

Lingulate brachiopods from the upper Cambrian (Sunwaptan) Hellnmaria Member of the Notch Peak Formation, western Utah, USA

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Bulk samples collected from the Hellnmaria Member of the Notch Peak Formation of western Utah, USA have yielded a lingulate brachiopod fauna with many new taxa. Two new lingulid genera are named, *Stittia* and *Tuleobolus*. Seven new species are described, the lingulid species *Stittia ornata*, *Tuleobolus cretatus* and *Discotreta? arcana*, and the acrotretid species *Quadrisonia congerensis*, *Q. rattlesnakensis*, *Q. sawtoothensis* and *Q. swaseyensis*. The genus *Quadrisonia* Rowell & Henderson, 1978 is emended. The species *Obolus (Westonia) notchensis* Walcott, 1908 is assigned to the new genus *Stittia*. *Zhanatella rotunda* Koneva, 1986 is documented from the lower beds of the Hellnmaria Member, establishing it as coeval with strata in Kazakhstan and southern France, from where this species was described previously. These collections extend downward the range of *Quadrisonia lavadamensis* Popov *et al.*, 2002, *Zhanatella utahensis* Popov *et al.*, 2002 and *Wahwahlingula* sp., which were described previously from Utah.

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LINGULATE brachiopods are common fossils in upper Cambrian strata of North America but are less frequently studied than co-occurring conodonts or trilobites. Popov *et al.* (2002) described lingulate taxa from the uppermost Millardan Series and overlying lower Ibexian Series in western Utah, and Holmer *et al.* (2005) described taxa from the overlying Ordovician (upper Skullrockian Stage and lower Stairsian Stage) in western Utah. This paper describes lingulate taxa from strata directly underlying the strata considered by Popov *et al.* (2002). The brachiopods are from two measured sections of the Hellnmaria Member of the Notch Peak Formation in which sequence stratigraphy and conodont zonation have been established (Miller *et al.* 2003). Few trilobites have been collected in the Hellnmaria Member, and conodonts are only useful for biostratigraphy in the upper part of the member.

LITHOSTRATIGRAPHY AND MEASURED SECTIONS

The two sections were measured by J. F. Miller and D. Freadly in 1991. Both are of the Hellnmaria

Member of the Notch Peak Formation as defined by Hintze *et al.* (1988). Miller *et al.* (2003) published detailed descriptions of the sections, with locality information, GPS coordinates, and conodont zonation. The names of the two sections, East Shoreline Butte (ESB) and Chalk Knolls North (CKN), refer to shoreline features and diatomaceous earth deposits associated with Pleistocene Lake Bonneville and Tule Lake. The sections are in small fault blocks in Tule Valley, west of the House Range, and these horst blocks were islands during the Pleistocene (Fig. 1). The East Shoreline Butte section begins at the base of the Hellnmaria Member, where it is in contact with the underlying Sneakover Limestone Member of the Orr Formation, and the Chalk Knolls North section starts stratigraphically higher. Together, the sections include all but the uppermost strata of the Hellnmaria Member. An interval of the East Shoreline Butte section is covered from 144-225 m above the base, but the upper part of the equivalent interval is exposed in the lower part of the Chalk Knolls North section. Seventy-three bulk samples were collected. From each sample, 2-5 kg of limestone was dissolved

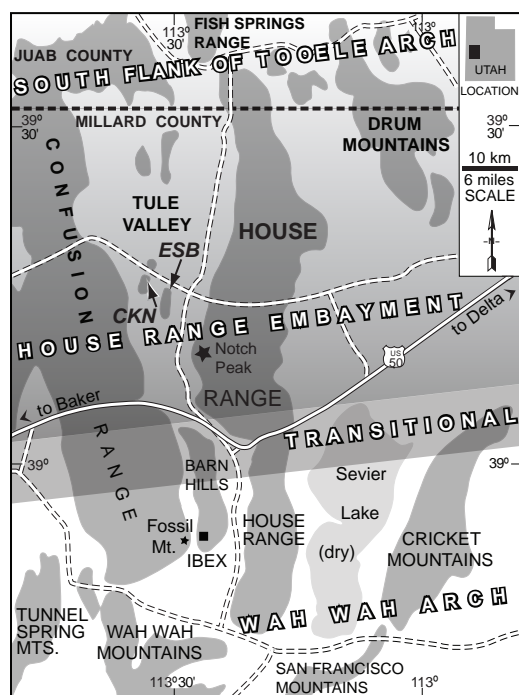


Figure 1. Map showing locations of measured sections. ESB is East Shoreline Butte section; CKN is Chalk Knolls North section.

and the insoluble residue picked. The majority of the samples were processed for conodonts by J.F. Miller. Sample numbers discussed herein are measured thicknesses in feet.

The sections are within the House Range Embayment (Fig. 1), interpreted by Rees (1986) as a fault-controlled deeper water basin on the Middle Cambrian carbonate platform. This pattern of sedimentation was shown to persist into the Late Cambrian during the deposition of the Orr Formation (Evans 1997, 1999) and Hellnmaria Member of the Notch Peak Formation (Miller *et al.* 2003). Miller *et al.* (in press) interpreted the embayment to be tectonically controlled, resulting from the breakup of the Neoproterozoic supercontinent. Faulting from the rifting was followed by thermal subsidence that produced accommodation space for the thick sequences of marine sediments deposited in the embayment.

Both measured sections include strata that are primarily lime mudstone interpreted to have been deposited in a deep subtidal environment on the continental shelf (Osleger & Read 1993). These limestones were deposited during the Hellnmaria Highstand (Evans *et al.* 2003; Miller *et al.* 2003) within the Sauk III Megasequence (Palmer 1981). The lithology is in contrast to peritidal dolomites, often stromatolitic, that comprise

the Hellnmaria Member to the north and south (Tooele Arch and Wahwah Arch, Fig. 1) of the House Range Embayment (Hintze *et al.* 1988). Both sections include a distinctive ooid grainstone bed, interpreted by Miller *et al.* (2003) to indicate higher energy during a period of shallowing of the depositional environment. The ooid grainstone bed allows lithostratigraphic correlation of the two sections, which together are 408.6 m (1340.5 ft) thick. No unconformities are known.

BIOSTRATIGRAPHY

Conodont and trilobite zonation

The upper parts of both sections yield conodonts of the *Proconodontus tenuiserratus* Zone, the lowest conodont zone established in North America, with overlying strata yielding conodonts of the *Proconodontus posterocostatus* Zone (Miller *et al.* 2003). Conodonts are present in the lower part of the Hellnmaria Member but are not useful for biostratigraphy. Macroscopic fossils are rare, although several trilobite collections have been made recently. Trilobite zones are not established in most of the Hellnmaria Member, but the top of the underlying Orr Formation is in the *Taenicephalus* Zone, and the top of the Hellnmaria Member occupies the *Rasettia magna* Subzone at the base of the *Saukia* Zone. These bracketing trilobite faunas establish the Hellnmaria as mid-Sunwaptan. Trilobites collected three feet above the base of the Chalk Knolls North section were identified as occupying the *Saratogia* Zone (Miller *et al.* 2003).

Brachiopod correlation

Brachiopods are used infrequently for correlation of North American Cambrian strata. Useful biostratigraphic zones for coeval strata in Oklahoma were established using calcitic-shelled brachiopods (Freeman & Stitt 1996). Zones using phosphatic-shelled brachiopods were established for slightly lower strata (Kurtz 1971) and for equivalent strata in Wyoming (Grant 1965).

Most of the species recovered are new and therefore not useful for correlation. Three species were reported previously in higher strata in the same field area (Popov *et al.* 2002), and this study establishes the base of their ranges. *Zhanatella utahensis* Popov *et al.*, 2002 ranges to the top of the *Cambroistodus minutus* conodont Subzone (*Eoconodontus* Zone), within the *Prosaukia serotina* trilobite Subzone. *Quadrisonia lavadamensis* Popov *et al.*, 2002 has its highest occurrence just below the top of the *Cambroistodus minutus* Subzone.

The species *Zhanatella rotunda* Koneva, 1986 was found in the lower part of the Hellnmaria Member, in samples taken from the East Shoreline

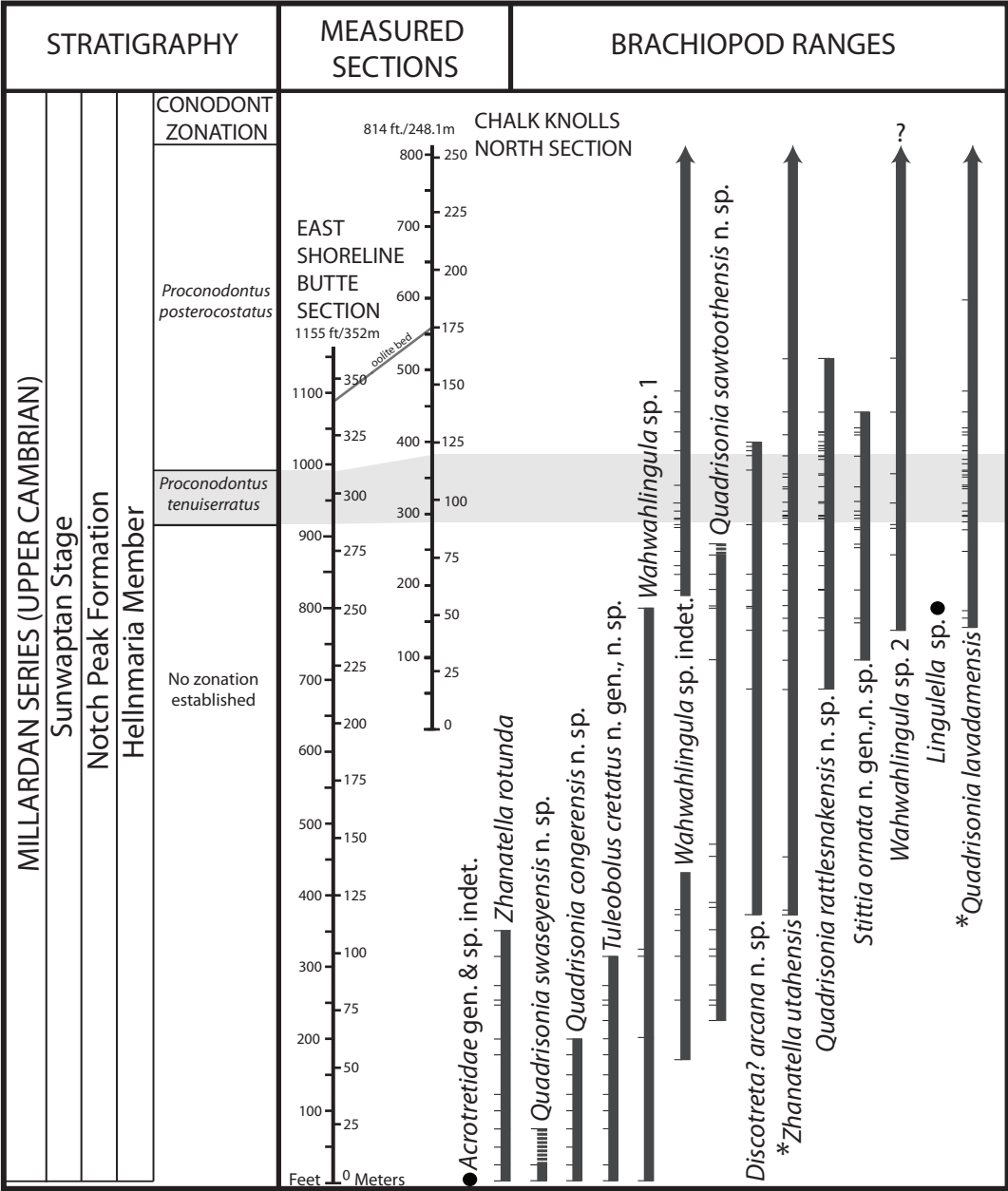


Figure 2. Ranges of lingulate brachiopod species in a composite of the two measured sections of the Hellnmaria Member of the Notch Peak Formation. The two sections are correlated biostratigraphically using the base of the *Proconodontus tenuiserratus* conodont Zone as a tie-point. Lithostratigraphic correlation is indicated by a distinctive oolite bed. The stratigraphic positions of collections are shown with tick-marks. Species described by Popov *et al.* (2002) are denoted with an asterisk.

Butte section. It ranges from the lowest sample collected, at 0.9 m above the base, to 107.3 m above the base (Fig. 2). The bed in which it was most abundant, ESB-200 (61 m above the base of the section), also yields trilobites and unidentified agnostoids.

The presence of *Z. rotunda* in Utah is especially

intriguing because it was described originally from the Malyi Karatau, southern Kazakhstan (Koneva 1986). It has since been documented in northeastern central Kazakhstan (Popov & Holmer 1994) as well as in the Montagne Noire region of southern France (González-Gómez 2005; Álvaro *et al.* 2007). Rieboldt (2005) also

Sample number (feet above section base)	3	25	50	75	100	125	150	178	200	226	247	254	275	315	325	352
Metres above base of section	0.9	7.6	15.2	22.9	30.5	37.9	45.7	54.3	61	68.7	75.3	77.4	83.8	96	99.1	107
<i>Tuleobolus cretatus</i> new gen. & sp.	10	10	18	20	33	7	111	11	56	8	3	5	1	23		
<i>Wahwahlingula</i> sp. 1	1								2							
<i>Wahwahlingula</i> sp. indet.								4				6			2	1
<i>Zhanatella rotunda</i> Koneva	1	5		1	8	11		6	53		1	20	6	23		1
<i>Quadrisonia congerensis</i> n. sp.	65	61	42	8	73	147	11	60	143							
<i>Quadrisonia sawtoothensis</i> n. sp.										105	48	159	36	67	112	88
<i>Quadrisonia swaseyensis</i> n. sp.	9	34		?												
<i>Quadrisonia</i> sp. indet.	6					6										
Acrotretidae gen. & sp. indet.	1															
Sample number (feet above section base)	373	380	454	471	779	800	825	847	859	879	912	916	920	925	929	935
Metres above base of section	114	116	138	144	237	244	252	258	262	268	278	279	280	282	283	285
<i>Lingulella</i> sp.						2										
<i>Stittia ornata</i> n. gen. & sp.					frag.		3			2	2			frag.	2	3
<i>Wahwahlingula</i> sp. 1			3			1										
<i>Wahwahlingula</i> sp. 2											2	4				
<i>Wahwahlingula</i> sp. indet.	1	9					10	1	1	8	31	66		1		1
<i>Zhanatella utahensis</i> Popov <i>et al.</i>	17	7	2				1	1	3	10		1		1	2	1
<i>Discotreta?</i> <i>arcana</i> n. sp.	1					1	6	3				4				
<i>Quadrisonia lavadamensis</i> Popov <i>et al.</i>										2					9	20
<i>Quadrisonia rattlesnakensis</i> n.sp.							?	80		23	?			54	43	
<i>Quadrisonia sawtoothensis</i> n. sp.	71	296	88	95		54		46		?	?					
<i>Quadrisonia</i> sp. indet.					15					21	2	1	16			
Sample number (feet above section base)	948	969	971	982	985	990	992	1001	1007	1012	1019	1032	1041	1051	1073	1157
Metres above base of section	289	295	296	299	300	302	302	305	307	309	311	315	317	320	327	353
<i>Stittia ornata</i> n. gen. & sp.	frag.	1								2			2	3		
<i>Wahwahlingula</i> sp. 2															2	
<i>Wahwahlingula</i> sp. indet.			1								2				1	
<i>Zhanatella utahensis</i> Popov <i>et al.</i>	2	2		5						1			2			
<i>Discotreta?</i> <i>arcana</i> n. sp.							6			1	6		1			
<i>Quadrisonia lavadamensis</i> Popov <i>et al.</i>		5	13	23	1	5	19	4	8		2			11	10	
<i>Quadrisonia rattlesnakensis</i> n. sp.	17	10			4				21	8	13	103	56		13	
<i>Quadrisonia</i> sp. indet.					8	5		6	11	33			10	34	12	14

Table 1. Distribution of brachiopods in collections from the Hellnmaria Member of the Notch Peak Formation by bed in the East Shoreline Butte measured section (ESB). Sample numbers refer to footage measured from the base of the section, at the base of the Hellnmaria Member. Equivalent measurements are given in metres. Specimens were counted if complete enough to be identified to valve type. “Frag.” refers to identifiable fragments with pseudointerarea details not intact; “?” refers to tentatively identified specimens. Total number of specimens is 4,367. Table does not include specimens identified as “juvenile lingulids”.

reported this species from deep subtidal facies of the Sneakover Limestone Member of the Orr Formation, the formation directly beneath the Notch Peak Formation in western Utah, as well as from the stratigraphically equivalent Catlin Member of the Windfall Formation in Nevada, the next state west of the field area.

A reconstruction of latest Cambrian palaeogeography (Cocks & Torvik 2002) placed Laurentia and Kazakhstan near the equator and placed the Montagne Noire area of France along the northern edge of the southern continent of Gondwana, far to the south of the equator. The distribution of a species over such a wide range of palaeoclimatic settings is unusual enough to call into question identification of specimens, but *Zhanatella rotunda* is a distinctive species and not easily mistaken for any other. The illustration of *Z. rotunda* by Álvaro *et al.* (2007, fig. 7H) appears

to be instead an acrotretid ventral valve, but this was apparently an error in plate construction or captioning. The species is illustrated and identified correctly by González-Gómez (2005).

All of the reported occurrences of *Zhanatella rotunda* are from strata that could be interpreted as outer shelf to upper slope deposits, most likely with access to the open ocean. Given the range of palaeolatitudes from which it is reported, it seems likely that this species was eurytopic as to water temperature and was adapted to deeper water environments.

