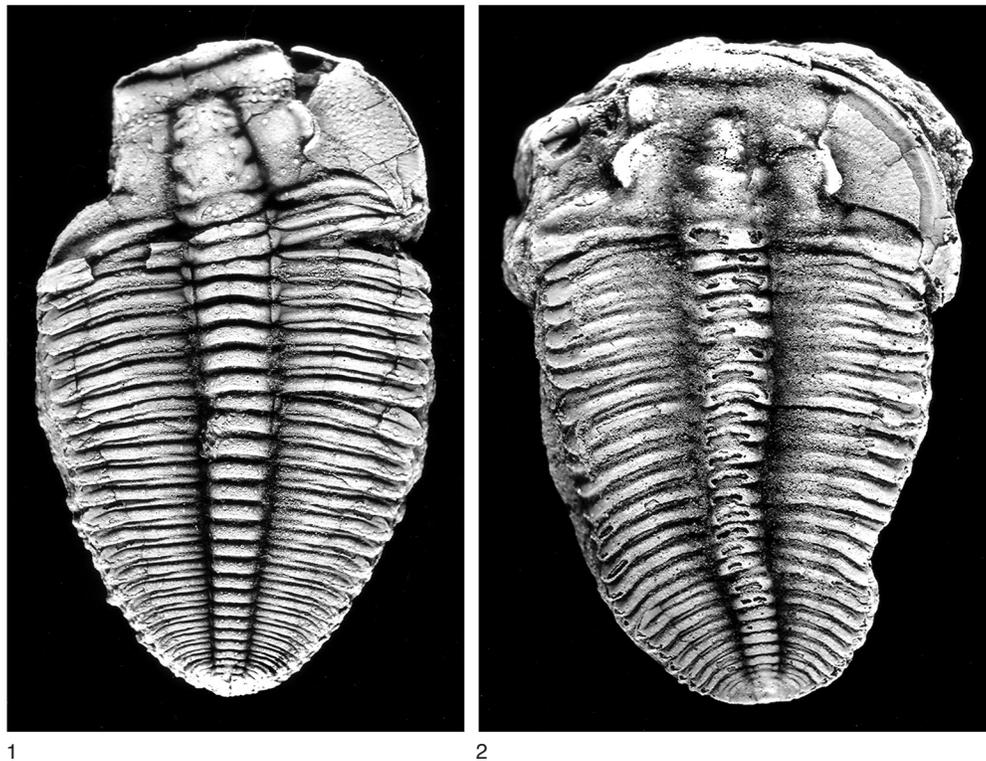
Figure 25. *Bolaspidella reesae* new species, with calcite cone-in-cone encrustation on the ventral surface, upper Wheeler Formation, locality 115, in Wheeler Amphitheater, House Range. 1, Holotype exoskeleton, UU 1021, length 22 mm; 2, paratype exoskeleton, UU 1024, length 21 mm.

ally deepen rearward. Occipital ring medially lengthened, with or without weak medial node. Genal spines short, tips opposite thoracic axial ring 3 or 4. Thorax containing 15 to 18 segments. Pygidium micropygous. Pygidial axis with 2 or 3 rings that weaken rearward.

Etymology.—After Professor Richard D. Jarrard, University of Utah, for contributions to knowledge of Cambrian fossils, stratigraphy, and depositional environments in Utah.

Types.—Holotype exoskeleton UU 10051.50 (Fig. 24.1) and several paratype exoskeletons (UU 10051.51, 11042.01–11042.24), all from locality 347.

Discussion.—The number of thoracic segments in *Bolaspidella jarrardi* is variable, ranging from 15 to 18 within single samples, with 18 being most common. *Bolaspidella jarrardi* is most similar to *B. reesae* n. sp. but has at least 4 fewer thoracic segments, and its glabella commonly is less tapered. It has a longer frontal area than *B. contracta* Robison, 1964. A disarticulated pygidium originally assigned to *B. contracta* is semicircular rather than alate, and it now seems likely to represent a different species and possibly a different genus.

Occurrence.—*Bolaspidella jarrardi* is rare to common in the Marjum Formation, mid-*Bolaspidella* Zone, at localities 347, 391, and 716 in the House Range.

BOLASPIDELLA REESAE new species
Figure 25

Bolaspidella wellsvillensis (Lochman and Denson). Robison, 1971, p. 801–802, pl. 91, *10–14;* Gunther and Gunther, 1981, p. 28, pl. 14.

Diagnosis.—*Bolaspidella* without axial spines. Glabella moderately tapered with moderately deep lateral furrows. Occipital ring having weak medial node. Genal spines short, tips opposite thoracic axial ring 3 or 4. Thorax containing 24 segments. Pygidium micropygous. Pygidial axis with three rings that weaken rearward. Dorsal surface covered with mixture of mostly scattered coarser granules and abundant finer granules. One bilateral pair of coarser granules per segment regularly occurs on axis.

Etymology.—After Professor Margaret N. Rees, University of Nevada, Las Vegas, for many contributions to the knowledge of Cambrian stratigraphy and depositional environments.

Types.—Holotype exoskeleton UU 1021 (Fig. 25.1); paratypes UU 1020–1024 (Fig. 25.2).

Discussion.—For reasons mentioned above, entire exoskeletons from the Wheeler Formation previously assigned by Robison (1971) to *Bolaspidella wellsvillensis* are here reassigned to a new species, *B. reesae*. Compared to other species of *Bolaspidella*, *B. reesae* has the greatest number of thoracic segments (24). It also reaches the largest size, with skeletal lengths ranging up to 22 mm. The co-occurring spiny type species of *Bolaspidella*, *B. housensis*, has only 15 thoracic segments and rarely exceeds 10 mm in length (Robison, 1964).

Occurrence.—Rare in the upper Wheeler Formation, lower *Bolaspidella* Zone, at locality 115 in the House Range.

Genus MENOMONIA Walcott, 1916a

Type species.—*Conocephalites calymenoides* Whitfield, 1878, p. 52.

Emended diagnosis.—Gonatoparian, elongated, micropygous menomoniids with strong convexity. Cephalon short, wide, and

subelliptical. Glabella short, moderate to strongly tapered, and truncate anteriorly in some species. Eyes small, near front of glabella, and may or may not be elevated on short stalks. Frontal area transversely narrow, commonly with upturned and lenticular border. Thorax long, with as many as 44 segments; axis weakly tapering and narrower than pleural regions; pleurae straplike with rounded terminal ends. Pygidium minute and subelliptical to alate.

Remarks.—The diagnosis of *Menomonia* by Pratt (1992, p. 77) is slightly emended to accommodate an expanded range of observed morphological variation. Depth of the axial furrow commonly is accentuated because of taphonomic flattening of the convex exoskeleton. The genus is most similar to *Dresbachia,* from which it differs by having a transversely wider frontal area, more widely set eyes, generally less triangular glabella, and generally more thoracic segments. Like Pratt (1992) and some other previous reviewers, we regard *Menomonia* to be a senior synonym of *Densonella.*

MENOMONIA SAHRATIANI new species
Figures 26, 28

Millardia semele Walcott, 1916a (in part), pl. 28, figs. 3c, 3c' (not figs. 3, 3a, 3b, 3b').

Nephalicephalus n. sp. Bonino and Kier, 2009 (*nom. nud.*), tavola 45.a.

Undetermined menomoniid trilobite Bonino and Kier, 2010, pl. 67.a.

Diagnosis.—*Menomonia* with small, weak, palpebral lobes and effacement of most cephalic furrows except rearmost parts of axial furrow, weak occipital furrow, and weak posterior border furrows. Anterior branches of facial suture only slightly divergent forward from eyes, curving inwardly near anterior cephalic margin; posterior branches strongly divergent, curving rearward to genal angle near lateral cephalic margin. Thorax contains as many as 44 segments. Pygidium minute, alate in outline, and otherwise nearly featureless.

Etymology.—After Quintin Sahratian, for promoting knowledge of the Cambrian fossils of Utah.

Types.—Holotype exoskeleton, UU 10051.52 (Fig. 26.1); paratype exoskeletons, UU 10051.53 (Figs. 26.2–26.3) and BPM 1010 (Figs. 26.4–26.5).

Discussion.—*Menomonia sahratiani* differs from other species of the genus by anterior effacement of the cephalic axial furrow and an absence of lateral glabellar furrows. *Menomonia sahratiani* also has low and ill-defined palpebral lobes, whereas lobes of the type species, *M. calymenoides* (Whitfield, 1878), are small but prominent, and the geographically widespread *M. semele* (Walcott, 1916a) has eyes on short stalks.

The maximum number of 44 thoracic segments observed in *M. sahratiani* (Fig. 26.4) is unusually high for trilobites. It is exceeded by few described examples, all from Cambrian Epoch 2 taxa. *Balcoracania dailyi* (Pocock, 1970), an emuellid from South Australia, has up to 103 thoracic segments, the greatest known number for a trilobite (Paterson and Edgecombe, 2006). *Olenellus fowleri* Palmer, 1998a, an olenellid from Nevada, has a maximum of 48 segments (Palmer, 1998a).

One fragmentary dorsal exoskeleton assigned by Walcott (1916a, pl. 28, figs. 3c, 3c') to *Millardia semele* is here reassigned to *Menomonia sahratiani*. The specimen was collected from the upper Weeks

Formation, in what Walcott referred to as Weeks Canyon (now North Canyon). Other illustrated specimens that are conspecific with *M. sahratiani* have been referred, especially on the Internet, to *Nephalacephalus*, a *nomen nudum*, first appearing in an unpublished doctoral dissertation (Peters, 2003).