Neuman (1984) recognised the importance of volcanic island arcs to brachiopod migration and used the distribution of Ordovician rhynchonelliform brachiopods to speculate on the existence of an island arc. Palaeogeographic reconstructions of the late Cambrian generally include subduction zones (Cocks & Torvik 2002)

Sample number (feet above section base)	61	102	143	160	177	200	248	260	283
Metres above base of section	18.6	31.1	43.6	48.7	54	61	75.6	79.2	86.3
Equivalent ESB bed in metres	209.4	221.9	234.4	239.6	244.8	251.8	266.4	270.1	277.1
<i>Stittia ornata</i> n. gen. & sp.		1		8			2		2
<i>Wahwahlingula</i> sp. 2			1				1		
<i>Wahwahlingula</i> sp. indet.									
<i>Zhanatella utahensis</i> Popov <i>et al.</i>	3	3	1	45	5				
<i>Discotretra?</i> <i>arcana</i> n. sp.	1		2		1				
<i>Quadrisonia lavadamensis</i> Popov <i>et al.</i>				11					1
<i>Quadrisonia sawtoothensis</i>		302			48	13	20		
<i>Quadrisonia rattlesnakensis</i> n. sp.	27		48	94		8			
<i>Quadrisonia</i> sp. indet.	4			120		20	10	7	1
Sample number (feet above section base)	288	294	297.5	302	320	340	361	385	396
Metres above base of section	87.8	89.6	90.7	92	97.5	103.6	110	117.3	120.7
Equivalent ESB bed in metres	278.6	280.4	281.5	282.9	288.3	294.4	300.8	308.2	311.5
<i>Stittia ornata</i> n. gen. & sp.							2		
<i>Wahwahlingula</i> sp. 2									
<i>Wahwahlingula</i> sp. indet.			2						
<i>Zhanatella utahensis</i> Popov <i>et al.</i>				1		54	1		
<i>Discotretra?</i> <i>arcana</i> n. sp.									
<i>Quadrisonia lavadamensis</i> Popov <i>et al.</i>		3		5	15	38			
<i>Quadrisonia rattlesnakensis</i> n. sp.			2	6	85		142	24	
<i>Quadrisonia</i> sp. indet.	5	2	9	31	11	21		1	2
Sample number (feet above section base)	400	419	447	476	521.5	540	599		
Metres above base of section	121.9	127.7	136.2	145.1	159	164.6	176.5		
Equivalent ESB bed in metres	312.7	318.5	327.1	335.9	349.8	355.4	373.4		
<i>Stittia ornata</i> n. gen. & sp.		1	1						
<i>Wahwahlingula</i> sp. 2			1		1				
<i>Wahwahlingula</i> sp. indet.		2	11	2					
<i>Zhanatella utahensis</i> Popov <i>et al.</i>			1		1				
<i>Discotretra?</i> <i>arcana</i> n. sp.	2								
<i>Quadrisonia lavadamensis</i> Popov <i>et al.</i>	1	4		137			7		
<i>Quadrisonia rattlesnakensis</i> n. sp.	46	76	81		52				
<i>Quadrisonia</i> sp. indet.	21	8				2			

Table 2. Distribution of brachiopods in collections from the Hellnmaria Member of the Notch Peak Formation by bed in the Chalk Knolls North measured section (CKN). Sample numbers refer to measurements in feet from the base of the section, at the base of the Hellnmaria Member. Equivalent measurements are given in metres. The position of equivalent beds in East Shoreline Butte section is given in metres; correlation between sections used the base of the *Proconodontus tenuiserratus* conodont Zone, with ESB-920 (280.4 m above the base of the section) equivalent to CKN-294 (89.6 m above the base of the section). “Frag.” and “?” as in Table 1. Total number of specimens is 1,676. Table does not include specimens identified as “juvenile lingulids”.

that could have served as “stepping stones” for migration. Lingulate brachiopods have long-lived planktotrophic larvae (Ushatinskaya 2003) and could have drifted for long distances over deeper water and then settled in the shallow water surrounding island arcs for metamorphosis. The presence of *Z. rotunda* in the Malyi Karatau region of Kazakhstan in an area interpreted as an early Palaeozoic seamount (Cook *et al.* 1991) supports the idea of isolated platforms around islands and seamounts serving as migration pathways.

Zhanatella rotunda was described from the *Pseudagnostus pseudangustilobus* trilobite Zone of the Malyi Karatau region of southern Kazakhstan (Koneva 1986). Holmer *et al.* (2001) documented its range in the Kyrshabakty section of the Malyi Karatau region as extending

from the *Pseudagnostus pseudangustilobus*-*Acrocephalalaspina* trilobite “bed” through the overlying *Euragnostus kazakhstanicus*-*Parabolina monstrosa* “bed” and into the lower part of the *Euragnostus ovaliformis*-*Pareuloma* “bed” of Abdulin *et al.* (1990). These three zones overlie the *Ivshinagnostus ivshini*-*Irvingella major* “bed” of Abdulin *et al.* (1990). *Irvingella major* Ulrich & Resser in Walcott, 1924 is a globally distributed trilobite species that is very useful for correlation. It occurs in coquina abundances in the *Irvingella major* Subzone of the *Elvinia* trilobite Zone in North America, which is the base of the Sunwaptan Stage of the Millardan Series of North America. Rieboldt (2005) collected *Zhanatella rotunda* from the *Taenicephalus* trilobite zone, directly above the

Irvingella major Subzone, in the Orr and Windfall Formations of Utah and Nevada, thus establishing the base of its range in the Great Basin of North America.

DISCUSSION OF FAUNA

The most abundant brachiopod in these Utah collections is the acrotetid *Quadrisonia*. Of the 6,042 specimens collected from bulk samples, 4,155 were assigned to the genus, and all collections yielded *Quadrisonia*. Five species of *Quadrisonia* are identified. Commonly, ranges of the species overlap and the species co-occur, although in most samples with two or more species of *Quadrisonia* present, one species is dominant. Also abundant (943 specimens) are early postlarval lingulids that are unidentifiable to genus or species. Species of *Zhanatella* commonly are associated with *Quadrisonia* but are generally not dominant. The distribution of taxa is summarised in Tables 1 and 2. Stratigraphic ranges of taxa and relationships with conodont zones are shown on Figure 2.

The genera *Quadrisonia* and *Wahwahlingula* are globally distributed. *Quadrisonia* has been reported from Australia (Rowell & Henderson 1978), Kazakhstan (Koneva & Popov 1988; Koneva *et al.* 1990), western Antarctica (Henderson *et al.* 1992), western Argentina (Holmer *et al.* 1999), possibly Sweden (Puura & Holmer 1993), as well as from stratigraphically lower upper Cambrian strata in the Great Basin of North America (Rowell & Henderson 1978; Popov *et al.* 2002), and questionably from the middle Cambrian Marjuman Stage of North America (Robson & Pratt 2007). *Wahwahlingula* was first reported from strata in the upper part of the Notch Peak Formation in Utah (Popov *et al.* 2002), as well as the overlying House Limestone and Fillmore Formation (Holmer *et al.* 2005) and has been reported from Russia (Popov *et al.* 2002). It has also been possibly reported from Australia (Brock & Holmer 2004) and Iran (Popov *et al.* 2008).

The occurrence of genera and species in Utah that also occur together in Kazakhstan is a pattern seen in strata just above those considered here (Popov *et al.* 2002). Holmer *et al.* (2005) also reported a genus common to Kazakhstan and Laurentia in the Fillmore Formation in the Stairian Stage of the Ibexian Series in Utah. These strata overlie those considered by Popov *et al.* (2002). This distribution suggests that there were at least sporadic migrations of brachiopods between Laurentia and Kazakhstan throughout the latest part of the Cambrian and into the earliest Ordovician.

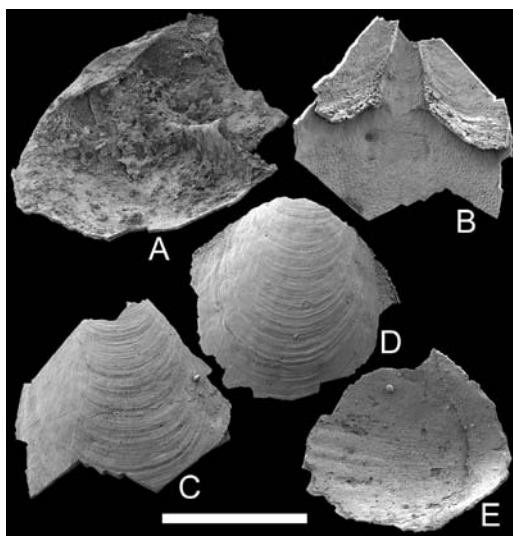


Figure 3. A, Acrotetid dorsal valve, gen. et sp. indet., from ESB-3, Hellnmria Member of the Notch Peak Formation, USMN 543034. Scale bar equals 500 µm; B-E, *Lingulella* sp. fragments from the Hellnmria Member of the Notch Peak Formation, ESB-800, B-C, ventral valve exterior and interior, USNM 543035; D-E, dorsal valve exterior and oblique view of interior, USNM 543036. Scale bar equals 1 mm.

SYSTEMATIC PALAEOLOGY

The classification used here follows Holmer & Popov (2000). Measurements in tables are reported in millimetres. Measurements were made on whole specimens, with a few exceptions for rare, poorly preserved taxa. In these cases, it was assumed that because brachiopods are bilaterally symmetrical, measurements involving width could be taken on half of a specimen and doubled.

Abbreviations used in tables of measurements are used as follows. For all valves, W, L and H refer to maximum width, length and height, respectively. For dorsal valves, Wm is the width of the cardinal muscle field, Wi is the width of the pseudointerarea, Wg is the width of the median groove, BS is the position of the posterior end of the median septum, LS is the position of the anterior end of the median septum, Lm is the length of the cardinal muscle field, and Li is the length of the pseudointerarea. For ventral valves, F refers to the distance between the posterior margin and the foramen, Wp is the width of the propareas, Lp is the length of the propareas, and Lg is the length of the pedicle groove. N refers to the number of specimens measured, X is the average value, S is standard deviation, MIN is the minimum value, MAX is the maximum value. The position of measurements follows Popov & Holmer (1994).

The material illustrated is housed in the

collections of the Department of Paleobiology, National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC.

Phylum BRACHIOPODA

Subphylum LINGULIFORMEA Williams *et al.*, 1996

Class LINGULATA Gorjansky & Popov, 1985

Order LINGULIDA Waagen, 1885

Superfamily LINGULOIDEA Menke, 1828

Family OBOLIDAE King, 1846

Subfamily OBOLINAE King, 1846

Lingulella Salter, 1866

Type species. *Lingula davisii* M'Coy, 1851 (by designation of Dall 1870).

Species included. The species of *Lingulella* are in need of revision, a project beyond the scope of this report.

Diagnosis. The type species, *Lingulella davisii*, was redescribed by Sutton *et al.* (2000), and their concept of the genus is followed here.

Lingulella? sp. (Fig. 3B-E)

Locality. Upper Cambrian (Sunwaptan) Hellnmaria Member of the Notch Peak Formation, Tule Valley, Millard County, western Utah. The two specimens were collected at 243.8 m above the base of the ESB section.

Material. One dorsal and one ventral valve fragment, USNM 543035 and USNM 543036.

Description. Exterior ornament on both valves consists of fine, closely spaced growth lines with frequent small disruptions of growth. Growth disruptions aligned laterally give the appearance of faint radial ornament.

Ventral valve with deep, narrow pedicle groove. Edges of propareas raised slightly along lateral edges of pedicle groove. Small round umbonal muscle scars lightly impressed anterolateral to the pedicle groove. Valve interior with many small, closely spaced epithelial imprints of varying size and shape, most commonly 20-30 μ m in maximum diameter (Fig. 3B).

Dorsal valve pseudointerarea forms crescent-shaped strip along posterior margin, not raised above valve floor. Flexure lines not observed. Visceral area pitted in same manner as ventral valve interior (Fig. 3E). Weakly developed median ridge bounded by two faint furrows.

Discussion. The material examined consists of

two fragments exhibiting internal pitting (Fig. 3B, E), a character of *Lingulella*. The pits are smaller and more closely spaced than on the type species.

Wahwahlingula is abundant in these collections and is very similar to *Lingulella* in morphology. Pitted exterior microornament on *Wahwahlingula*, which is virtually undetectable under the light microscope on juveniles, distinguishes the two genera. The microornament of *Wahwahlingula* can be obscured or destroyed when a specimen is exfoliated, adding to the difficulty of distinguishing the two genera.

Stittia n. gen.

Etymology. In honor of the Cambrian trilobite specialist, the late Dr. J.H. Stitt, advisor to the first author and friend to the second author.

Type species. *Stittia ornata* n. sp.

Species included. *Obolus (Westonia) notchensis* Walcott, 1908.

Occurrence. Upper Cambrian (Sunwaptan): Hellnmaria and Red Tops members of the Notch Peak Formation, western Utah, USA.

Diagnosis. Elongate suboval, nearly equibiconvex valves with prominent larval shell. Larval shell with fine growth lines and subtle radial ornamentation. Larval-postlarval shell boundary prominent, generally marked by slightly raised rim on latest larval growth, followed by depressed, but not undercut, area of postlarval growth. Mature growth marked by strongly expressed roughly concentric, raised transverse terrace lines, evenly spaced, with slightly irregular margins. Transverse terrace lines truncate against larval shell laterally and cross growth lines, deflecting towards posterior at median part of valve. Dorsal pseudointerarea with prominent elongated median groove. Dorsal propareas with lateral grooves.

Discussion. A number of early Palaeozoic obolid genera have been described with similar patterns of transverse ridges, including *Westonia* Walcott, 1901, *Libecoviella* Mergl, 1997, *Agalatassia* Popov & Holmer, 1994, and *Westonisca* Havlíček, 1982. *Stittia* is easily distinguished from these genera by its distinctive elongate dorsal median groove (Fig. 4E, J-K, P) and transverse grooves along the posterior margin of the dorsal pseudointerarea (Fig. 4E, G, K, P). Externally, it is most similar to *Libecoviella* in that the deflections of the transverse ridges occur only in the median part of the shell.

Although two species are distinguished, the

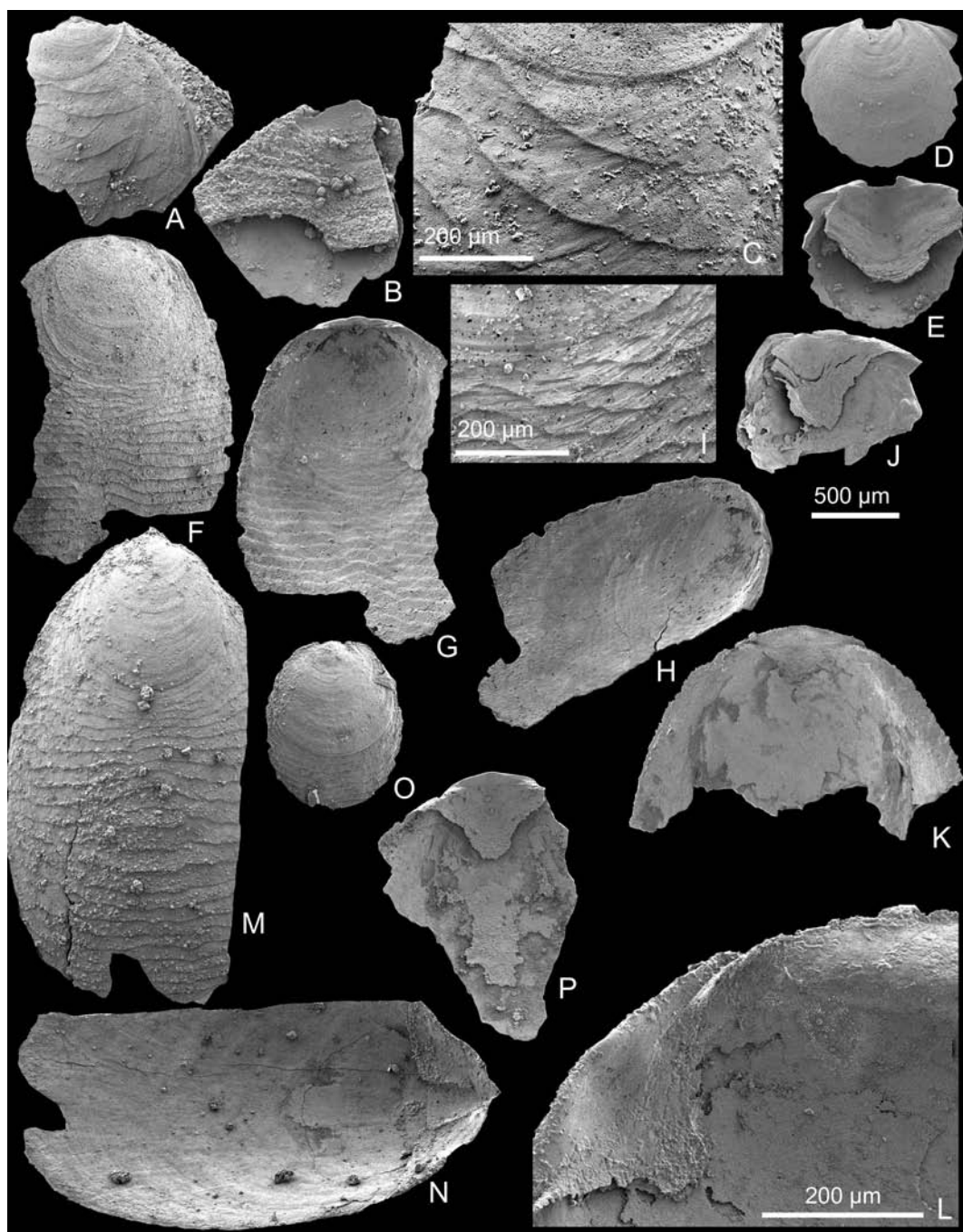


Figure 4. A-E, *Stittia* cf. *notchensis* (Walcott, 1908) n. gen., Red Tops Member, Notch Peak Formation, Millard County, Utah; collected at the summit of Notch Peak by Lehi Hintze. A-C, dorsal valve fragment, A, exterior, B, interior, showing part of robust elongate median groove characteristic of very mature specimens, C, detail of anterior margin of larval shell and postlarval ornamentation, USNM 542976; D-E, interior and exterior of a dorsal valve fragment, USNM 542977; F-P, *Stittia ornata* n. gen., n. sp., Hellnmaria Member, Notch Peak Formation, Millard County, Utah; F-I, dorsal valve fragment from ESB-912, F, exterior, G, interior, H, oblique lateral interior, I, anterior margin of larval shell and postlarval ornamentation, USNM 542978; J, dorsal valve fragment interior from ESB-825, USNM 542979; K-L, dorsal valve fragment from CKN-283, K, interior, L, detail of proparea showing transverse groove, USNM 542980; M-N, holotype, ventral valve from CKN-248, M, exterior, N, oblique view of interior, USNM 542983; O, postlarval juvenile dorsal valve exterior from CKN-160, USNM 542881; P, dorsal valve fragment interior from ESB-935, USNM 542982.

descriptions are based on mostly fragmentary material from insoluble residue or highly exfoliated hand samples. The most complete specimens are of *Stittia ornata*, but only one nearly complete valve was found in insoluble residue. The previously described species *S. cf. notchensis* was described from two exfoliated ventral valves, only one of which was illustrated (Walcott 1908, pl.7, fig. 13; 1912, pl. 63, fig. 9). New material is described below, but the specimens are fragmentary. Shell structure was not determined for either species due to recrystallisation.

***Stittia ornata* n. sp. (Figs. 4F-P)**

2011 Genus and species indeterminate; Freeman & Miller, p. 698, figs. 1-2.

Etymology. Latin, *ornatus*, in reference to the shell ornament.

Type locality. The holotype is from 75.6 m above the base of the CKN section, 14 m below the base of the *Proconodontus tenuiserratus* Zone in the Upper Cambrian (Sunwaptan) Hellnmaria Member of the Notch Peak Formation, Tule Valley, Millard County, western Utah. The lowest occurrence of the species is 31.1 m above the base of the CKN section, 58.5 m below the base of the *Proconodontus tenuiserratus* Zone, and the highest occurrence of the species is 136 m above the base of the CKN section, 18.7 m above the base of the *Proconodontus posterocostatus* Zone.

Type material. Holotype, ventral valve USNM 542983 (Fig. 4M-N). Paratypes, USNM 542978, dorsal valve from 278 m above the base of the ESB section; USNM 542979, dorsal valve from 251.5 m above the base of the ESB section; USNM 542980, dorsal valve from 86.3 m above the base of the CKN section; USNM 542981, dorsal valve from 48.8 m above the base of the CKN section; USNM 542982 dorsal valve from 285 m above the base of the ESB section. Unfigured topotype material consists of 14 dorsal valve fragments and 3 ventral valve fragments from the ESB section, and 12 dorsal valve fragments from the CKN section, along with many shell fragments unidentifiable to valve.

Diagnosis. *Stittia* characterised by transverse ornament of asymmetrical ridges spaced 40-55 μm apart in early postlarval growth. Dorsal valve pseudointerarea with prominent elongate median groove, rounded in lateral cross-section.

Description. Valves almost equibiconvex,

elongate suboval in outline, with maximum width of the valve at midlength or slightly to anterior. Larval shells more nearly equidimensional in outline, only slightly longer than wide, maximum length varying from 600 to 950 μm . Maximum height of valves situated towards posterior with maximum height of the one well preserved ventral valve at about 15% of maximum length of valve. Ventral valve slightly more inflated than dorsal valve. Dorsal posterolateral area of valve less convex than rest of valve. Both anterior and posterior slopes gently convex in lateral profile, with the posterior slope especially rounded near umbo and the anterior slope more tapered.

Both valves with relatively large larval shells ornamented by fine, sometimes irregularly spaced growth lines, crossed by occasional finely developed radial ornamentation (Fig. 4F, M, O). Boundary between larval and postlarval growth marked by prominent raised disturbance of growth accompanied by depressed areas to either side (Fig. 4I). Abrupt transition to postlarval ornamentation of strongly developed concentric, evenly spaced transverse ridges, with gently and irregularly scalloped anterior margins (Fig. 4I). Transverse ridges generally laterally continuous across valve, crossing growth lines. Ridges sometimes truncate against growth lines. Line of ridge deflected towards posterior at mid-valve, sometimes with subtle deflections towards anterior on either side. Transverse ridges terminate against lateral margins of larval shell in early growth stages. In lateral profile, ridges slope more gently towards posterior and more steeply towards anterior, with sharply defined anterior margin.

Suboval ventral valve, slightly more than half as wide as long, with subacuminate posterior margin. Ventral pseudointerarea with narrow, shallow pedicle groove, triangular in outline. Maximum width of groove less than 25% of maximum width of pseudointerarea. Pedicle groove bounded by low ridges along edges of the propareas (Fig. 4N). Orthocline propareas only slightly elevated above valve floor. Flexure lines barely discernible. Pseudointerarea about half as long as wide. Slightly thickened ventral visceral area with median tongue extending anteriorly a short distance, to approximately one-third valve length (Fig. 4N). Central part of visceral area bounded by two faintly impressed furrows, interpreted as impressions of pedicle nerve. Furrows extend from position approximately at maximum length of the pseudointerarea to anterolateral edge of the visceral area.

Central muscle scars bound median tongue of visceral area laterally. Anterior lateral muscle scars small and crescent-shaped, positioned with

posterior margin approximately coinciding with anterior end of flexure lines of propareas, then divergent laterally.

Suboval dorsal valve with short, slightly curved posterior margin. Posterior margin of larval shell thickened and upturned slightly. Orthocline pseudointerarea, with wide, shallow, laterally elongate median groove (Fig. 4G-H, K, P). Anterior edge of propareas elevated laterally on either side of median groove during juvenile growth stages, forming short, transverse groove that extends from edge of median groove to lateral margin of valve (Fig. 4L). Grooves less pronounced but still apparent on more mature specimens. Median groove U-shaped in transverse profile, with median part of the groove gently concave. Median groove extends towards anterior as much as three times the maximum length of remainder of pseudointerarea. Posterior lateral muscle scars small, crescent-shaped and lightly impressed, with maximum width of muscle field slightly wider than width of pseudointerarea. Slightly thickened visceral area. Other features of dorsal interior not observed.

Discussion. The material is fragmentary, with the most complete specimen (Fig. 4M, N) being a ventral valve from CKN-248. It is approximately 2.4 mm long, and, measuring width from lateral margin to midwidth and doubling (due to incomplete specimen), width is 1.6 mm. The largest dorsal valve (Fig. 4F-H) is clearly missing much of its anterior margin, but the maximum length of the fragment is 1.8 mm long. The reconstructed maximum width of this specimen is approximately 1.5 mm. Many of the specimens are fragments of the dorsal pseudointerarea with all or some of the elongate median groove present. The median groove varies considerably in size along the specimens, from smaller examples interpreted to be juveniles (Fig. 4G), to very large, robust median grooves interpreted to have been on mature individuals (Fig. 4J, P). The extremely large size of the median groove on some fragments indicates that *Stittia ornata* reached a mature size larger than indicated by the largest nearly complete individuals found in insoluble residues. This is supported by a large specimen collected as a hand sample at ESB-1051, a stratum that also yielded the species as insoluble residue. The specimen is exfoliated but does display the characteristic ornamentation of the genus. Although the entire shell is not preserved, the maximum dimension of the specimen is 9 mm long and 6 mm wide. This specimen was collected from a bed associated with abundant trilobites, both fragments and whole cranidia and pygidia. Trilobites are extremely rare in most

Hellnmaria strata. Siliceous sponge spicules are more abundant in insoluble residue from ESB-1051 than in residues from other Hellnmaria strata. This may indicate a temporary change in the depositional environment to shallower and possibly more high-energy conditions.

Stittia is rare in these collections, occurring in only 18 samples, generally as fewer than five fragmentary specimens. Brachiopods with transverse terrace-like ornament, as seen in *Stittia*, are interpreted to have been burrowers (Savazzi 1986; Seilacher 1973) and to have been adapted to higher energy environments (Mergl 1997). Mergl (1997) described a “*Westonia* Community” of obolids with morphology similar to *Stittia* as being characteristic of sandy-bottomed, shallow marine environments. He interpreted the deep, narrow pedicle groove exhibited by these brachiopods as being evidence for a well developed pedicle, which would be necessary in such an environment. Savazzi (1986) postulated that brachiopods with this type of ornament may have burrowed umbodown, which would necessitate a stout pedicle. The unusually prominent elongate median groove seen on the dorsal valve of *Stittia* (Fig. 4E, K, M) is consistent with a well developed pedicle. Another characteristic of *Stittia* is its large larval shell. The size of the larval shell may correlate to the amount of time spent as a planktotrophic larva (Freeman & Lundelius 1999). Perhaps the physical requirements of burrowing favored larger individuals at the time of settlement onto the substrate. The rarity of *Stittia* in the two Hellnmaria measured sections may be facies-related, as this brachiopod may have inhabited higher energy environments and occasionally been swept into the quieter, deeper environment.

Stittia* cf. *notchensis (Walcott, 1908) (Figs. 4A-E)

1908 *Obolus* (*Westonia*) *notchensis*; Walcott, p. 69, fig. 13.

1912 *Obolus* (*Westonia*) *notchensis* Walcott; Walcott, p. 463, pl. 63, fig. 9.

Locality. Summit of Notch Peak, House Range, Millard County, western Utah, in the upper Cambrian (Sunwaptan) Red Tops Member of the Notch Peak Formation.

Material. Two topotype dorsal valve fragments, USNM 542976 and USNM 542977.

Diagnosis. Transverse ornament of rounded ridges, asymmetrical in profile, spaced 100-200 μ m apart in early postlarval growth.

Description. Dorsal valve with large larval shell, unornamented except for growth lines. Boundary between larval and postlarval growth distinct, marked by depressed area of growth disruption. Postlarval growth with ornament of transverse ridges, asymmetrical in profile, spaced 100-200 μm apart (Fig. 4C), crossing growth lines and deflected towards posterior at mid-valve. Wide median groove elongated towards anterior. Median groove rounded and concave in transverse profile. Propareas with transverse groove extending along posterior margin laterally from either side of beak (Fig. 4E).

Discussion. Walcott's *Obolus* (*Westonia*) *notchensis* description is based on the exterior of two ventral valves, both described (and one illustrated) as being badly exfoliated. Nothing of the interior was described. The ornamentation was described as being similar to that of *Obolus* (*Westonia*) *stoneanus* (Whitfield, 1882) or *Obolus* (*Westonia*) *iphis* (Walcott, 1905), both of which are described as having transverse lines with undulations near the median part of the shell.

Walcott (1908) described *O. (W.) notchensis* from the Notch Peak Formation, with the type locality given as the summit of Notch Peak, in the House Range, Millard County, western Utah. Although Walcott considered the type locality of *O. (W.) notchensis* to be Ordovician, it has since been confirmed (Hintze *et al.* 1988) that strata at the summit of Notch Peak are assignable to either the *Saukiella junia* or *Prosaugia serotina* Subzones of the *Saukia* trilobite zone and are therefore upper Cambrian and Sunwaptan in age. They are assigned to the Red Tops Member of the Notch Peak Formation. Hintze collected a bulk sample at the top of Notch Peak in 1974 which J. F. Miller processed for conodonts and phosphatic brachiopods. Hintze *et al.* (1988) lists "linguloid brachiopod, gen. and sp. undet." from this collection. The sample consists of two very fragmentary dorsal valves, one of which exhibits the distinctive elongate dorsal median groove and transverse grooves along the posterolateral margins of the pseudointerarea, which are characters of *Stittia* (Fig. 4E). Both valves have part of an intact smooth larval shell that appears to have been similar in size to that of *Stittia ornata* (Fig. 4A, D). The intact ornament on one fragment (Fig. 4A) is clearly different from that of *S. ornata*. The transverse ridges are more widely spaced, from a minimum of 100 μm to a maximum of 200 μm apart (Fig. 4C). The fragment preserves only a few transverse ridges in an area of early postlarval growth, but the transverse ridges on similar areas of *S. ornata* are spaced twice or more as closely (Fig. 4I). The lateral profile of

the ridges of *S. cf. notchensis* is more rounded in profile than those on *S. ornata*, although the *S. cf. notchensis* specimens likely are abraded.

The transverse ridges are similar to those of *S. ornata* in cross-cutting growth lines, and they appear to deflect towards the posterior at the median part of the valve (Fig. 4A).

Tuleobolus n. gen.

Etymology. In reference to Tule Valley in Utah, and to the superficial similarity of the genus to *Obolus* von Eichwald 1829.

Type species. *Tuleobolus cretatus* n. sp.

Other species included. *Obolella discoida* Hall & Whitfield 1877 is provisionally included.

Occurrence. Upper Cambrian (Sunwaptan): Hellnmaria Member of the Notch Peak Formation, western Utah, USA. Possibly also from the upper Cambrian (Steptoean) Dunderberg Shale, Eureka County, Nevada, USA.

Diagnosis. Small, slightly dorsibiconvex shells, subrounded and nearly equidimensional in outline. Ornamented with unevenly spaced rugellae. Prominent larval shells on both valves marked by growth disruption. Ventral larval shell inflated relative to rest of valve, with low lateral ridge. Interior of both valves with wide limbus. Pedicle groove short, shallow, terminating as a short tubular projection at beak, and at anterior end with shallow groove extending towards anterior. Ventral pseudointerarea with microornament of small hemispherical pits on lateral margins.

Discussion. *Tuleobolus* is unique in having microornament confined to the outer margins of the ventral pseudointerarea. The tubular projection of the beak is similar to that of *Aksarinaia* Koneva, 1992, described as an emarginature. That genus was assigned to Family Zhanatellidae by Koneva (1992) because of the emarginature, but assigned to Family Obolidae by Holmer *et al.* (2001) because of lack of pitted microornament. A similar feature of the beak is also seen in Obolinae n. gen.? and n. sp.? of Streng *et al.* (2011). This feature is seen as well on the zhanatellid genus *Wahwahlingula* Popov *et al.*, 2002. Although *Tuleobolus* is assigned to the Family Obolidae based on the lack of microornament on external larval and postlarval growth, the growing number of taxa which share features of both families suggests that the relationship between the two families should be re-examined.

The few known characters of the species

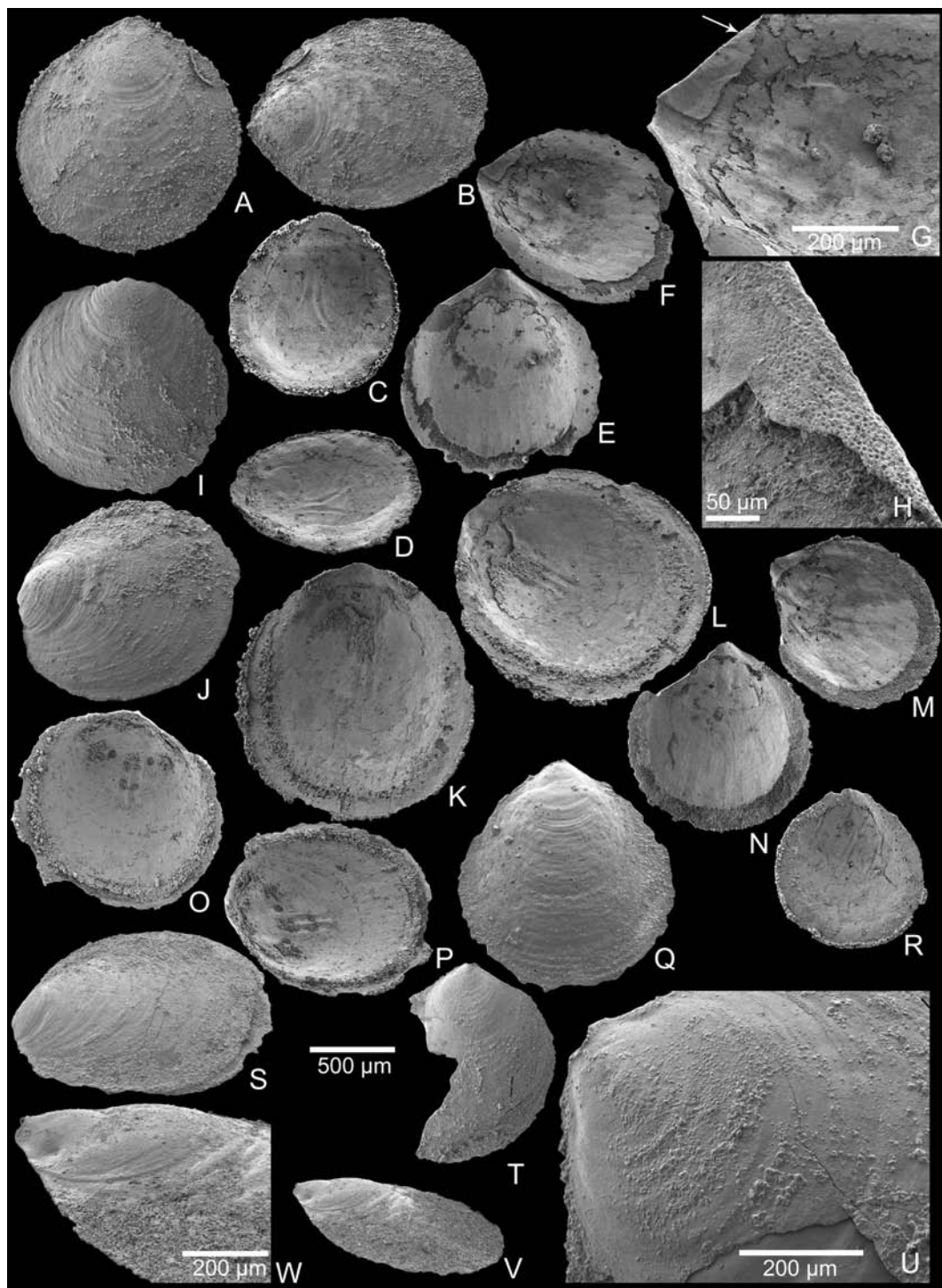


Figure 5. A-W, *Tuleobolus cretatus* n. gen., n. sp., Hellnmaria Member, Notch Peak Formation, Millard County, Utah. Scale bar 500 µm unless indicated. A-B, ventral valve from ESB-150, A, exterior, B, oblique view of exterior, USNM 542964; C-D, dorsal valve from ESB-150, C, interior, D, oblique view of interior, USNM 542965; E-H, holotype, ventral valve from ESB-150, E, interior, F, oblique view of interior, G, pseudointerarea and interior, arrow shows location of H, H, micro-ornament along outer margin of pseudointerarea, USNM 542966; I-J, dorsal valve from ESB-150, I, exterior, J, oblique lateral view, USNM 542967; K-L, dorsal valve from ESB-150, K, interior, L, oblique lateral view USNM 542968; (continued opposite)

Obolella discoida Hall & Whitfield appear to fit the diagnosis of this genus and it is provisionally assigned to it. Walcott (1912) mentioned that the umbo of *O. discoida* is raised slightly towards the posterior margin, a diagnostic character of *Tuleobolus*. The interiors of the valves were not described, but Walcott (1912, pl.18, fig. 6d) illustrated a partially exfoliated dorsal valve with two subparallel grooves. These grooves appear to be similar to the posterior ends of the vascula media, which are relatively prominent on *Tuleobolus cretatus*.

The maximum size reported by Walcott (1912) was 4.25 mm in length, with a width of 4 mm. This is larger than material from the Hellnmaria Member. The type material of *O. discoida* was collected from a limestone in the Eureka District of Nevada, and Walcott (1908, 1912) documented it from the Dunderberg Shale in the Eureka District, Nevada. The Dunderberg Shale is stratigraphically equivalent to the Orr Formation of western Utah, which underlies the Hellnmaria Member of the Notch Peak Formation.

***Tuleobolus cretatus* n. sp. (Figs. 5)**

Etymology. Latin, *cretatus*, meaning “surrounded by chalk” in reference to the diatomaceous earth deposits (locally called “chalk”) from Pleistocene Lake Bonneville; these deposits surround the type locality.

Type locality. Upper Cambrian (Sunwaptan) Hellnmaria Member of the Notch Peak Formation, Tule Valley, Millard County, western Utah. The holotype was collected from the ESB section, 45.7 m above the base of the Hellnmaria Member of the Notch Peak Formation, 233.5 m below the base of the *Proconodontus tenuiserratus* Zone. The lowest occurrence of the species is in the lowest sample collected, at 0.9 m above the base of the ESB section, 278.3 m below the base of the *P. tenuiserratus* Zone. The highest occurrence of the species is at 96 m above the base of the ESB section, 183.2 m below the base of the *P. tenuiserratus* Zone.

Type material. Holotype, ventral valve USNM 542966 (Fig. 5E-H). Paratypes from 15.2 m above the base of the ESB section, USNM 542970, dorsal valve and USNM 542971, ventral valve. Paratypes from 45.7 m above the base of the ESB

section, USNM 542964, ventral valve; USNM 542965, dorsal valve; USNM 542967, dorsal valve; USNM 542968, dorsal valve; USNM 542969, ventral valve; USNM 542972, ventral valve; USNM 542973, dorsal valve; USNM 542974, ventral valve; and USNM 542975, ventral valve. Unfigured topotype material consists of 145 dorsal valves, 168 ventral valves, and 3 juvenile whole shells, all from the ESB section.

Diagnosis. As for genus.

Description. Slightly dorsibiconvex, with both valves only slightly inflated. Valves subrounded to suboval in outline, slightly longer than wide, with dorsal valve more nearly equidimensional. Maximum height of both valves at approximately midlength or slightly to posterior. Anterior and posterior slopes are gently and evenly inflated in lateral profile. Internal shell structure was not determined due to recrystallisation of the study material.

Ornament of irregularly spaced concentric rugellae, approximately 2-4 distinct rugellae per 100 μm , not evenly spaced, nor of equal size. Fine, faint, radial ornamentation observed on some mature, well preserved specimens (Fig. 5I). Microornament of hemispherical pits, 1-2 μm in diameter, on outer parts of ventral pseudointerarea (Fig. 5H).