Occurrence.—Rare to locally common in the *Cedaria* Zone of the upper Weeks Formation in North Canyon, House Range.

Family NORWOODIIDAE Walcott, 1916a
Genus NORWOODIA Walcott, 1916a

Type species.—*Norwoodia gracilis* Walcott, 1916a, p. 169–170. The generic diagnosis by Pratt (1992, p. 75) is followed.

NORWOODIA BONINOI new species
Figures 27–28

Norwoodia bellaspina Bonino and Kier, 2009 (*nom. nud.*), fig. 21.c; tavola 45.b.

Norwoodia sp. Bonino and Kier, 2010, fig. 24.b; pls. 67.b, 68.

Diagnosis.—*Norwoodia* with wide anterior and lateral cephalic border furrow. Glabella short, slightly tapered, diminishing in relative length through ontogeny; lateral furrows weak to effaced. Occipital furrow weak to effaced. Occipital ring, with medial node, merging rearward into long, stout, variably flattened occipital spine. Palpebral lobes about half as long as glabella, opposite anterior glabella. Anterior sections of facial suture weakly divergent, posterior sections diverge laterally and slightly forward to border furrow and then gently curve rearward to lateral cephalic margin. Genal spines long and stout, similar in length to occipital spine, all three approximately reaching an imaginary transverse line near thoracic-pygidial boundary. Cephalic doublure with small anterior rostellum and posterior median suture. Thorax containing nine segments; unusually narrow and subcircular in outline, being slightly more than half as wide as maximum width of cephalon. Fourth thoracic segment having exceptionally long, slender, posteriorly directed, medial spine, its length greater than exoskeleton without spine. Pygidium tiny, short, and alate; width more than three times length; axis with two rings.

Etymology.—After Enrico Bonino, for promoting knowledge of trilobites (Bonino and Kier, 2009, 2010).

Types.—Holotype, USNM 437971 (Fig. 27.1), and paratypes KUMIP 204396 (Fig. 27.2) and 204397 (Fig. 27.4); all collected from the south side of North Canyon, House Range, by George Melloy.

Discussion.—*Norwoodia boninoi* is a macrocephalic trilobite that has a general morphology reminiscent of, and probably convergent with, some mid-Paleozoic bellinurid xiphosurans.

Several species of *Norwoodia* have been described, mostly based on fragmentary cranidia, which greatly limits morphologic comparisons with the entire exoskeletons illustrated here. *Norwoodia boninoi* differs from all species of the genus by its combination of weak to effaced occipital furrow, unusually long and stout occipital spine, and very short and wide pygidium.

A reconstruction by Lochman-Balk (1959, fig. 224.2) of the type species of *Norwoodia*, *N. gracilis* Walcott (1916a), has a moderately long medial spine on thoracic segment 8. Walcott (1916a) illustrated two disarticulated thoracic segments of *N. gracilis*, each with a long medial spine, and illustrated two exoskeletons, each of which has a damaged axial lobe with no preserved evidence as
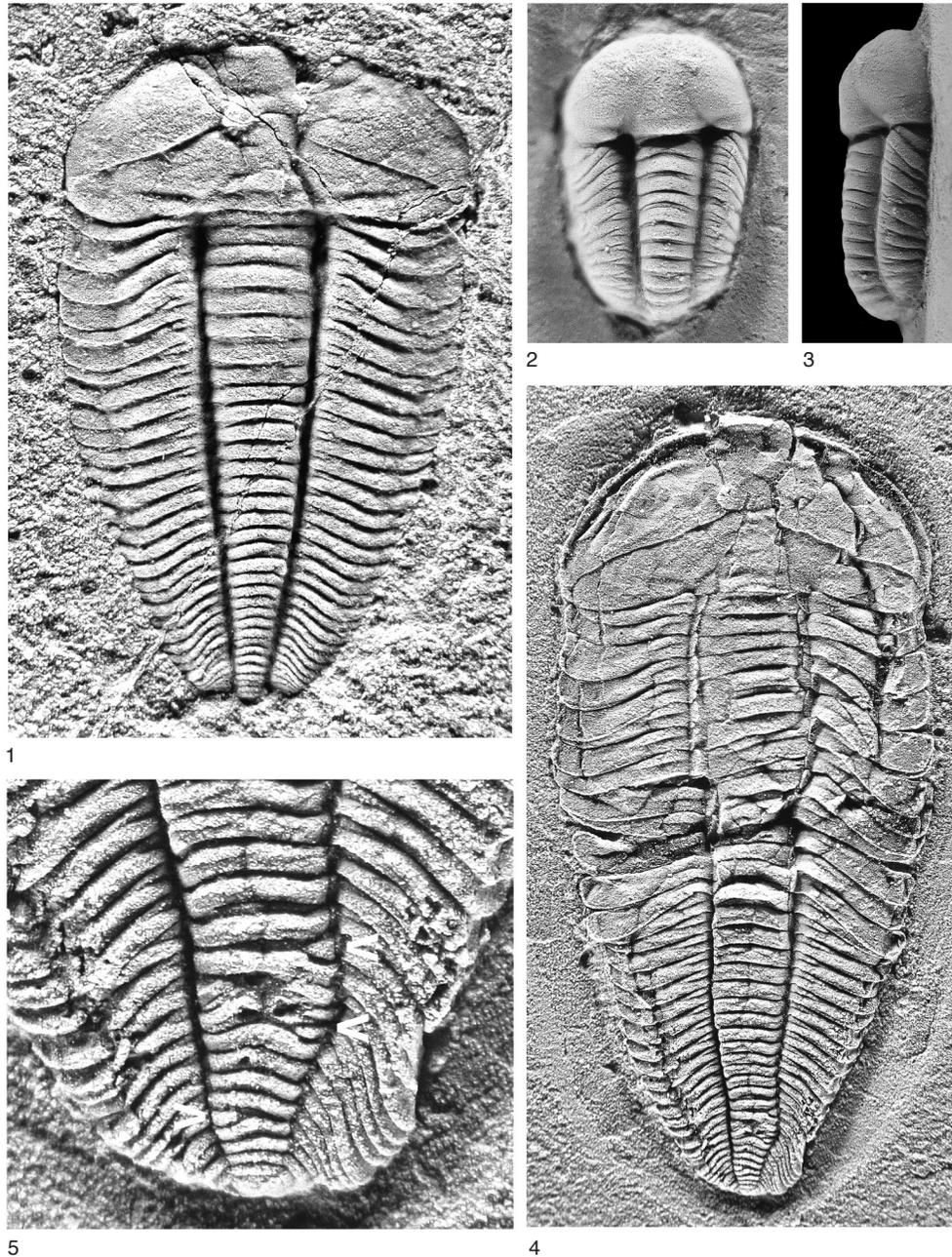
Figure 26. *Menomonia sahratiani* new species, locality 824 in the upper Weeks Formation, House Range. *1*, Holotype exoskeleton, flattened with pygidium not exposed, UU 10051.52, length 19 mm; *2–3*, immature paratype exoskeleton in dorsal and lateral views, retaining high convexity with cephalon displaced rearward over anterior thorax, UU 10051.53, length 7.5 mm; *4–5*, paratype exoskeleton, flattened and unusually large with 44 thoracic segments, BPM 1010, length 39 mm; *4*, entire specimen; *5*, enlarged view of posterior thorax showing some malformed segments (*arrows*) and the minute, featureless pygidium.

to which thoracic segment had a spine. A thoracopygon assigned to *N. gracilis* by Resser (1938, pl. 10,*37*) was stated by Resser (pl. 10,*37*, caption) to have an axial spine on the last thoracic segment. Comparison of specimens illustrated by Walcott (1916a) and Resser (1938), and specimens of *N. boninoi* illustrated here suggest that the reconstruction by Lochman-Balk (1959) is erroneous in both the location and length of the medial spine on the thorax of *N. gracilis*.