Interior margin of both valves marked by broad limbus extending from anterolateral edge of the pseudointerareas, widening towards the anterior (Fig. 5E-F, K-M). Limbus not well developed on juveniles. Interior with faint radial ornament (Fig. 5F).

Subacuminate ventral posterior margin, with posterolateral margins straight to slightly concave in outline. Angle formed by posterolateral margins at apex approximately 100°, with juvenile valves more sharply acuminate. Ventral pseudointerarea slightly raised above valve floor along anterior edge, divided by poorly developed flexure lines. Short, shallow pedicle groove, gently flared towards anterior, terminating in small (approximately 50-60 μm diameter) tubular projection at beak (Fig. 5G, U-W). Shallow internal groove extends from anterior margin of pedicle groove to about one-third length of valve (Fig. 5G).

Ventral visceral area slightly thickened and

M-N, ventral valve from ESB-150, **M**, oblique lateral view, **N**, interior, USNM 542969; **O-P**, dorsal valve from ESB-50, **O**, interior, **P**, oblique lateral view, USNM 542970; **Q**, ventral valve exterior from ESB-50, USNM 542971; **R**, ventral valve interior from ESB-150, USNM 542972; **S**, oblique lateral view of dorsal valve exterior from ESB-150, USNM 542973; **T-U**, ventral valve from ESB-150, **T**, exterior, **U**, detail of larval shell, USNM 542974; **V-W**, ventral valve exterior from ESB-150, **V**, exterior, **W**, larval shell showing elongated apical projection of pedicle groove, USNM 542975.

Dors.	W	L	L/W	Vent.	W	L	Lg	Lp	Wp	W/L	Wp/Lp	Lp/L	Wp/W	Lg/Lp	L/W
N	14	14	14	N	10	10	10	10	10	10	10	10	10	10	10
X	0.91	0.90	0.99	X	0.84	0.91	0.09	0.16	0.48	0.93	2.9653	0.181	0.574	0.54	1.083
S	0.15	0.15	0.03	S	0.14	0.12	0.01	0.03	0.08	0.07	0.3323	0.018	0.042	0.047	0.09
MIN	0.64	0.63	0.94	MIN	0.61	0.69	0.06	0.12	0.37	0.76	2.5714	0.15	0.517	0.467	1
MAX	1.07	1.12	1.07	MAX	1.10	1.16	0.10	0.22	0.66	1.00	3.7778	0.212	0.667	0.6	1.311

Table 3. *Tuleobolus cretatus* n. gen., n. sp., average dimensions and ratios of dorsal and ventral valves, all specimens from ESB-150. See first part of ‘Systematic Palaeontology’ for explanation of abbreviations.

poorly defined, apparently not extending past midlength. Vascula lateralia baculate, located submarginally and slightly arcuate, not visible past posterior half of valve. Central muscle scars small, round, lightly impressed. Anterior lateral muscle scars narrow and crescent-shaped, set just lateral to terminations of pseudointerarea flexure lines.

Ventral larval shell prominent, with low, subtle lateral ridge (Fig. 5V-W). Larval shell wider than long, about 475 µm wide and 375 µm long. Anterior half of larval shell inflated and rounded relative to postlarval growth, giving prominence to larval shell boundary. Larval/postlarval boundary marked by slight growth disruption.

Dorsal valve nearly equidimensional in outline, varying from transversely to laterally suboval, with gently rounded posterior margin in outline. Dorsal pseudointerarea forms crescent-shaped strip not raised above the floor of the valve. Wide median groove poorly differentiated from propareas, with flexure lines poorly developed.

Narrow, transversely suboval central muscle scars placed near posterior end of low median ridge. Median ridge bounded by two low ridges laterally. Combined (?) posterior lateral muscle scars are lightly impressed narrow crescents. Vascula lateralia arcuate, submarginal and lightly impressed. Vascula media extending from position just anterior to central muscle scars, subparallel, then becoming widely divergent, arcing strongly anterolaterally, extending to slightly past midlength of the valve (Fig. 5C-D).

Prominent dorsal larval shell boundary formed by disruption of growth, but shape and convexity

of larval shell similar to that of postlarval growth.

Measurements. See Table 3.

Discussion. Both dorsal and ventral valves were measured, but the lightly impressed interior features, such as muscle scars and the dorsal median ridge, were impossible to measure accurately and meaningfully.

Although the specimens are small and the interior features are lightly impressed, the majority of the specimens examined are interpreted as mature, or nearly mature, individuals. Four macroscopically visible specimens were collected at ESB-200, a bed yielding many of the specimens recovered from insoluble residue. Although the specimens visible in the field were exfoliated and pseudointerarea details were not visible, maximum dimensions were measured as accurately as possible. The largest of these valves had a width of 2.4 mm. These valves are not included in the measurement tables due to the inaccuracy of the measurements. No fragments of extremely large individuals were observed in insoluble residue.

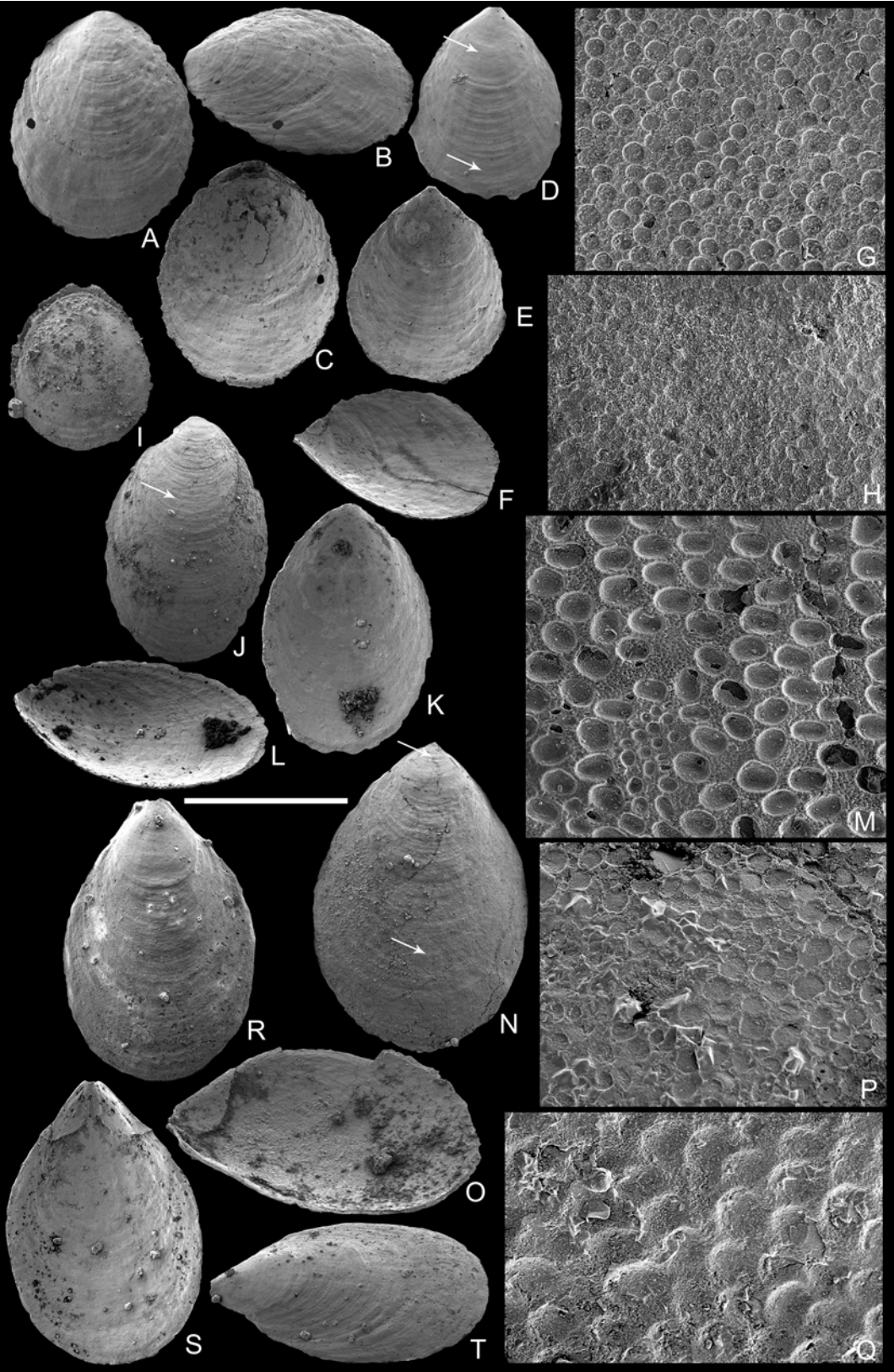
Family ZHANATELLIDAE Koneva, 1986

Wahwahlingula Popov *et al.*, 2002

Type species. *Lingula antiquissima* Jeremejew, 1856.

Other species included. *Wahwahlingula* sp. Popov *et al.*, 2002; *Wahwahlingula sevierensis*

Figure 6. *Wahwahlingula* spp., Hellnmaria Member, Notch Peak Formation, Millard County, Utah. Scale bar indicates 300 µm for J, K, and L; 20 µm for G, H, M, P, Q; and 500 µm for other images. **A-I**, *Wahwahlingula* sp. 1. **A-C**, dorsal valve from ESB-454, **A**, exterior, **B**, oblique exterior, **C**, interior view USNM 542984; **D-H**, ventral valve from ESB-454, **D**, exterior view with arrows pointing to location of H (top) and G (bottom), **E**, interior, **F**, oblique interior, **G**, detail of postlarval microornament, and **H**, detail of larval microornament, USNM 542985; **I**, dorsal view of whole shell of juvenile from ESB-200, USNM 542986. **J-T**, *Wahwahlingula* sp. 2. **J-M**, dorsal valve from ESB-916, **J**, exterior with arrow indicating position of M, **K**, interior, **L**, oblique interior, **M**, detail of postlarval pitting, USNM 542987; **N-Q**, ventral valve from ESB-916, **N**, exterior with arrows pointing to location of P (top) and Q (bottom), **O**, interior oblique, **P**, detail of larval ornamentation, **Q**, detail of exfoliated postlarval ornamentation, USNM 542988; **R-T**, ventral valve from ESB-916, **R**, exterior, **S**, interior, **T**, oblique exterior, USNM 542989.



Holmer *et al.*, 2005. Questionably included is *Wahwahlingula? emanuelensis* Brock & Holmer, 2004.

Diagnosis. The diagnosis of Popov *et al.* (2002) is followed here.

Discussion. The majority of specimens were exfoliated juveniles that were not assigned to a species. These are shown as *Wahwahlingula* sp. indet. in Figure 2 and listed in the same manner in Tables 1 and 2. The study material was too recrystallized to determine the shell structure with certainty.

Wahwahlingula sp. 1 (Fig. 6A-I)

Locality. Upper Cambrian (Sunwaptan) Hellnmaria Member of the Notch Peak Formation, Tule Valley, Millard County, western Utah. All specimens were collected from the ESB section. The lowest occurrence of the species was in the lowest sample collected, at 0.9 m above the base of the section, 278.3 m below the base of the *P. tenuiserratus* Zone, and the highest sample was collected 244 m above the base of the section, 35.2 m below the base of the *P. tenuiserratus* Zone.

Material. Illustrated specimens USNM 542984, dorsal valve, and USNM 542985, ventral valve, both collected 138.4 m above the base of the ESB section, and USNM 542986, juvenile whole shell, collected 61 m above the base of ESB section. Additional material is four dorsal valves and two ventral valves from the ESB section.

Description. The description is based on a few juvenile postlarval shells. Larval shell of both valves well defined, exterior with round, closely spaced and sometimes overlapping, flat-bottomed pits, 2-2.5 μm in diameter (Fig. 6H). Larval shell nearly equidimensional in outline or transversely suboval. Length of larval shell 200-225 μm and width 200-300 μm . Larval/postlarval boundary marked by change in ornamentation and pronounced disruption of growth. Both valves with postlarval microornament of slightly larger, flat-bottomed, round pits, 2.5-3.5 μm in diameter, with clusters of smaller, 1-1.5 μm diameter, flat-bottomed, round pits between (Fig. 6G). Larger pits arranged in clusters and irregular anastomosing chains, with smaller pits forming clusters between. Irregularly spaced growth lamellae and faint radial ornamentation present. Radial ornamentation also visible on valve interiors.

Ventral valve subtriangular, with length about 130% of width. Maximum width anterior

to midlength. Posterior margin subacuminate, with elongated pedicle groove forming short tubular projection. Pseudointerarea with length approximately 18% of valve length and width 60% of valve width. Shallow, well defined triangular pedicle groove and low, triangular propareas. Flexure lines faintly defined or absent on juvenile individuals.

Dorsal valve suboval with rounded posterior margin. Dorsal pseudointerarea forms crescent-shaped strip along the posterior margin, not raised above the valve floor. Median groove wide, poorly defined.

Other interior features of both valves not discerned.

Discussion. *Wahwahlingula* sp. 1 differs from *Wahwahlingula sevierensis* Holmer *et al.*, 2005 and *Wahwahlingula antiquissima* (Jeremejew, 1856), as well as *Wahwahlingula* sp. 2 (below) in having flat-bottomed pits on postlarval growth that are similar to pits on the larval shell. The flat-bottomed pits are similar to those of *Wahwahlingula? emanuelensis* Brock & Holmer, 2004 but differ in being larger in diameter. Additionally, the larval shell of *W.? emanuelensis* is smooth.

Wahwahlingula sp. 2 (Fig. 6J-T)

2002 *Wahwahlingula* sp.; Popov *et al.*, fig. 20-27.

Locality. Upper Cambrian (Sunwaptan) Hellnmaria Member of the Notch Peak Formation, Tule Valley, Millard County, western Utah. The lowest occurrence of the species is 43.6 m above the base of the CKN section, 46 m below the base of the *Proconodontus tenuiserratus* Zone, and the highest occurrence is 159 m above the base of the CKN section, 41.7 m above the base of the *Proconodontus posterocostatus* Zone.

Material. Illustrated specimens USNM 542987, dorsal valve, and USNM 542988-542989, ventral valves, all collected at 279.2 m above the base of the ESB section. Additional material is 2 dorsal and 3 ventral valves from ESB section, 3 dorsal and 4 ventral valves from CKN section.

Description. Larval shell of both valves well defined, with ornament of round, closely spaced and sometimes overlapping, flat-bottomed pits, 2-2.5 μm in diameter (Fig. 6P). Larval shell nearly equidimensional in outline to transversely suboval, with length of larval shell 200-275 μm and width 200-325 μm . Larval/postlarval boundary marked by pronounced disruption of growth and change in ornamentation. Postlarval

growth with microornament of rounded-bottom pits, oval in outline and 4-5 μm in length, sometimes with clusters of smaller, more nearly circular pits (Fig. 6M, O). Long axis of oval pits most commonly parallel to growth. Pits sometimes aligned laterally, forming irregular columns, especially in later postlarval growth. Irregularly spaced growth lamellae on exterior.

Suboval ventral valve with subacuminate posterior margin. Length approximately 150% of width, with maximum width at about midlength or slightly anterior to it. Posterior end of pedicle groove elongate forming short tube-like projection at posterior margin (Fig. 6T). Well defined triangular pseudointerarea with shallow, triangular pedicle groove. Pseudointerarea occupies about 65% of valve width and 22% of valve length. Posterior margin thickened and rounded. Flexure lines faint.

Poorly defined dorsal valve pseudointerarea not raised above valve floor, forms a strip along posterior margin. Median groove not observed.

Interior features not discerned on either valve.

Discussion. *Wahwahlingula* sp. 2 is slightly more elongate than *Wahwahlingula* sp. 1 and has different microornament. Under the light microscope, early postlarval specimens of *Wahwahlingula* sp. 1 and *W.* sp. 2 are difficult to distinguish from each other and also from the co-occurring genus *Lingulella*.

The microornament of *Wahwahlingula* sp. 2 is similar in shape to the stratigraphically higher species, *Wahwahlingula sevierensis* Holmer *et al.*, 2005, but the pits are larger. The microornament also appears to differ in pattern from that of *Wahwahlingula antiquissima* (Jeremejew), as illustrated by Popov *et al.* (2002, fig. 4.16). The microornament appears to be similar to *Wahwahlingula*? sp. 1 of Popov *et al.* (2008), but that taxon is significantly more equidimensional in outline.

The description is based on a few early postlarval juveniles, but they appear to be similar to specimens identified by Popov *et al.* (2002) as *Wahwahlingula* sp. and excluded from *W. sevierensis* by Holmer *et al.* (2005). Similarities to the Popov *et al.* (2002) material includes microornament of the same shape and size (Popov *et al.* 2002, fig. 4.25), similarity in shape of specimens, and a thickened and enrolled dorsal posterior margin (Popov *et al.* 2002, fig. 4.26).

Zhanatella Koneva, 1986

Type species. *Zhanatella rotunda* Koneva, 1986.

Other species included. *Zhanatella utahensis*

Popov *et al.*, 2002.

Diagnosis. The diagnosis of Popov & Holmer (1994) is followed here.

Zhanatella rotunda Koneva, 1986 (Fig. 7A-H)

1986 *Zhanatella rotunda*; Koneva, p. 50, pl. 5, figs. 1-12.

1992 *Zhanatella rotunda* Koneva; Popov & Ushatinskaya, pl. 2, figs. 5-6; pl. 3, figs. 1-3.

1994 *Zhanatella rotunda* Koneva; Popov & Holmer, p. 70-71, figs. 40, 65.

1995 *Zhanatella rotunda* Koneva; Ushatinskaya, figs. 8, 14.

2001 *Zhanatella rotunda* Koneva; Holmer *et al.*, p. 48-49, pl. 10, figs. 8-11.

Locality. Upper Cambrian (Sunwaptan) Hellnmaria Member of the Notch Peak Formation, Tule Valley, Millard County, western Utah. The species occurs in the stratigraphically lowest sample at 0.9 m above the base of the Hellnmaria Member and the base of the ESB section. The highest occurrence of the species is 107.3 m above the base of that section, 171.9 m below the base of the *Proconodontus tenuiserratus* Zone.

Material. Illustrated specimens USNM 542956, dorsal valve, from 61 m above the base of the ESB section; USNM 542955 and 542958, ventral valves, both from 61 m above the base of the ESB section; and USNM 542957, ventral valve from 107.3 m above the base of the ESB section. Additional material is 46 dorsal valves and 16 ventral valves from the ESB section.

Diagnosis. The diagnosis of Popov & Holmer (1994) is followed here.

Discussion. The specimens appear to be identical to previously described and illustrated occurrences in almost every way, except that the pattern of concentric rugae is, in some cases, less regular than on specimens illustrated by Popov & Holmer (1994) and Holmer *et al.* (2001).

This brachiopod is abundant only in sample ESB-200, a bed which is unusual for the Hellnmaria Member in bearing abundant trilobites and agnostoids.

Zhanatella utahensis Popov *et al.*, 2002 (Fig. 7I-V)

2002 *Zhanatella utahensis*; Popov *et al.*, p. 221, figs. 5.1-5.19.