Bonino and Kier (2009, fig. 21.c; 2010, fig. 24.b) documented the presence of a rostellum and associated median suture on the ventral cephalic doublure of specimens here assigned to *Norwoodia boninoi*. The connective sutures laterally bounding the rostellum and the following median suture together form a distinctive Y-shaped pattern on the doublure (Fig. 27.3). The taxonomic significance of these characters is discussed in the section on High-level Classification of Trilobites (p. 6–7 herein).
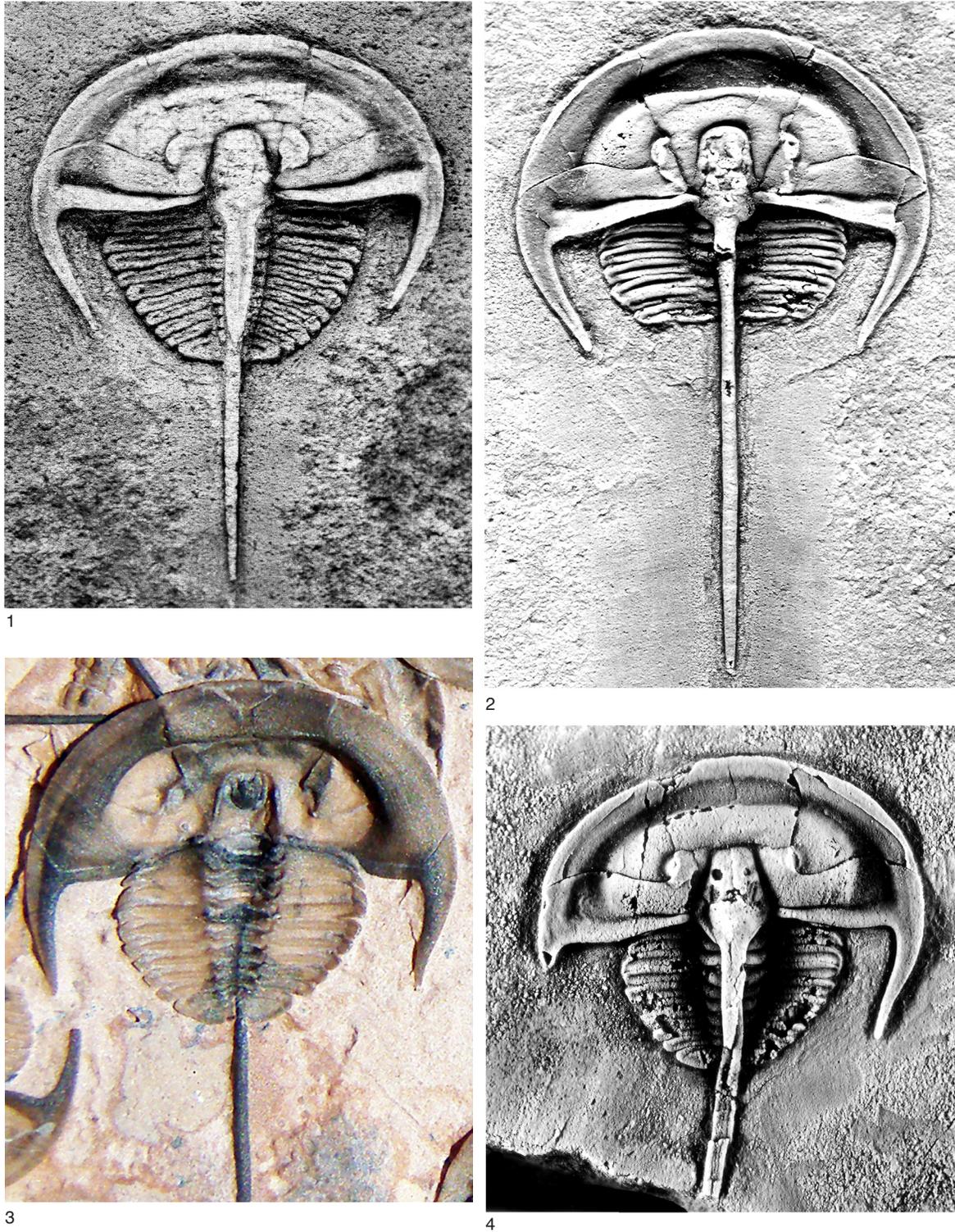
Figure 27. *Norwoodia boninoi* new species, upper Weeks Formation, North Canyon, House Range. *1*, Holotype exoskeleton, USNM 437971, length including thoracic spine 15 mm; *2*, paratype exoskeleton, KUMIP 204396, length including thoracic spine 15 mm; *3*, ventral view of exoskeleton (from near center of Fig. 28) showing Y-shaped pattern of the rostellum and median suture on anterior doublure, natant hypostome is collapsed onto ventral surface of anterior glabella, BPM 1011, length of exoskeleton excluding thoracic spine 9 mm (photo courtesy of Enrico Bonino); *4*, paratype exoskeleton, KUMIP 204397, length including thoracic spine 12 mm.

Figure 28. *1*, Trilobites and rare brachiopods preserved on argillaceous surface of thin limestone bed, upper Weeks Formation. The fauna, likely buried during a storm event, mostly consists of *Norwoodia boninoi*, with fewer *Menomenia sahratiani* (the largest of which is 15 mm in length), *Coosella kieri*, *Triadaspis bigeneris, Genevievella* sp., and undetermined agnostoids and inarticulated brachiopods. Overturned specimens of *N. boninoi* show a characteristic rostellum and median suture on the anterior cephalic doublure (compare Fig. 27.3, an exoskeleton whose length excluding thoracic spine is 9 mm); BPM 1011, locality 824 in North Canyon, House Range (photo courtesy of Carlo Kier); *2*, rose diagram showing orientations of trilobite exoskeletons on slab in *1*. Specimens (n = 56) were measured along mean axial direction with the cephalon pointing forward and plotted in 15° classes.

Some specimens of *N. boninoi* show wrinkling of the exoskeleton in the frontal area, without obvious breakage except along the facial sutures (Figs. 27.1–27.2). This suggests that some exoskeletons were rather pliable at the time of burial and could withstand some deformation related to compression under the weight of overlying sediment layers.

Occurrence.—*Norwoodia boninoi* is rare to locally abundant in the upper Weeks Formation, *Cedaria* Zone, House Range.

Family Undetermined
Genus MENISCOPSIA new genus

Type species.—*Meniscopsia beebei* n. sp.

Diagnosis.—Opisthoparian ptychoparioid with crescent-shaped cephalon, long and slightly tapered glabella, stout genal spines, 10 short thoracic segments, and semicircular isopygous to macropygous pygidium.

Etymology.—From Greek *meniskos*, crescent, and *ops*, face, alluding to the crescent-shaped cephalon.

Discussion.—*Meniscopsia*, known from a single species, has a unique combination of characters not closely similar to those of any named trilobite genus. Its family affinities are obscure.

MENISCOPSIA BEEBEI new species
Figure 29

Selenocoryphe platyura Bonino and Kier, 2009 (*nom. nud.*), figs. 4, 48.a; tavola 45.c.
New genus and new species Bonino and Kier, 2010, fig. 53.a, pl. 67.c.

Diagnosis.—Exoskeleton ovate with low relief and somewhat variable width. Cephalon crescent shaped. Lateral cephalic borders widen rearward into stout, broad-based genal spines. Anterior sections of facial suture moderately divergent, posterior sections strongly divergent. Glabella unfurrowed, long, slightly tapered, bluntly rounded anteriorly, reaching anterior border furrow. Occipital ring short. Palpebral lobes slightly posterior to glabellar midpoint. Hypostome conterminant, with front margin broadly abutting laterally wide and sagittally narrow rostral plate along hypostomal suture. Thorax containing 10 sagittally short, weakly falcate segments. Pygidium large, semicircular, with broad, smooth border that widens rearward. Pygidial axis tapering to rounded terminus, length about 0.6 times that of pygidium; containing eight weakly defined rings and terminal piece. Pleural fields of pygidium triangular and very weakly furrowed. Exoskeletal doublure significantly widens rearward beneath cephalon, showing slight abrupt increase beneath posterior cephalic border, then similar width beneath thorax, further slight broadening beneath pygidium, and slight medial constriction behind axial terminus.

Etymology.—After Matthew A. Beebe, for unpublished contributions (1990) to knowledge of the Weeks Formation and its fauna. Revision for publication of work on the Weeks Formation by Beebe ended with his untimely death in 1994.

Types.—Holotype exoskeleton, USNM 437980 (Fig. 29.1); paratype exoskeleton, BPM 1012 (Fig. 29.2); paratype exoskeleton, UU 10051.54 (Fig. 29.4).

Discussion.—During holaspid ontogeny, the pygidium of *Meniscopsia beebei* increased disproportionately in size relative to the cephalon. For example, the pygidium of a paratype, 15 mm in length (Fig. 29.4), is slightly shorter than the cephalon in sagittal length, whereas the pygidium of the holotype, 33 mm in length (Fig. 29.1), is almost 1.5 times longer than the cephalon in sagittal length. Variation in late holaspid exoskeletal width may be related to differences in postmortem compression.

Two specimens of *M. beebei* (Figs. 29.2–29.3) show a narrow, dark, central feature interpreted to be an early diagenetic filling of the alimentary tract and bilateral foregut and midgut digestive glands (compare Butterfield, 2002; Babcock, 2003; Babcock and Peel, 2007). These axial features, which are presumably phosphatic, lack sediment fill and broken skeletal matter. One specimen (Fig. 29.2) has two dark nodules of unequal size and unknown origin flanking the pygidial axis.

Occurrence.—Upper Weeks Formation, *Cedaria* Zone, locality 824 in North Canyon, House Range.

Order Undetermined
Family BURLINGIIDAE Walcott, 1908
Genus BURLINGIA Walcott, 1908

Type species.—*Burlingia hectori* Walcott, 1908, p. 15.

The generic diagnosis by Whittington (1994, p. 8) is followed. Ebbestad and Budd (2003) described additional burlingiids and assessed broader phyletic relationships of *Burlingia*, which remain obscure. Specimens of this genus are among the smallest of trilobites and characteristically are proparian and micropygous. They have global distribution in open-marine deposits and probably were planktonic.

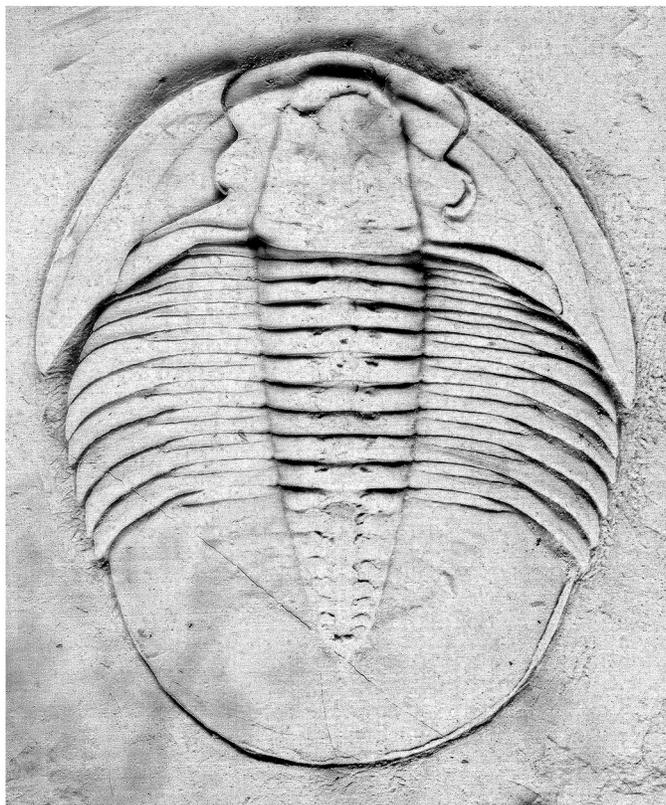### BURLINGIA HALGEDAHLAE new species
Figure 30