Locality. Upper Cambrian (Sunwaptan)

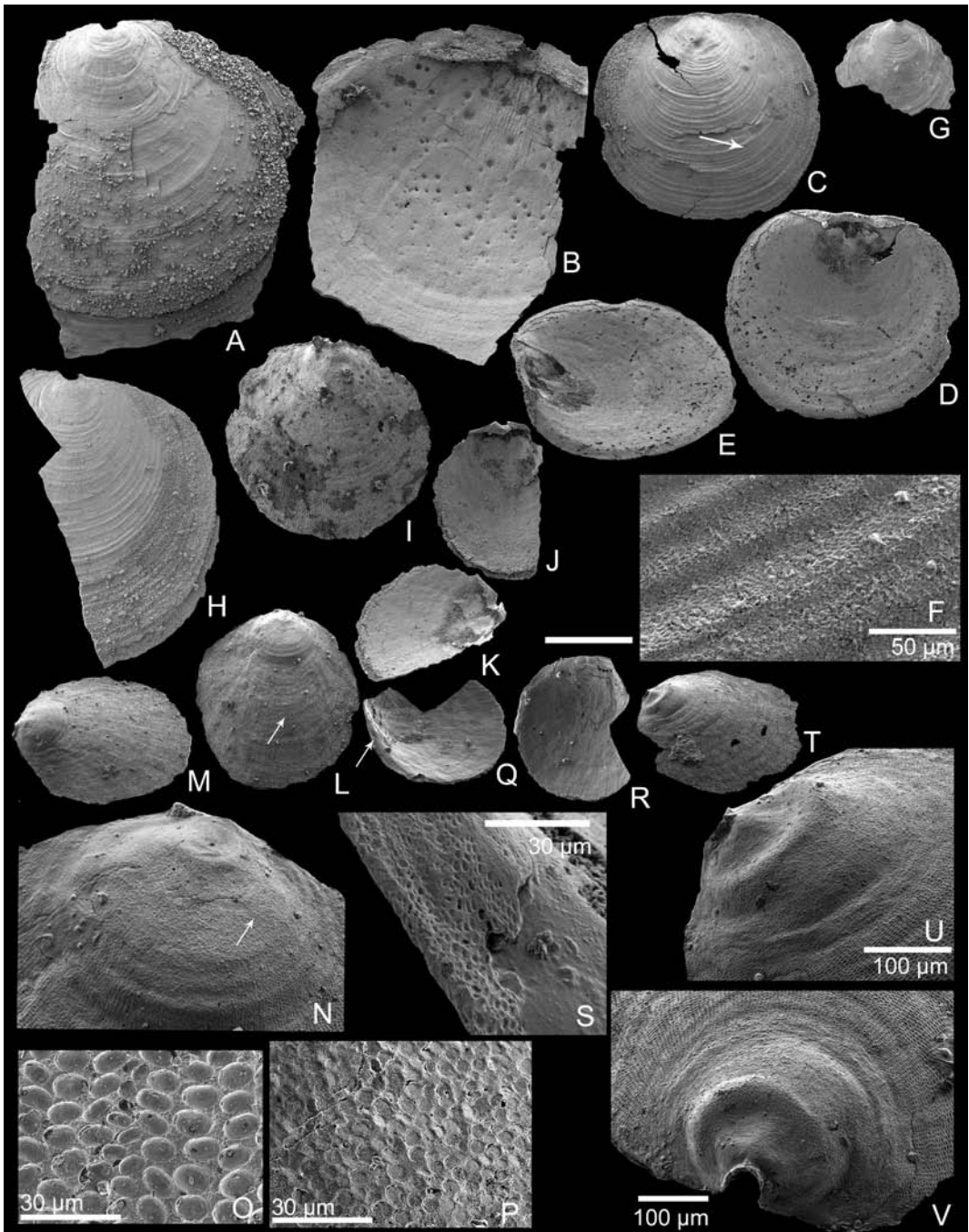


Figure 7. **A-H**, *Zhanatella rotunda* Koneva, 1986, Hellnmaria Member, Notch Peak Formation, Millard County; Scale bar indicates 1 mm for figures A, B, and H, 500 μ m for all others unless indicated otherwise. **A-B**, ventral valve from ESB-200, **A**, exterior **B**, interior, USNM 542955; **C-F**, dorsal valve from ESB-200, **C**, exterior with arrow showing location of **F**, **D**, interior, **E**, lateral view, **F**, microornament, USNM 542956; **G**, exterior of juvenile ventral valve fragment from ESB-352, USNM 542957; **H**, exterior of ventral valve from ESB-200, USNM 542958; **I-V**, *Zhanatella utahensis* Popov *et al.*, 2002, Hellnmaria Member, Notch Peak Formation, Millard County; **I**, ventral valve exterior from CKN-361, USNM 542959; **J-K**, ventral valve from ESB-969, **J**, interior, **K**, oblique interior view, USNM 542960; **L-P**, dorsal valve from ESB-373, **L**, exterior, **M**, oblique lateral view, **N**, larval shell, **O**, microornament in postlarval growth at position indicated by arrow on **L**, **P**, microornament on larval shell at position marked by arrow on **N**, USNM 542961; (*continued opposite*)

Hellnmria Member of the Notch Peak Formation, Tule Valley, Millard County, western Utah. The lowest occurrence of the species is 114 m above the base of the ESB section, 165.2 m below the base of the *Proconodontus tenuiserratus* conodont zone. The highest occurrence of the species is 159 m above the base of the CKN section, 41.7 m above the base of the *Proconodontus posterocostatus* Zone.

Material. Illustrated material includes USNM 542959, ventral valve, from 110 m above the base of the CKN section; USNM 542960, ventral valve, from 295.4 m above the base of the ESB section; and USNM 542963, ventral valve, from 103.6 m above the base of the CKN section; and USNM 542961-542962, dorsal valves, both from 113.7 m above the base of the ESB section. Additional material is 43 dorsal and 15 ventral valves from ESB section; 58 dorsal and 54 ventral valves from CKN section.

Diagnosis. The diagnosis of Popov *et al.* (2002) is followed here.

Discussion. These specimens match the description of the species in Popov *et al.* (2002) in all respects except that the ridges on the larval shells are often less distinct than in their illustrations. The ridges are especially subtle on larger individuals.

A detail not mentioned in the original species description is that the outer margins of the dorsal pseudointerarea bear microornament similar to the postlarval exterior. Oval micropits are ranged in irregular rows that are subparallel the margin of the valve (Fig. 7S). The observed maximum diameter of the micropits (from 2-3 μm up to 10 μm) depends on the maturity of the specimen.

The species was reported previously from the *Cambrooistodus minutus* conodont Subzone of the Red Tops Member of the Notch Peak Formation, Utah (Popov *et al.* 2002).

Superfamily ACROTHELOIDEA Walcott & Schuchert, in Walcott, 1908

Family ACROTHELIDAE Walcott & Schuchert, in Walcott, 1908

Subfamily CONODISCINAE Rowell, 1965

Discotreta Ulrich & Cooper, 1936

Type and only named species. *Discotreta*

levisensis (Walcott, 1908).

Diagnosis. The diagnosis of Holmer & Popov (2000) is followed here.

Discotreta? arcana n. sp. (Fig. 8A-Q)

Etymology. From the Latin *arcanus*, meaning enigmatic, in reference to its uncertain affinities.

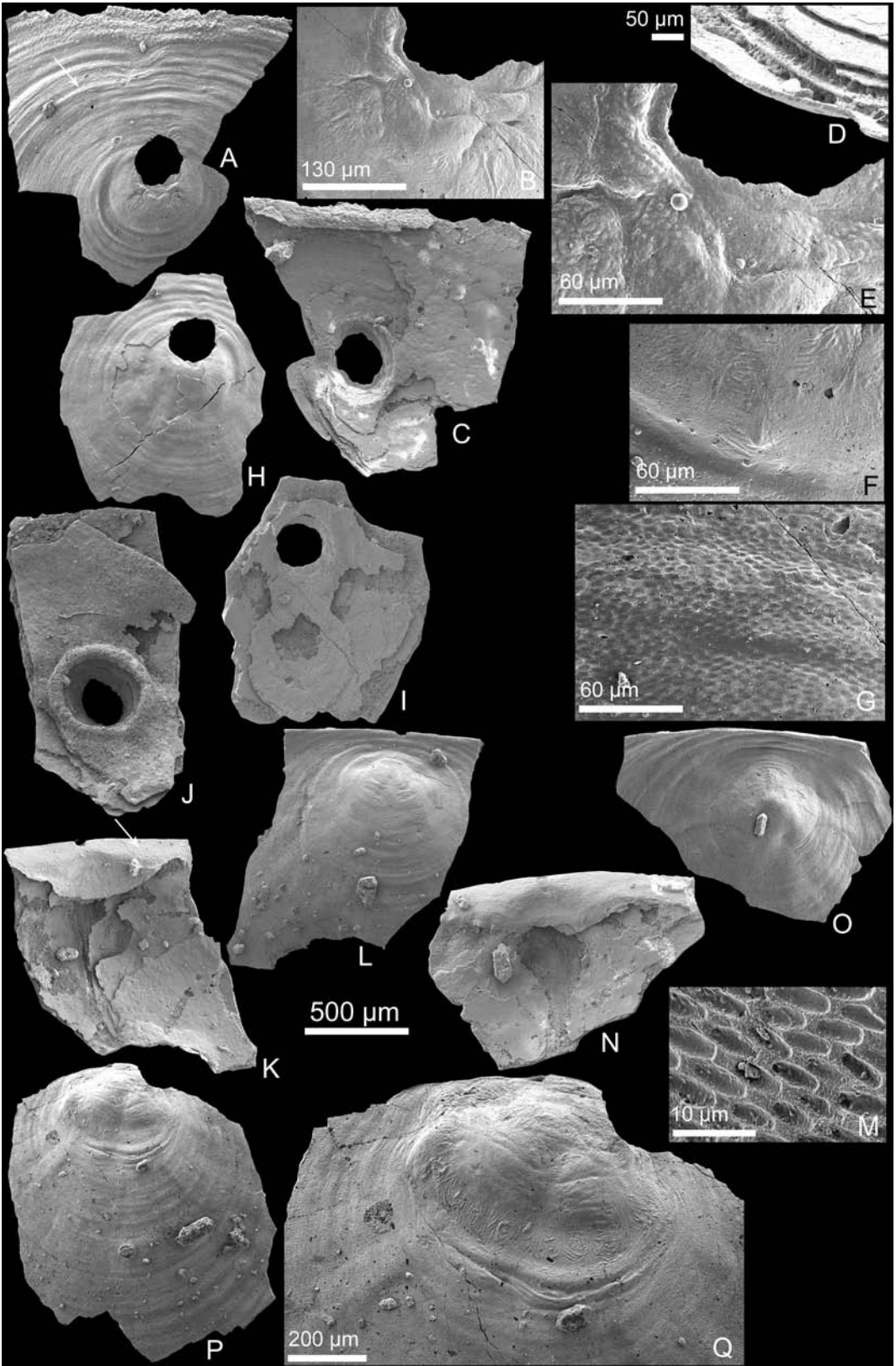
Type Locality. The type specimen was collected 251.5 m above the base of the ESB section, from the upper Cambrian (Sunwaptan) Hellnmria Member of the Notch Peak Formation, Tule Valley, Millard County, western Utah. The lowest occurrence of the species is 18.6 m above the base of the CKN section, 71 m below the base of the *Proconodontus tenuiserratus* Zone, and the highest occurrence of the species is 317 m above the base of the ESB section, 14.6 m above the base of the *Proconodontus posterocostatus* Zone.

Material. Holotype USNM 542997, ventral valve. Paratypes, USNM 542997-USNM 542988, ventral valves from 251.5 m above the base of the ESB section; USNM 542999, ventral valve, from 243.8 m above the base of the ESB section; USNM 543000-543002, dorsal valves, from 251.5 m above the base of the ESB section. Additional material is 5 dorsal and 18 ventral valves from ESB section, and 2 dorsal and 4 ventral valves from CKN section, all fragmental.

Diagnosis. Submarginal dorsal beak, subcentral ventral beak. Irregularly pitted and pustulose larval shell on both valves. Dorsal larval shell with lobed appearance. Ventral larval shell with furrows radiating from foramen. Postlarval growth with pitted microornament. Short internal pedicle tube surrounded by raised rim on interior of ventral valve. Foramen somewhat restricted by shell material within pedicle tube. Dorsal valve with broad shallow median groove and propareas with pitted microornament.

Description. Biconvex valves, with outline of valves not known due to fragmentation. Larval shell of both valves with irregularly pitted and pustulose microornament. Postlarval growth of both valves ornamented with 5-7 μm oval pits, with long axis of pits generally arranged parallel to growth lines (Fig. 8G). Irregularly spaced rugellae of variable width on postlarval growth.

Q-S, dorsal valve from ESB-373, **Q**, lateral interior view with arrow indicating location of **S**, **R**, interior, **S**, microornament on proparea in position indicated by arrow on **Q**, USNM 542962; **T-V**, ventral valve from CKN-340, **T**, oblique lateral view, **U**, anterolateral oblique detail of larval shell, **V**, view of larval shell and emarginature from posterior, USNM 542963.



Faint radial ornamentation sometimes observed as well (Fig. 8P). The shells are recrystallised but the interlaminar surfaces do not appear to be perforated and the columnar elements between the laminae do appear to be inclined, therefore the structure appears to be baculate (Fig. 8D)

Ventral valve with large foramen, approximately 250 μm in length, not contained within larval shell. Foramen and beak apparently subcentrally located. Foramen extending from just posterior to centre of larval shell into postlarval growth, with many postlarval growth lines truncating against foramen. Pustulose ornament especially expressed on larval shell near foramen (Fig. 8B, E). Entire larval shell covered with fine, irregularly spaced, rounded pits about 3 μm in diameter (Fig. 8F). Branching canal-like furrows extending from posterior edge of foramen towards anterolateral areas of larval shell, not completely reaching larval shell margin (Fig. 8B). Both larval and postlarval growth with occasional small interruptions of growth, causing “nick points” and “draping” of rugellae.

Ventral valve interior not well known. Short internal pedicle tube. Interior pedicle opening surrounded by raised, thickened, rounded rim (Fig. 8J). External foramen restricted by shell material filling exterior margin of the pedicle tube (Fig. 8C, J). Internal pedicle opening nearly round, but external foramen suboval to pyriform in outline. Vestigial pseudointerarea present as narrow strip along posterior interior margin (Fig. 8C).

Dorsal valve exterior with gently convex posterior margin. Submarginal beak. Area between apex of larval valve and posterior margin concave in lateral profile, sharply concave along midline of valve but more gently tapered laterally (Fig. 8O). Posterior edge of valve upturned, thickened and rounded. Larval shell with frequent small disruptions of growth at irregular locations, forming lobes and furrows in shell (Fig. 8Q). Pronounced furrow extending from apex of larval shell towards anterior margin of valve on most specimens, but lobes and furrows variable in number, arrangement and strength of expression. Continued disruption of growth on postlarval growth, but becoming less pronounced.

Anacline dorsal pseudointerarea, with wide,

shallow, broadly triangular median groove not extending to the posterior margin of valve (Fig. 8N). Propareas with microornament of pits near posterior margin (Fig. 8K, M). Pits are oval in outline and rounded in cross-section. Long axis of oval pits parallels margin of shell. Visceral area thickened. Median ridge apparently present, although exfoliated on these fragmentary specimens (Fig. 8K, N).

Discussion. This material does not fit well into either of the two subfamilies of the Family Acrothelidae. It is most similar to Subfamily Acrothelinae in having a gently convex dorsal valve with a marginal beak, although the beak appears to be more submarginal than truly marginal. It differs from both Subfamily Acrothelinae and Subfamily Conodiscinae in having a well developed dorsal pseudointerarea.

The oval pitted microornament of the postlarval growth of this species resembles that of some species of the Family Zhanatellidae, but the vestigial ventral pseudointerarea and the position of the foramen suggest affinities with the Superfamily Acrotheloidea. The species does not exhibit certain characteristics of the superfamily as defined by Holmer & Popov (2000), namely spines or tubercles ornamenting the larval shell.

The species is similar to some genera of Family Siphonotretidae Kutorga, 1848, such as *Schizambon* Walcott, 1884 and *Oaxaquiatreta* Streng *et al.*, 2011 in having a pedicle opening which expanded by resorption during growth, filling in the pedicle opening with shell material. It differs in that the foramen expands and truncates growth lines towards the posterior rather than the anterior, and in that shell material was secreted around the margin of the pedicle opening to the posterior as well as laterally and does not form a separate plate as in *Schizambon*. A short internal pedicle tube is also seen on some siphonotretids, such as *Siphonobolus* Havlíček, 1982. The lobed larval shell is similar to that of the siphonotretid species *Oaxaquiatreta labrifera* Streng *et al.*, 2011, as well as species of *Siphonobolus* (Popov *et al.* 2009a, b). Unlike the siphonotretids, *Discotreta? arcana* lacks spines. The overlap of features characteristic of the Family Acrothelidae and the Family Siphonotretidae seen in *Discotreta?*

Figure 8. *Discotreta? arcana* n. sp., Hellnmaria Member, Notch Peak Formation, Millard County. Scale bar indicates 500 μm unless indicated otherwise. **A-G**, holotype, ventral valve from ESB-825, **A**, exterior, with arrow indicating position of G, **C**, interior, **D**, detail of shell structure, **B** and **E**, pustulose ornament and pitting on larval shell, **F**, nick points and drapes near larval/postlarval boundary, **G**, microornament on postlarval growth, USNM 542997; **H-I**, ventral valve from ESB-825, **H**, exterior, **I**, interior, USNM 542998; **J**, ventral valve interior from ESB-800, USNM 542999; **K-M**, dorsal valve from ESB-825, **K**, interior oblique view with arrow indicating position of M, **L**, exterior, **M**, microornament on propareas, USNM 543000; **N-O**, dorsal valve from ESB-825, **N**, interior, **O**, exterior, USNM 543001; **P-Q**, dorsal valve from ESB-825, **P**, exterior, **Q**, detail of larval shell and early postlarval growth, USNM 543002.

arcana n. sp. suggests that these two families may be closely related.

Of genera assigned to the Family Acrothelidae, ventral valves of this species are most similar to *Discotreta* Ulrich & Cooper, 1936, which Holmer & Popov (2000) tentatively assigned to the Subfamily Conodiscinae. *Discotreta* is a poorly known genus comprising only the type species, *D. levisensis* (Walcott, 1908). This species is similar to the type in the apparent shape and convexity of the valves and in having a similar pattern of concentric rugellae and a faint radial ornamentation. Additionally, the interior foramen is bounded by an elevated rim in *D. levisensis*, a feature similar to the Utah material. The posterior part of the foramen of *D. levisensis* is filled with shell material, similar to this material, although none of the Utah specimens examined had the foramen filled in to the half or more that was described for *D. levisensis*. Ulrich & Cooper (1938) described it as having a low fold on either side of the exterior of the foramen, a feature not present on this material. The rest of the ventral interior features described for *D. levisensis* are not preserved on this fragmentary material.

The dorsal valve of *Discotreta levisensis* is not well known, but it is described as having a median ridge, a feature that appears to be present on this material. The overall shape of the dorsal valve of *D. ? arcana* is not clear from these fragments.

Order ACROTRETIDA Kuhn, 1949

Superfamily ACROTRETOIDEA Schuchert, 1893

Family ACROTRETIDAE Schuchert, 1893

Quadrisonia Rowell & Henderson, 1978

Type species. Quadrisonia minor Rowell & Henderson, 1978.

Other species included. Quadrisonia declivis Koneva & Popov, 1988; *Quadrisonia suspensa* Koneva & Popov, 1988; *Quadrisonia simplex* Koneva, Popov & Ushatinskaya (in Koneva *et al.*, 1990) *Quadrisonia? lavadamensis* Popov *et al.*, 2002; *Quadrisonia congerensis* n. sp.; *Quadrisonia rattlesnakensis* n. sp.; *Quadrisonia sawtoothensis* n. sp.; *Quadrisonia swaseyensis* n. sp. Not included is *Quadrisonia? sigmoidea* Robson & Pratt, 2007.

Emended diagnosis. Subconical ventral valve with short posterior margin, varying from gently convex to gently concave in outline. Ventral pseudointerarea poorly defined from lateral margins, variable from procline to apsacline, with poorly developed intertrough. Apical process

present and variably developed, extending along either anterior slope or both anterior and posterior slope. Apical pits variable from lightly to deeply impressed, positioned posterolateral or lateral to internal foramen.

Dorsal valve gently convex in profile. Dorsal pseudointerarea orthocline. Small cardinal muscle scars closely set on dorsal valve. Median ridge variably developed, but not developed into a median septum. Mantle canal system baculate.

Larval shell with hemispherical pits, round in outline, variable in size. Foramen contained within larval shell, usually surrounded by short external tube.

Discussion. The diagnosis of *Quadrisonia* is emended to include species with apsacline ventral pseudointerareas, such as *Q. lavadamensis* and to exclude species with a median septum rather than a median ridge. The orientation of the pseudointerarea is variable in several species, particularly *Q. lavadamensis* and *Q. swaseyensis* n. sp. The original diagnosis of the genus (Rowell & Henderson 1978) described a “low to absent median septum”, while the remarks section allowed the possibility of a septum developed into a “low blade”. The morphologic difference between a median ridge and a median septum is gradational, and the two terms have often been used interchangeably. Herein, the term “ridge” is restricted to features with a maximum height equal to or less than the maximum width of the feature, and “septum” refers to features with a maximum height greater than maximum width of the feature, often a height equal to or higher than the line of commissure of the dorsal valve. Large, possibly gerontic specimens of some species, such as *Q. sawtoothensis* and *Q. swaseyensis*, sometimes exhibit a median ridge that is very nearly a median septum (Figs. 12P, Q, 13E, F) but in such cases the majority of the specimens within the population have a more subdued median ridge.

The apical process of *Quadrisonia* is also quite variable, generally elongated to the anterior, but sometimes it is developed along the posterior wall of the shell as well, as in *Q. sawtoothensis* n. sp., and frequently it bridges both the anterior and posterior slopes to some extent. Apical pits are generally positioned posterolateral to the internal foramen on the ventral valve, but may also be positioned directly lateral to it, as in *Q. lavadamensis* and the type species, *Quadrisonia minor*.

Five species of *Quadrisonia*, four new, are distinguished from the Hellnmaria Member of the Notch Peak Formation. Interestingly, all have ventral valves whose average height is greater than 50% of maximum length. This

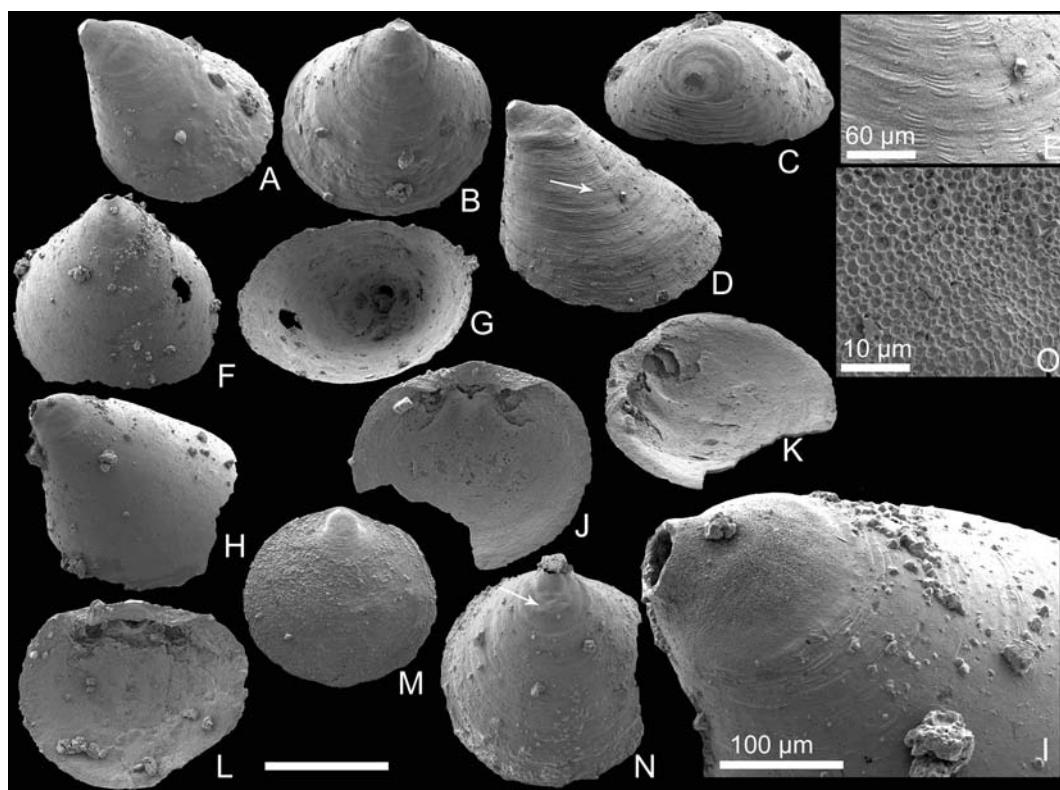


Figure 9. *Quadrisonia lavadamensis* Popov, Holmer & Miller, 2002, Hellnmaria Member, Notch Peak Formation, Millard County. Scale bar indicates 500 µm for J-M; 300 µm for others unless indicated otherwise. **A-C**, ventral valve from ESB-1073, **A**, oblique exterior view, **B**, exterior, **C**, oblique posterior view, USNM 542990; **D-E**, ventral valve from ESB-1073, **D**, ventral lateral view with arrow indicating position of **E**, **E**, ornamentation of postlarval growth, USNM 542991; **F-I**, ventral valve from CKN-476, **F**, exterior, **G**, interior, **H**, lateral view, **I**, larval shell, USNM 542992; **J-K**, dorsal valve from ESB-1073, **J**, interior, **K**, oblique view of interior, USNM 542993; **L**, dorsal valve interior from ESB-1073, USNM 542994; **M**, dorsal valve exterior from ESB-1073, USNM 542995; **N-O**, ventral valve from CKN-476, **N**, ventral exterior with arrow indicating position of **O**, **O**, microornament on larval shell, USNM 542996.

is in contrast to other species of *Quadrisonia* for which measurements are available. These include the type species, *Q. minor* Rowell & Henderson, 1978, which was described from the Orr Formation of the Great Basin, directly below the Hellnmaria Member considered herein.

Quadrisonia? sigmoidea Robson & Pratt, 2007 is excluded from the genus because of its anacline dorsal pseudointerareas and well developed sigmoidally shaped median septum. Material described as *Quadrisonia* sp. by Robson & Pratt (2007) is also excluded because the external foramen is not contained within the larval shell. Material with a blade-like median septum on the dorsal valve described as *Quadrisonia* sp. by Engelbreetsen (2006) is likewise excluded. Other taxa excluded from the genus because they have a moderately to well developed median septum are *Quadrisonia?* sp. of Puura & Holmer (1993) and *Quadrisonia* sp. nov. of Henderson *et al.* (1992).

Quadrisonia cf. *minor* described by Holmer *et al.* (1999) is poorly preserved but exhibits diagnostic characters of *Quadrisonia*. *Quadrisonia* sp. of Holmer *et al.* (2001) is too poorly known to be included or excluded with certainty.

***Quadrisonia lavadamensis* Popov *et al.*, 2002 (Fig. 9)**

2002 *Quadrisonia? lavadamensis*; Popov *et al.*, p. 225, figs. 8.1-8.9.

Locality. Upper Cambrian (Sunwaptan) Hellnmaria Member of the Notch Peak Formation, Tule Valley, Millard County, western Utah. The lowest occurrence of the species is 268 m above the base of the ESB section, 11.2 m below the base of the *Proconodontus tenuiserratus* Zone, and the highest occurrence of the species is 599 m above the base of the CKN section, 59.7 m above the

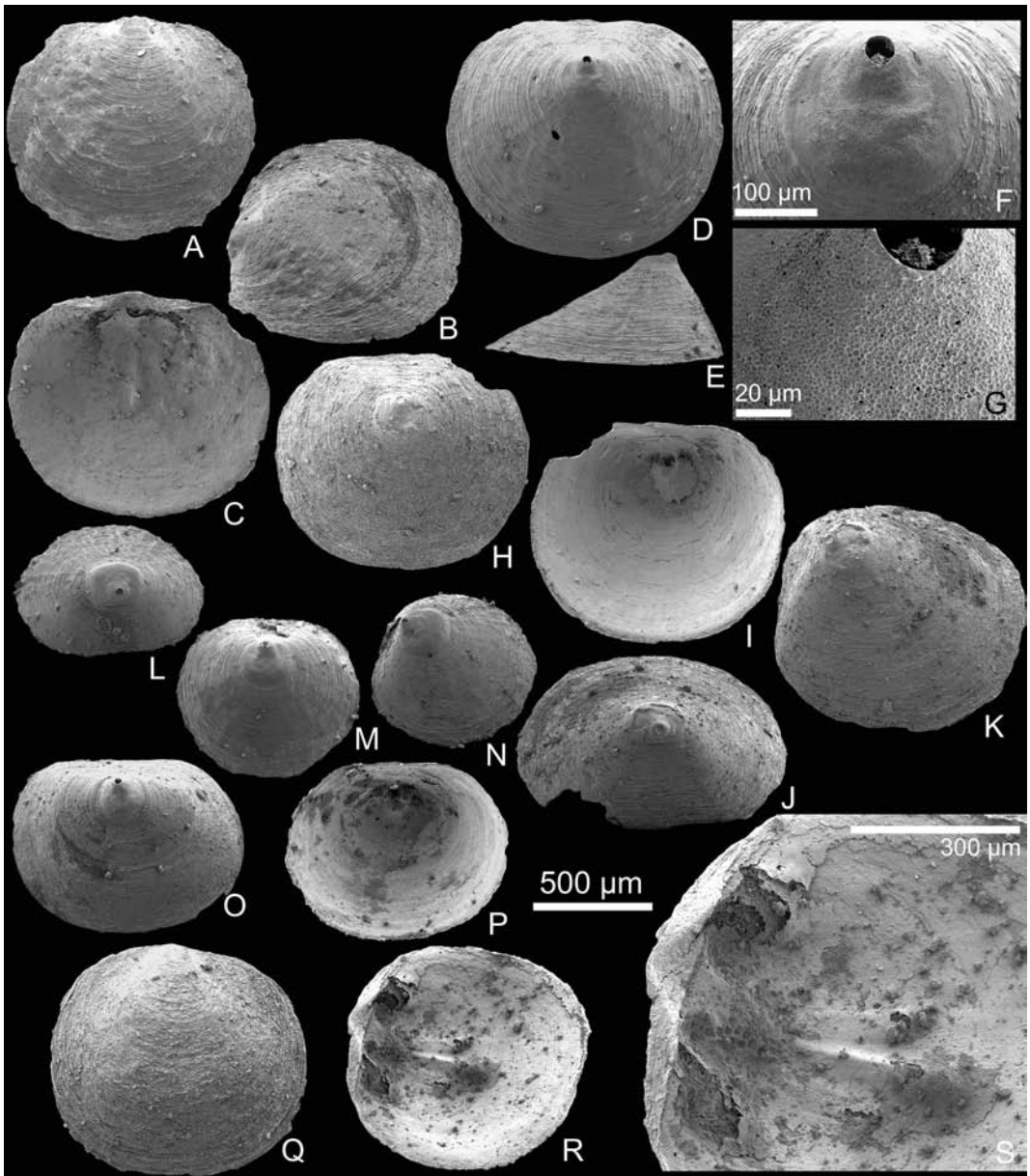


Figure 10. *Quadrisonia congerensis* n. sp., Hellnmaria Member, Notch Peak Formation, Millard County. Scale bar indicates 500 µm unless indicated otherwise. **A-C**, dorsal valve from ESB-25, **A**, exterior, **B**, oblique view of exterior, **C**, interior, USNM 543003; **D-G**, holotype, ventral valve from ESB-25, **D**, ventral exterior, **E**, ventral lateral profile, **F**, larval and postlarval shell microornament, **G**, larval shell microornament, USNM 543004; **H-K**, ventral valve from ESB-25, **H**, exterior, **I**, interior, **J**, oblique view of posterior, **K**, oblique lateral view of exterior, USNM 543005; **L-N**, juvenile ventral valve from ESB-25, **L**, oblique view of posterior, **M**, exterior, **N**, oblique lateral view of exterior, USNM 543006; **O**, ventral valve exterior from ESB-200, USNM 543007; **P**, ventral interior from ESB-200, USNM 543008; **Q-S**, dorsal valve from ESB-25, **Q**, exterior, **R**, oblique view of interior, **S**, interior showing possible epithelial imprints on median buttress, USNM 543009.

base of the *Proconodontus posterocostatus* Zone.

Material. Illustrated material USNM 542993-542995, dorsal valves, from 327 m above the base of the ESB section; USNM 542990-542991,

ventral valves from 327 m above the base of the ESB section; USNM 542992, USNM 542996, ventral valves from 145.1 m above the base of the CKN section. Additional material is 59 dorsal, 70 ventral, 2 tentatively identified dorsal valves, and

one whole shell from ESB section; 96 dorsal, 97 ventral, 27 tentatively identified dorsal valves and one whole shell from CKN section.

Diagnosis. As given by Popov *et al.* (2002).

Occurrence. Also in the *Cambroostodus minutus* conodont Subzone and *Saukia* trilobite Zone in the Lava Dam Member of the Notch Peak Formation (Popov *et al.* 2002).

Discussion. The majority of specimens examined are juveniles, but fit the description of this species given by Popov *et al.* (2002), particularly in being steeply procline to apsacline. The proportions of measured dimensions are also within the same range, with the ventral valve slightly more than 90% as long as wide and slightly more than half as high as long. Some specimens exhibit pronounced ornamentation of “nick points” or disruptions of growth resulting in a drapery-like arrangement of growth lines (Fig. 9E), but the development of this ornamentation is variable among individuals in the population. Although this ornamentation was not mentioned by Popov *et al.* (2002) in the species description, it is visible on their figured material (fig. 8.7).

The median ridge of the dorsal valve was not well developed on these juvenile specimens, but the material appears to match in every other way, including in having apical pits positioned lateral to the internal foramen on the ventral valve (Fig. 9G). This detail was not mentioned in the original species description, but is visible on figured material (Popov *et al.* 2002, fig. 8.9). This is in contrast to most species of *Quadrisonia* which have apical pits at a posterolateral position relative to the internal foramen.

Quadrisonia lavadamensis co-occurs with *Q. rattlesnakensis* n. sp., and dorsal valves of the two species are difficult to distinguish. The propareas of *Q. lavadamensis* are generally more robust, with the lateral margins of the propareas more strongly deflected towards the posterior. The propareas project further over the cardinal muscle scars than those of *Q. rattlesnakensis*. All of these features are variable, however, and are more readily used to separate populations than individual specimens. Juveniles are particularly difficult to identify to species. The drapery-like arrangements of growth line “nick points” on *Q. lavadamensis* can sometimes be seen under the light microscope and aids in identification if observed.

***Quadrisonia congerensis* n. sp. (Fig. 10)**

Etymology. In reference to Conger Mountain,

in the Confusion Range, to the west of the type locality.

Type locality. The holotype valve was collected 7.6 m from the base of the ESB section in the upper Cambrian (Sunwaptan) Hellnmaria Member of the Notch Peak Formation, Tule Valley, Millard County, western Utah. The lowest occurrence of the species is 0.9 m above the base of the ESB section, in the lowest sample collected, 278.3 m below the base of the *Proconodontus tenuiserratus* Zone, and the highest occurrence was 61 m above the base of the ESB section, 218.2 m below the base of the *Proconodontus tenuiserratus* Zone.

Type material. Holotype, ventral valve, USNM 543004 (Fig. 10D-G). Paratypes from 7.6 m above the base of the ESB section USNM 543003, dorsal valve; USNM 543005, ventral valve; USNM 543006, ventral valve; and USNM 543009 dorsal valve. Paratypes from 61 m above the base of the ESB section USNM 543007, ventral valve, and USNM 543008 ventral valve. Unfigured topotype material consists of 371 dorsal valves, 295 ventral valves, all from the ESB section.

Diagnosis. Small, thin-shelled species with subconical ventral valve slightly over half as high as long. Ornament of rounded, regularly spaced filae, well developed on both valves. Ventral valve pseudointerareas gently procline, flattened, with poorly developed intertrough. Poorly developed, short apical process occludes apex of ventral valve. Poorly developed apical pits positioned posterolateral to internal foramen. Dorsal valve with narrow orthocline pseudointerarea and poorly developed to absent median ridge. Larval shell pits measuring 1-3 μ m in diameter.

Description. Ventribiconvex, with low conical ventral valve and gently inflated dorsal valve. Shells transversely suboval in outline. Both valves with prominent, fine, closely spaced growth lines forming rounded filae (Fig. 10F). Filae with many disruptions of growth, causing drapery-like effect. Growth disruptions continue through many growth lines, with resulting “nick points” often aligned laterally, giving appearance of faint radial ornamentation (Fig. 10L). Larval shells of both valves well defined by growth disruption. Larval shell microornament of hemispherical pits, 1-3 μ m in diameter and round in outline (Fig. 10G).