Diagnosis.—Exoskeleton generally oval in outline, width greatest along anterior thorax, medial posterior margin weakly indented. Cephalon subtriangular, lacking dorsal furrows. Anterior sections of facial suture straight, moderately divergent; posterior sections weakly curved, diverging laterally and slightly forward. Site of effaced occipital ring having small median node. Thorax containing as many as 15 segments, axis widest along midlength. Anterior border of thoracic pleurae raised to form low, narrow ridge. Pygidium narrowly rectangular.

Etymology.—After Professor Susan L. Halgedahl, University of Utah, for contributions to knowledge of Cambrian fossils, stratigraphy, and depositional environments in Utah.
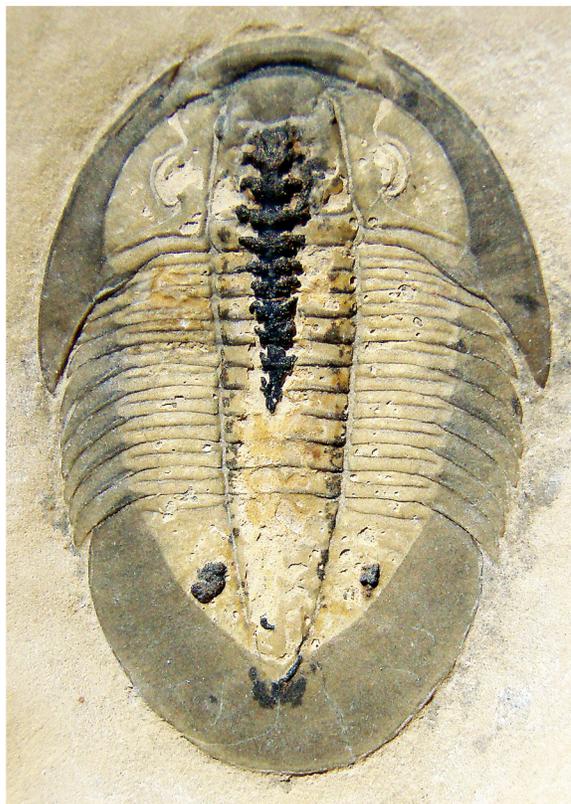
Holotype.—Exoskeleton, UU 10051.55 (Fig. 30.1).

Discussion.—*Burlingia halgedahlae* most closely resembles *B. hectori* Walcott, 1908, from the Stephen Formation of British Columbia

Figure 29. *Meniscopsia beebei* new genus and new species, upper Weeks Formation, North Canyon, House Range. *1*, Dorsal exoskeleton of holotype, USNM 437980, length 35 mm; *2*, dorsal exoskeleton with partly exposed interior dark filling of anterior and posterior alimentary canal and digestive glands; dark peripheral area is underlain by doublure, BPM 1012, length 40 mm (photo courtesy of Enrico Bonino); *3*, ventral view of exoskeleton showing central dark fillings of the alimentary canal and digestive glands, somewhat damaged rostral plate and hypostome separated slightly along the hypostomal suture, and the wide lateral and posterior doublure, length 36 mm (photo courtesy of Ru Smith); *4*, immature exoskeleton with relatively short pygidium, UU 10051.54, length 15 mm (photo courtesy of Quintin Sahratian).
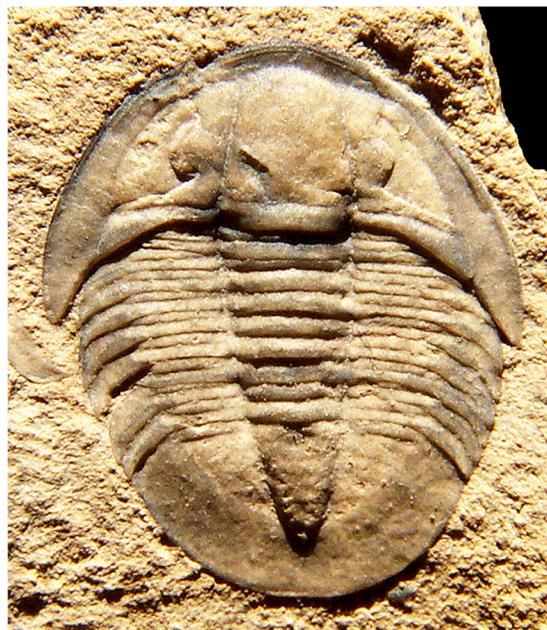
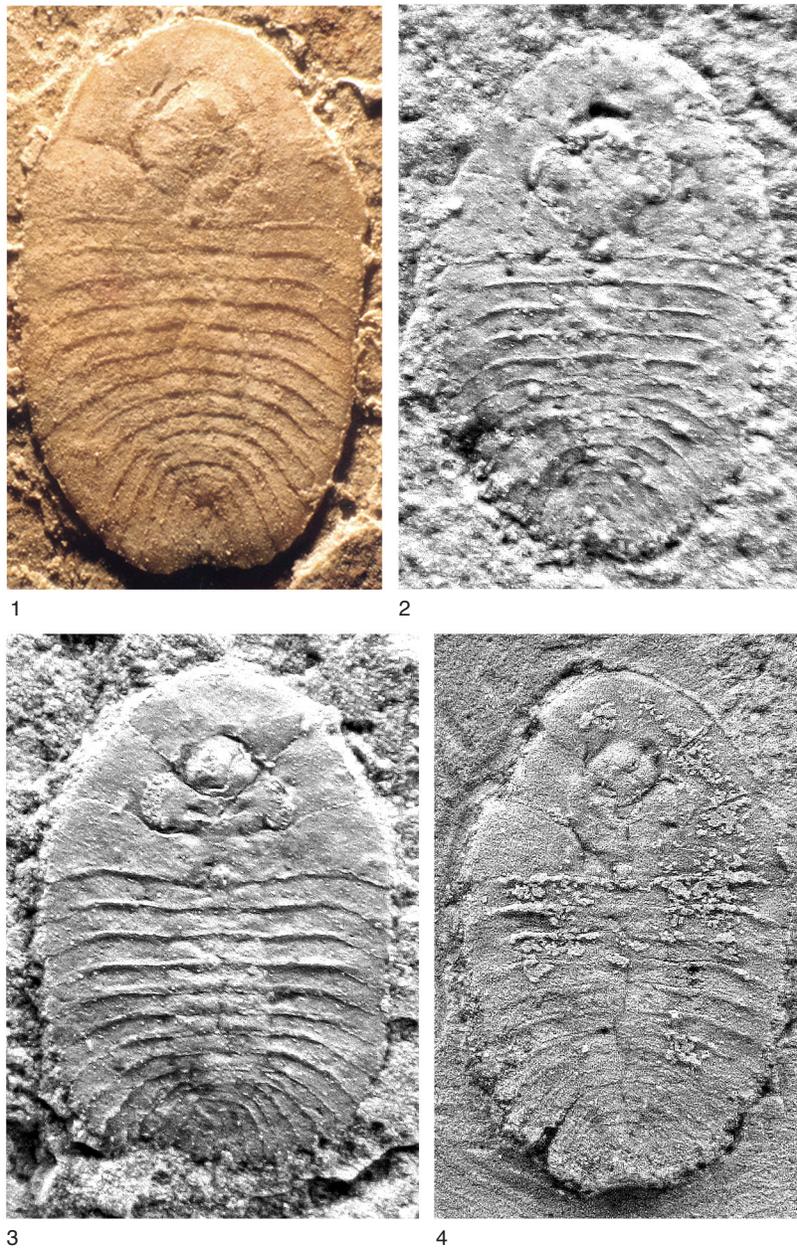Figure 29. *(For explanation, see facing page).*

Figure 30. *Burlingia halgedahlae* new species, Marjum Formation, House Range. *1*, Dorsal exoskeleton of holotype, UU 10051.55, length 4 mm, collected at locality 347 by Susan Halgedahl and Richard Jarrard; *2*, dorsal exoskeleton, UU 10051.56, length 4 mm, collected at locality 716 by J. A. (Denny) Sutherland; *3*, dorsal exoskeleton, UU 10051.57, length 4 mm, collected at locality 716 by Loy Crapo; *4,* dorsal exoskeleton, UU 10051.58, length 4 mm, collected at locality 716 by Val, Lloyd, and Metta Gunther.

and *B. jagoi* Whittington, 1994, from the Alum Shale of Sweden and Norway. It is similar to *B. hectori* in general outlines of the exoskeleton and thoracic axis but has a more triangular cephalon, one more thoracic segment, and a shallower medial indentation of the rear skeletal margin. It is similar to *B. jagoi* in having a subtriangular cephalon but differs in outline of the raised axial lobe, in having one more thoracic segment, and a deeper and wider indentation of the rear skeletal margin. *Burlingia halgedahlae* appears to differ from all other species of *Burlingia* by its greater effacement of dorsal furrows, but that feature may have a taphonomic rather than genetic origin.

Occurrence.—*Burlingia halgedahlae* is rare in the middle part of the Marjum Formation, mid-*Bolaspidella* Zone, at localities 347 and 716 in the House Range.

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