Subconical ventral valve averages 51% as high as long. Ventral valve transversely suboval in outline, with length 86% of width on average. Anterior slope of valve gently and evenly convex in lateral profile, posterior slope

Ventral	W	L	F	H	L/W	H/L	F/L
N	47	47	47	46	47	46	47
X	0.61	0.53	0.09	0.27	0.86	0.52	0.17
S	0.10	0.10	0.04	0.07	0.05	0.06	0.05
MIN	0.39	0.31	0.03	0.13	0.73	0.36	0.08
MAX	0.93	0.81	0.19	0.43	0.95	0.66	0.30

Dorsal	W	L	Wm	Wi	Wg	BS	Lm	LS	Li	H
N	45	45	43	44	40	28	43	28	45	43
X	0.67	0.58	0.29	0.34	0.13	0.16	0.12	0.34	0.05	0.11
S	0.14	0.13	0.06	0.09	0.03	0.04	0.03	0.07	0.01	0.02
MIN	0.39	0.34	0.16	0.18	0.06	0.09	0.06	0.21	0.03	0.06
MAX	1.04	0.96	0.45	0.60	0.21	0.25	0.21	0.57	0.10	0.16

Dorsal	L/W	Li/Wi	Wi/W	Lm/L	Wm/W	LS/L	BS/L	Li/L	H/L	Wm/Wi
N	45	44	44	43	43	28	28	45	43	43
X	0.87	0.14	0.50	0.21	0.43	0.59	0.27	0.08	0.20	0.87
S	0.04	0.03	0.05	0.03	0.06	0.19	0.04	0.01	0.04	0.15
MIN	0.78	0.09	0.39	0.13	0.35	0.32	0.18	0.05	0.09	0.64
MAX	0.97	0.22	0.62	0.26	0.67	1.12	0.33	0.12	0.30	1.38

Table 4. *Quadrisonia congerensis* n. sp., average dimensions and ratios of dorsal and ventral valves. Ten dorsal valves were measured from ESB-3, 10 from ESB-25, 10 from ESB-100, 9 from ESB-124.5, and 6 from ESB-178. Ten ventral valves were measured from ESB-3, 10 from ESB-25, 3 from ESB-75, 9 from ESB-100, 10 from ESB-124.5, and 5 from ESB-178.

straight. Foramen located within larval shell, to posterior of apex. Foramen slightly higher or at same level as apex (Fig. 10E). Pedicle opening surrounded by short external tube directed slightly towards posterior (Fig. 10L). Foramen located at position 16% length of the valve on average. Procline pseudointerarea flattened and straight in lateral profile (Fig. 10E). Faint, poorly defined intertrough (Fig. 10K, L). Narrow propareas poorly defined with rounded lateral margins (Fig. 10D, L). Posterior margin straight in outline.

Internal pedicle opening located posterior to short, poorly developed apical process. Apical process occludes apex and expands slightly towards anterior. Poorly defined apical pits posterolateral to internal pedicle opening on some mature specimens, more commonly not developed at all (Fig. 10I, P). Vascula lateralia baculate, lightly impressed or not observed.

Gently convex dorsal valve, transversely suboval in outline. Length averages 87% of width. Height of dorsal valve variable, but averages 20% of valve length. Delicately developed orthocline dorsal pseudointerarea with wide median groove. Lateral margins of propareas deflected only slightly towards posterior or straight laterally (Fig. 10S). Cardinal buttress of some specimens with rounded pits, 7-10 µm in diameter, impressed on lateral margins (Fig. 10S).

Closely spaced dorsal cardinal muscle scars with lateral edges not usually extending beyond

lateral edges of dorsal pseudointerarea. Muscle scars suboval in outline, with length of muscle scar field averaging 21% of maximum length of valve and width of muscle scar field averaging 43% of maximum width of valve.

Median ridge low, faintly developed and only present on some mature specimens. When present, expressed as small callosity (Fig. 10C, R). Median ridge extending to approximately 59% of length of valve.

Measurements. See Table 4.

Discussion. The ornamentation of *Q. congerensis* is not unique, as filae and “nick points”, together with the resulting drapery-like appearance, are common features of many acrotretids and can be seen developed to some extent on other species of *Quadrisonia*. The regular, robust nature of the filae and their often regularly arranged “nick points” do seem to be useful characteristics for distinguishing this species, however.

The valves are generally smaller than those of the co-occurring *Q. swaseyensis* n. sp., and are more delicate in appearance even when of comparable size. The ventral intertrough is less well defined and the apical process less developed. In lateral profile, the ventral valve of *Q. congerensis* is less strongly convex. The dorsal valves of *Q. congerensis* may be distinguished by the less developed median ridge, the more delicate

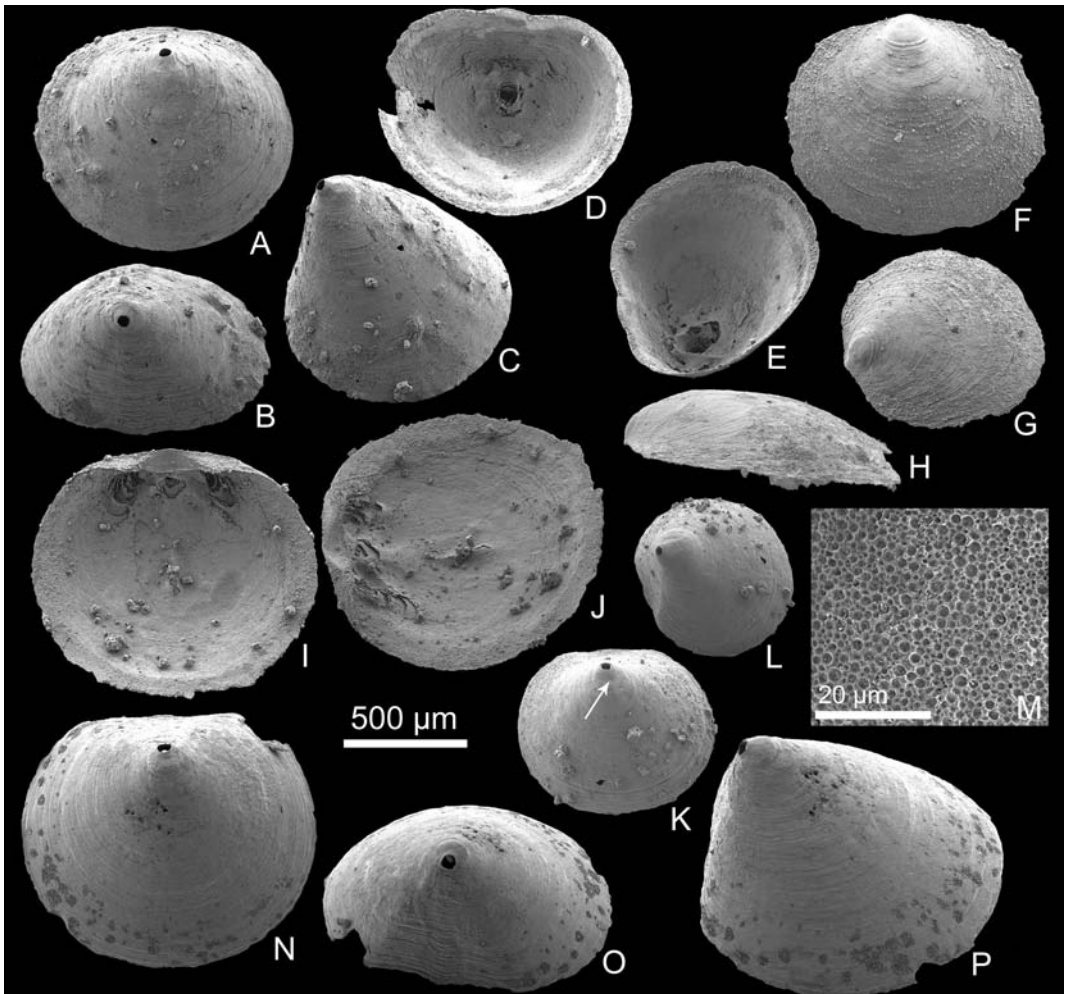


Figure 11. A-M, *Quadrisonia rattlesnakensis* n. sp. Hellnmaria Member, Notch Peak Formation, Millard County. Scale bar indicates 500 μ m unless indicated otherwise. A-C, holotype, ventral valve from CKN-361, A, exterior, B, oblique view of posterior, C, oblique lateral view, USNM 543027; D-E, ventral valve from CKN-361, D, interior, E, oblique view of interior, USNM 543028; F-G, dorsal valve from ESB-1041, F, exterior, G, oblique lateral view, USNM 543029; H, dorsal valve from ESB-1041, lateral profile view, USNM 543030; I-J, dorsal valve from ESB-1041, I, interior, J, oblique view of interior, USNM 543031; K-M, ventral valve from ESB-1041, K, exterior with arrow indicating location of M, L, oblique lateral view, M, detail of larval shell microornament, USNM 543032; N-P, *Quadrisonia rattlesnakensis*? n. sp. Hellnmaria Member, Notch Peak Formation, Millard County. ventral valve from ESB-825, N, ventral exterior, O, oblique posterior view, P, oblique lateral view, USNM 543033.

nature of the pseudointerarea, as well as by the difference in shape of the propareas. The shape of the propareas is especially useful in distinguishing juvenile dorsal valves of the two species.

***Quadrisonia rattlesnakensis* n. sp. (Fig. 11A-M)**

Etymology. In reference to Rattlesnake Summit, in the Confusion Range, to the west of the type locality.

Type locality. The holotype valve was collected

110 m above the base of the CKN section, from the upper Cambrian (Sunwaptan) Hellnmaria Member of the Notch Peak Formation, Tule Valley, Millard County, western Utah. The lowest occurrence of the species is 18.6 m above the base of the CKN section, 71 m below the base of the *Proconodontus tenuiserratus* Zone, and the species ranges through the *P. tenuiserratus* Zone and into the overlying *Proconodontus posterocostatus* Zone. The highest occurrence of the species is 159 m above the base of the CKN section, 137 m above the base of the *P.*

Ventral	W	L	F	H	L/W	H/L	F/L
N	25	25	24	25	25	25	24
X	0.64	0.54	0.09	0.36	0.85	0.68	0.17
S	0.21	0.17	0.03	0.12	0.05	0.19	0.05
MIN	0.39	0.33	0.03	0.15	0.75	0.36	0.09
MAX	1.13	0.91	0.16	0.63	0.93	1.30	0.27

Dorsal	W	L	Wm	Wi	Wg	BS	Lm	LS	Li	H
N	32	32	32	32	32	6	32.00	6	32	31
X	0.80	0.69	0.39	0.39	0.22	0.28	0.16	0.51	0.08	0.16
S	0.15	0.14	0.07	0.09	0.05	0.05	0.03	0.09	0.02	0.04
MIN	0.57	0.49	0.27	0.24	0.16	0.22	0.10	0.37	0.04	0.10
MAX	1.27	1.04	0.54	0.57	0.39	0.37	0.22	0.63	0.15	0.25

Dorsal	L/W	Li/Wi	Wi/W	Lm/L	Wm/W	LS/L	BS/L	Li/L	H/L	Wm/Wi
N	32	32	32	32	32	6	6	32	31	32
X	0.87	0.19	0.49	0.23	0.49	0.64	0.35	0.11	0.23	1.01
S	0.05	0.03	0.06	0.03	0.06	0.05	0.01	0.02	0.06	0.12
MIN	0.77	0.13	0.40	0.18	0.40	0.58	0.33	0.07	0.00	0.76
MAX	1.02	0.27	0.73	0.30	0.63	0.72	0.37	0.14	0.35	1.29

Table 5. *Quadrisonia rattlesnakensis* n. sp., average dimensions and ratios of dorsal and ventral valves. Six dorsal valves were measured from ESB-1032, 12 from CKN-361, 5 from CKN-447, and 9 from CKN-521.5. Seven ventral valves were measured from ESB-1032, 8 from CKN-361, 7 from CKN-447, and 3 from CKN-521.5.

posterocostatus Zone.

Type material. Holotype, ventral valve, USNM 543027 (Fig. 11A-C). Paratypes, USNM 543028, ventral valve from 110 m above the base of CKN; USNM 543029-543031, dorsal valves from 317.3 m above the base of the CKN section; USNM 543032, ventral valve from 317.3 m above the base of the CKN section. Specimen USNM 543033, ventral valve from 251.5 m above the base of the ESB section is questionably assigned to the species. Unfigured topotype material is 247 dorsal valves and 93 ventral valves from the ESB section and 533 dorsal valves and 126 ventral valves from the CKN section.

Diagnosis. High, subconical ventral valve. Steeply procline with gently convex anterior slope. Intertrough well defined for genus. Apical process occludes apex, not expanding far along anterior slope of valve. Large, prominent apical pits placed posterolateral to internal pedicle opening. Dorsal pseudointerareas approximately as wide as deeply impressed cardinal muscle scars, slightly overhanging them. Dorsal valve with poorly developed median ridge, sometimes absent. Larval shell pitting measuring 1-3 μ m in diameter.

Description. Ventribiconvex shell, transversely suboval in outline. Larval shell of both valves well

defined by marked growth disruption and change in ornamentation. Larval shells ornamented with hemispherical pits, circular in outline and 1-3 μ m in diameter (Fig. 11M). Larval shells generally nearly equidimensional in outline, approximately 190 μ m in length and width.

High subconical ventral valve with height averaging 68% of length. External foramen contained within larval shell, positioned to posterior of apex and directed towards posterior. Pseudointerarea steeply procline, with external foramen at position averaging 17% of valve length. Pseudointerarea flattened in lateral profile and anterior slope gently convex. Pseudointerarea divided by intertrough, well defined for the genus (Fig. 11B). Deflection of growth lines across intertrough towards the posterior gives scalloped effect to the posterior margin of some specimens (Fig. 11D, O).

Internal pedicle opening at end of short internal pedicle tube, surrounded by apical process. Apical process occludes apex and expands slightly along anterior slope of valve, never more than about one-third of length of valve slope (Fig. 11E). Baculate vascula lateralia moderately impressed on mature specimens, creating ridge-like effect on lateral margins of apical process. Apical pits well developed and large on all but very juvenile specimens. Apical pits placed posterolateral to internal pedicle opening (Fig. 11D). Small, moderately impressed suboval cardinal muscle

scars on posterior slope of valve, posterolateral to internal pedicle opening and apical pits.

Dorsal valve transversely suboval in outline, length averaging 87% of width. Transverse profile gently and evenly convex with height averaging 23% of length. Maximum height at midlength or slightly to posterior. Orthocline pseudointerarea with maximum width nearly equal to maximum width of cardinal muscle scars and very slightly overhanging them (Fig. 11I). Cardinal muscle field deeply impressed, occupying approximately 49% of width of valve and 23% of maximum length of valve. Cardinal muscle scars transversely suboval in outline.

Lateral margins of dorsal propareas only slightly deflected towards posterior (Fig. 11G). Wide, concave median groove. Well developed median buttress extends towards anterior, sometimes with impressed pits, irregularly suboval in outline, and approximately 3–4 μ m in width. Median ridge arises anterior to median buttress on some mature specimens at position averaging 35% of the length of the valve and ends at position at 64% of the length of valve. Median ridge not well defined and often absent.

Measurements. See Table 5.

Discussion. *Quadrisonia rattlesnakensis* is similar to *Q. swaseyensis* n. sp. and *Q. lavadamentis* in having a high ventral valve. *Quadrisonia rattlesnakensis* differs in being uniformly steeply procline, never approaching truly catacline. It is also similar to *Q. swaseyensis* and *Q. sawtoothensis* n. sp. in having a dorsal median ridge. The median ridge of *Q. rattlesnakensis* is less robust than that of either of those species. The apical process of *Q. rattlesnakensis* does not expand as far towards the anterior as that of *Q. lavadamentis*, and it also differs in having large, pronounced apical pits in all but the most juvenile specimens and in having a more well defined intertrough.

The dorsal valves are difficult to distinguish from those of *Q. sawtoothensis* and the co-occurring species *Q. lavadamentis*, and this is particularly true of juveniles. In addition to the less robust nature of the median septum, the dorsal valves of *Q. rattlesnakensis* are less inflated and the width of the cardinal muscle field is more nearly equal to the width of the pseudointerarea when compared to *Q. sawtoothensis*. These features are variable, and there is a great deal of overlap in the populations. In comparison to *Q. lavadamentis*, the dorsal propareas are slightly less robust and do not project as far over the muscle scars.

The measured specimens are from collections

high in the range of the species. Four collections were measured (ESB-1032, CKN-361, CKN-447, and CKN-521.5) and average proportions are consistent from one bed to another. Collections tentatively assigned to this species from lower beds consist mostly of smaller amounts of fragmentary and juvenile material. A low collection with good preservation at ESB-825 yielded some measureable material. Seven ventral valves and 6 dorsal valves were measured. The average height of the dorsal valves was 26% of length, shorter than the averages of collections higher in the range, yet higher than the averages of populations of *Q. sawtoothensis*. The average height of the ventral valve of specimens from ESB-825 is 56% of the maximum average length, slightly higher than the average for *Q. sawtoothensis* and significantly lower than the averages for stratigraphically higher specimens of *Q. rattlesnakensis*. The specimens from ESB-825 are steeply procline, which is consistent with *Q. rattlesnakensis* rather than *Q. sawtoothensis*. The average distance from the posterior margin to the foramen is 11% of the maximum length of the valve, less than the average for other measured specimens of *Q. rattlesnakensis* and much less than averages for *Q. sawtoothensis*.

Because so few specimens were measureable, it is unclear if the differences in low versus high specimens are significant. Because of the potential that the lower material may represent yet another species of *Quadrisonia*, the lower measured material is not included in the measurement tables for this species, and that material (Fig. 11N-P) is only tentatively assigned to *Q. rattlesnakensis*.

***Quadrisonia sawtoothensis* n. sp. (Fig. 12A-R)**

Etymology. In reference to Sawtooth Mountain, in the House Range, to the east of the type locality.

Type locality. The holotype valve was collected 68.7 m above the base of the ESB section, upper Cambrian (Sunwaptan) Hellnmaria Member of the Notch Peak Formation, Tule Valley, Millard County, western Utah. The lowest occurrence of the species is 68.7 m above the base of the ESB section, 210.5 m below the base of the *Proconodontus tenuiserratus* Zone, and the highest occurrence of the species is 75.6 m above the base of the CKN section, 14 m below the base of the *Proconodontus tenuiserratus* Zone.

Type material. Holotype, ventral valve, USNM 543016, (Fig. 12A-B). Paratypes from 68.7 m above the base of the ESB section USNM 543017, dorsal valve; USNM 543018, ventral valve; and USNM 543019, whole shell. Paratypes from 96 m

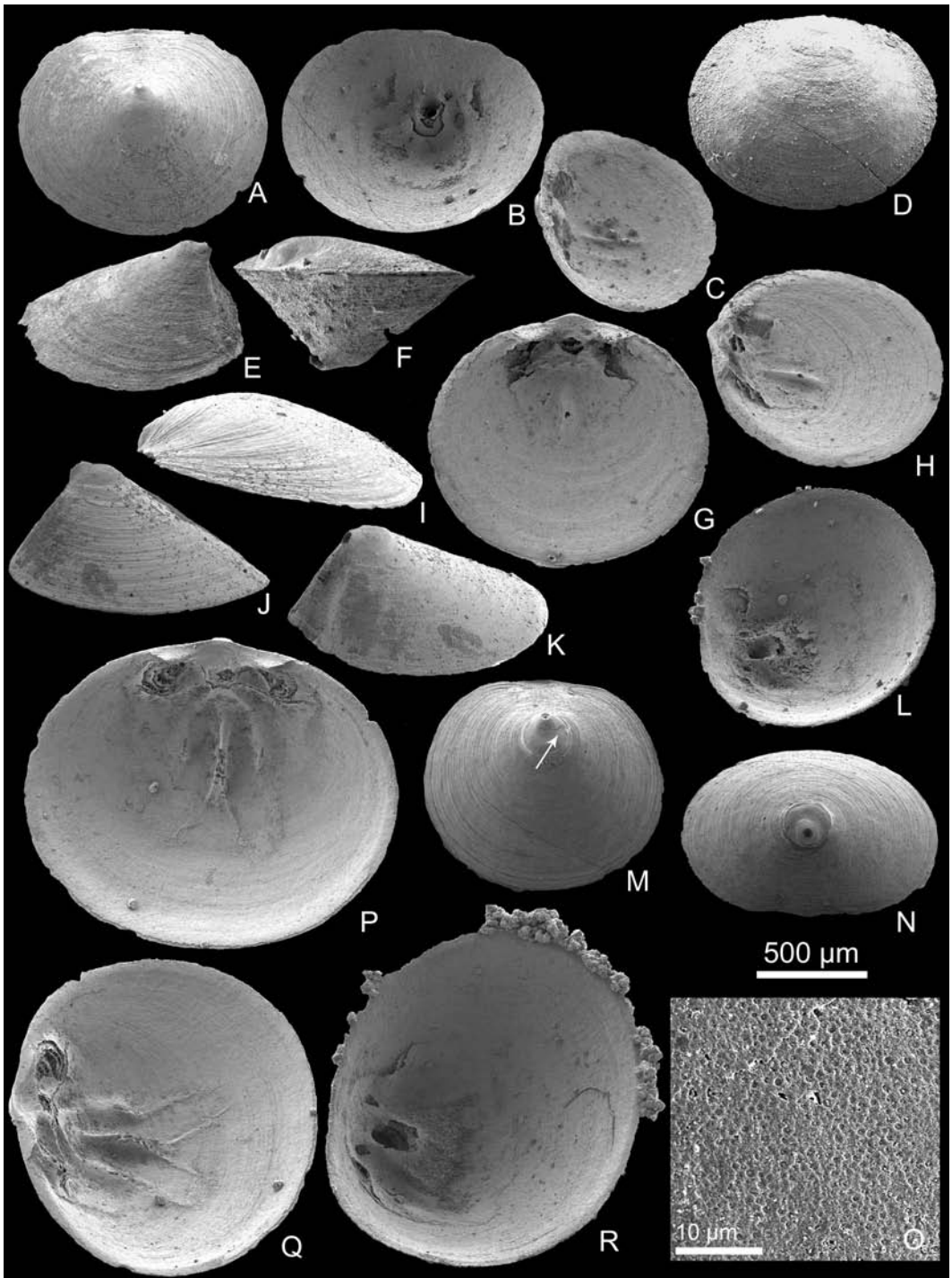


Figure 12. *Quadrisonia sawtoothensis* n. sp., Hellnmaria Member, Notch Peak Formation, Millard County. Scale bar indicates 300 µm for F, and 500 µm for others, unless indicated otherwise. **A-B**, holotype, ventral valve from ESB-225.5, **A**, exterior, **B**, interior, USNM 543016; **C-D**, dorsal valve from ESB-225.5, **C**, oblique view of interior, **D**, exterior, USNM 543017; **E**, ventral valve from ESB-225.5, oblique view of exterior, USNM 543018; **F**, juvenile whole shell from ESB-225.5, USNM 543019; **G-H**, dorsal valve from ESB-315, **G**, interior, **H**, oblique view of interior, USNM 543020; **I**, dorsal valve from ESB-380, lateral profile, USNM 543021; **J-K**, ventral valve from ESB-315, **J**, lateral profile, **K**, oblique lateral view, USNM 543022; (continued opposite)

Ventral	W	L	F	H	L/W	H/L	F/L
N	55	55	55	55	55	55	55
X	0.68	0.59	0.12	0.31	0.87	0.53	0.20
S	0.19	0.14	0.05	0.09	0.06	0.09	0.06
MIN	0.30	0.28	0.03	0.13	0.70	0.30	0.11
MAX	1.07	0.93	0.30	0.54	1.08	0.68	0.35

Dorsal	W	L	Wm	Wi	Wg	BS	Lm	LS	Li	H
N	63	63	63	63	62	60	63	60	63	60
X	0.93	0.81	0.40	0.42	0.21	0.21	0.18	0.44	0.08	0.24
S	0.25	0.22	0.12	0.11	0.06	0.07	0.06	0.14	0.02	0.07
MIN	0.28	0.24	0.10	0.15	0.04	0.04	0.04	0.13	0.03	0.13
MAX	1.51	1.31	0.64	0.61	0.31	0.39	0.37	0.81	0.13	0.45

Dorsal	L/W	Li/Wi	Wi/W	Lm/L	Wm/W	LS/L	BS/L	Li/L	H/L	Wm/Wi
N	63	63	63	63	63	60	60	63	60	63
X	0.87	0.20	0.46	0.22	0.43	0.54	0.26	0.11	0.31	0.94
S	0.06	0.04	0.06	0.04	0.05	0.11	0.05	0.02	0.09	0.15
MIN	0.74	0.12	0.33	0.13	0.32	0.17	0.18	0.07	0.17	0.64
MAX	1.03	0.30	0.62	0.30	0.55	0.71	0.38	0.17	0.69	1.38

Table 6. *Quadrisonia sawtoothensis* n. sp., average dimensions and ratios of dorsal and ventral valves. Ten dorsal valves were measured from ESB-225.5, 4 from ESB-247, 8 from ESB-325, 10 from ESB-352, 3 from ESB-373, 11 from ESB-380, 8 from ESB-454, and 9 from ESB-471. Ten ventral valves were measured from ESB-225.5, 5 from ESB-247, 6 from ESB-325, 6 from ESB-352, 3 from ESB-373, 13 from ESB-380, 7 from ESB-454, and 5 from ESB-471.

above the base of the ESB section USNM 543020, dorsal valve, and USNM 543022, ventral valve. Paratypes from 115.9 m above the base of the ESB section are USNM 543021, dorsal valve; USNM 543023, ventral valve; USNM 543024, ventral valve; USNM 543025, dorsal valve; and USNM 543026, ventral valve. Unfigured topotype material consists of 849 dorsal valves, 477 ventral valves, and 4 whole shells from ESB section and 81 dorsal valves and 32 ventral valves from CKN section.

Diagnosis. Robust species with subconical, gently procline ventral valve, with height approximately 50% of length. Foramen placed at 20% of length of valve from posterior margin. Ventral pseudointerarea flattened, gently procline with poorly developed intertrough. Elongate internal pedicle tube parallels posterior slope, with apical process developed along posterior slope of valve around it. Apical process extends along anterior slope for short distance. Small but well developed apical pits posterolateral to internal pedicle opening. Dorsal valve somewhat inflated, with small narrow propareas and prominent cardinal

muscle scars. Well developed narrow median ridge. Larval shell microornament of pits usually measuring approximately 1 μ m in diameter.

Description. Large and robust ventribiconvex shell, transversely suboval in outline. Larval shell of both valves well defined by marked growth disruption and change in ornamentation. Larval shells ornamented with small hemispherical pits, 1 μ m or less in diameter and round in outline (Fig. 12O).

Moderately high subconical ventral valve, with height averaging just over 50% of length. Foramen placed at approximately 20% of length of valve. Foramen contained within larval shell, slightly posterior to apex and directed towards posterior. Gently procline, flattened posterior slope with shallow, poorly defined intertrough (Fig. 12E, N). Posterior margin gently convex in outline, with lateral margins of propareas poorly defined. Anterior slope straight to gently convex in lateral outline.

Internal pedicle tube elongate and parallel to posterior slope of valve. Apical process surrounds internal pedicle opening and expands along

L, ventral valve from ESB-380, oblique view of interior, USNM 543023; **M-O**, ventral valve from ESB-380, **M**, exterior with arrow indicating location of **O**, **N**, posterior oblique view of exterior, **O**, larval shell microornament, USNM 543024; **P-Q**, dorsal valve from ESB-380, **P**, interior, **Q**, oblique view of interior, USNM 543025; **R**, ventral valve from ESB-380, oblique view of interior, USNM 543026.

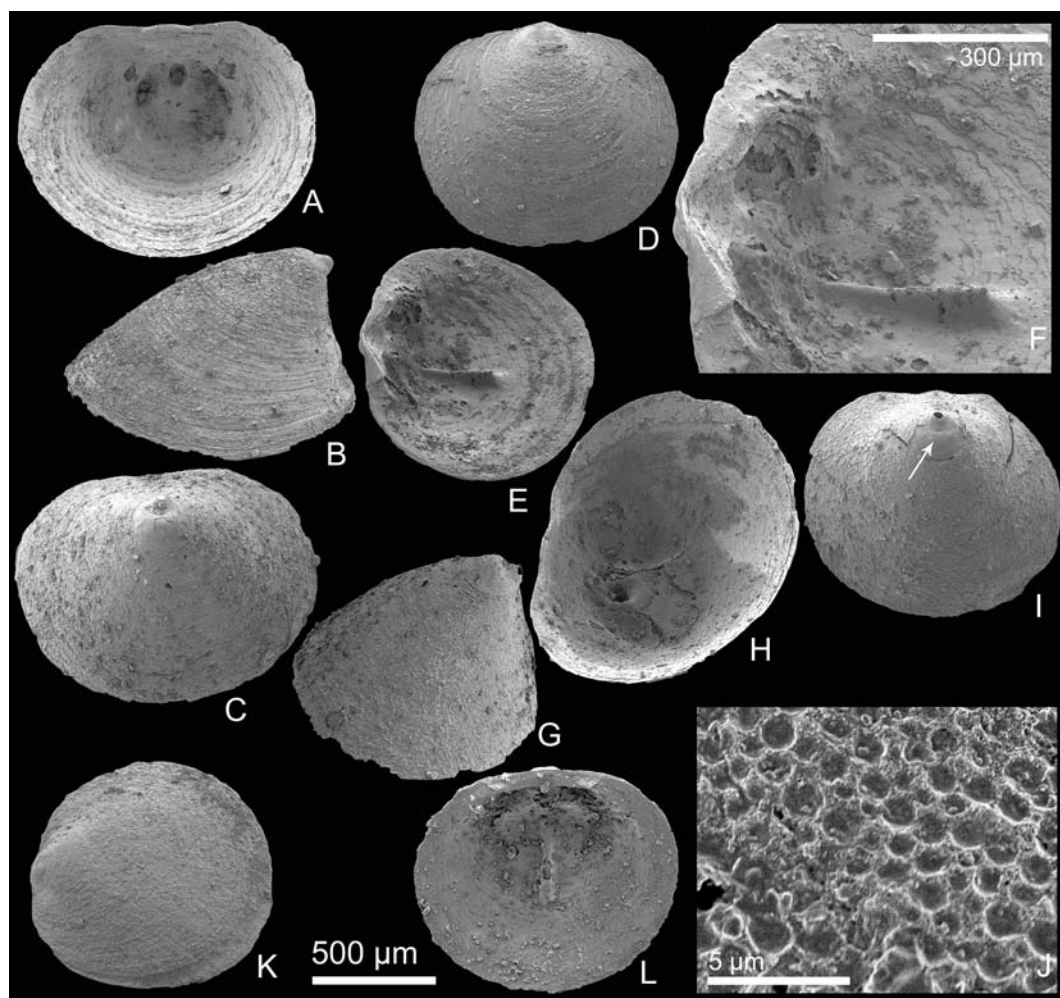


Figure 13. *Quadrisonia swaseyensis* n. sp., Hellnmaria Member, Notch Peak Formation, Millard County. Scale bar indicates 500 μ m unless indicated otherwise. **A-C**, holotype, ventral valve from ESB-25, **A**, interior, **B**, profile, **C**, exterior, USNM 543010; **D-F**, dorsal valve from ESB-25, **D**, exterior, **E**, oblique interior, **F**, propareas, median buttress with epithelial imprints, and median ridge, USNM 543011; **G**, ventral valve from ESB-25, profile view, USNM 543012; **H**, ventral valve from ESB-25, oblique interior view, USNM 543013; **I-J**, ventral valve from ESB-25, **I**, exterior, with arrow indicating location of **J**, **J**, larval shell microornament, USNM 543014; **K-L**, dorsal valve from ESB-25, **K**, oblique view of exterior, **L**, interior, USNM 543015.

posterior and anterior slope of valve (Figs. 12L, R). Apical process depressed ventrally to anterior of internal pedicle opening and expanded towards anterior for short distance. Apical pits small but prominent, especially on mature individuals, located posterolateral to internal pedicle opening (Fig. 12R). Baculate vascula lateralia divergent, not generally deeply impressed except on large, mature specimens. Moderately impressed cardinal muscle scars, suboval in outline, situated on posterior slope of valve posterolateral to internal pedicle opening.

Dorsal valve transversely suboval in outline, gently to robustly inflated, and evenly convex in lateral profile. Maximum height of dorsal valve

relative to maximum length varies considerably, averaging 31% of valve length. Orthocline pseudointerarea with short, narrow propareas (Fig. 12G, P). Width of pseudointerarea 46% of maximum width of valve and maximum length of pseudointerarea 11% of maximum length of valve. Lateral margins of propareas strongly deflected posteriorly in outline, not extending far past cardinal muscle field (Fig. 12G, P). Median groove wide, gently concave. Cardinal muscle scars deeply impressed, closely spaced, and transversely suboval in outline. Cardinal muscle field occupies approximately 43% of maximum width of valve and 22% of maximum length of valve. Median buttress robust, with narrow, well

defined median ridge arising anterior of median buttress at position approximately 26% maximum length of valve and extending anteriorly to approximately 54% of maximum length of valve. Median ridge very nearly a median septum on large individuals (Fig. 12P, Q). Impressions of vascula media prominent on mature specimens, diverging widely near anterior end of median ridge (Figs. 12P, Q).

Measurements. See Table 6.

Discussion. *Quadrisonia sawtoothensis* is similar to *Q. swaseyensis* n. sp. in having a well defined dorsal median ridge, but the ridge is shorter in length proportional to valve length, narrower and sharply defined laterally. *Quadrisonia sawtoothensis* is most similar to *Q. rattlesnakensis* n. sp. but differs in having a less inflated and more gently procline ventral valve and more inflated dorsal valve, as well as a more well developed median ridge.

The development of the pedicle tube and apical process along the posterior slope of the ventral valve is more pronounced on this species than on other species of *Quadrisonia* and can serve as a useful diagnostic character. However, it is most apparent on larger, more mature specimens.

***Quadrisonia swaseyensis* n. sp. (Fig. 13)**

Etymology. In reference to Swasey Peak, in the House Range, to the east of the type locality.

Type locality. The holotype valve was collected 7.6 m above the base of the ESB section in the upper Cambrian (Sunwaptan) Hellnmaria Member of the Notch Peak Formation, Tule Valley, Millard County, western Utah. The species was identified in the two lowest samples collected at the ESB section, at 0.9 m and 7.6 m above the base of the section. Four questionably assigned valves were collected at 22.9 m above the base.

Type material. Holotype, ventral valve, USNM 543010 (Fig. 13A-C). Paratypes, USNM 543011, dorsal valve; USNM 543012, ventral valve; USNM 543013, ventral valve; USNM 543014, ventral valve; and USNM 543015, dorsal valve. All paratypes are from 7.6 m above the base of the ESB section. Unfigured topotype material consists of 19 dorsal valves, 18 ventral valves, and 2 tentatively identified ventral valves.

Diagnosis. Robust species with high subconical ventral valve and steeply procline to nearly catacline ventral valve. Flattened to barely concave ventral pseudointerarea, with shallow

intertrough well defined for genus. Apical process short, expanding slightly towards anterior with a slight depression of the surface just anterior to the internal pedicle opening. Small apical pits situated posterolateral to internal pedicle opening. Lateral margins of dorsal valve propareas sharply deflected towards posterior in outline. Well developed median ridge. Larval shell with microornament of pitting generally measuring 1 μ m or less in diameter.

Description. Ventribiconvex shell with high subconical ventral valve and slightly inflated dorsal valve. Larval shells of both valves well defined, with ornament of hemispherical pits, most 1 μ m or less in diameter and round in outline (Fig. 13J). Strong growth lines on postlarval growth.

Ventral valve transversely suboval in outline with length averaging 82% of the width. Maximum height averaging 58% of length. Foramen enclosed within the larval shell, posterior to apex, usually at end of short tube directed slightly towards the posterior. Foramen just posterior to apex, at a position approximately 8% the length of the valve measured from posterior margin. Steeply procline to almost catacline pseudointerarea, flattened or gently convex in lateral profile, with well defined but shallow intertrough bounded by disruptions in growth lines. Outline of intertrough expands gently towards the posterior margin. Posterior margin of valve straight to slightly concave in outline. Lateral margins of propareas poorly defined. Anterior slope gently and evenly convex in profile.

Moderately developed apical process present in ventral interior, often bounded by baculate, widely divergent ventral vascula lateralia, forming sharply defined lateral margins of apical process if deeply impressed (Fig. 13H). Apical process expanding slightly anteriorly, with a slight depression on the surface anterior to the pedicle opening (Fig. 13H). Apical process short, never reaching a length greater than one-third of distance from the internal pedicle opening to anterior edge of the valve. Internal opening of pedicle tube positioned at posterior edge of apical process, with small, moderately well developed apical pits just posterolateral to pedicle opening. Apical process subtly elevated around margin of internal pedicle opening. Lightly impressed suboval cardinal muscle scars on posterior slope, posterolateral to internal pedicle opening.

Dorsal valve transversely suboval in outline, with length of valve averaging 82% of width. Dorsal valve gently inflated, with maximum height averaging 17% of valve length. Dorsal pseudointerarea orthocline, well developed, with

Ventral	W	L	F	H	L/W	H/L	F/L
N	11	12	11	11	11	11	11
X	0.91	0.78	0.06	0.45	0.85	0.58	0.08
S	0.11	0.11	0.02	0.09	0.06	0.07	0.03
MIN	0.75	0.55	0.03	0.28	0.74	0.45	0.04
MAX	1.12	0.94	0.09	0.63	0.97	0.68	0.12

Dorsal	W	L	Wm	Wi	Wg	BS	Lm	LS	Li	H
N	13	12	11	12	8	7	12.00	5	13	12
X	0.84	0.75	0.39	0.43	0.19	0.19	0.20	0.42	0.08	0.13
S	0.10	0.06	0.05	0.07	0.03	0.02	0.03	0.07	0.01	0.05
MIN	0.64	0.63	0.30	0.33	0.12	0.15	0.15	0.27	0.06	0.07
MAX	1.00	0.87	0.48	0.57	0.21	0.21	0.25	0.49	0.10	0.24

Dorsal	L/W	Li/Wi	Wi/W	Lm/L	Wm/W	LS/L	BS/L	Li/L	H/L	Wm/Wi
N	12	12	12	12	11	5	7	12	12	11
X	0.82	0.19	0.51	0.27	0.48	0.58	0.26	0.11	0.17	0.96
S	0.23	0.02	0.05	0.03	0.04	0.09	0.03	0.02	0.07	0.07
MIN	0.80	0.17	0.43	0.21	0.40	0.38	0.21	0.09	0.09	0.82
MAX	0.98	0.24	0.60	0.33	0.54	0.65	0.30	0.14	0.30	1.07

Table 7. *Quadrisonia swaseyensis* n. sp., average dimensions and ratios of dorsal and ventral valves. Five dorsal valves were measured from ESB-3 and 8 from ESB-25. Three ventral valves were measured from ESB-3 and 10 from ESB-25.

wide median groove. Outline of lateral margins of propareas strongly deflected posteriorly, giving propareas a triangular, tab-like appearance in outline (Fig. 13E, L). Anterior margins of propareas projecting in a shelf-like fashion over cardinal muscle scars (Fig. 13F).

Dorsal cardinal muscle scars thickened, impressed, set close together, with lateral edges generally not extending beyond lateral edges of pseudointerarea. Cardinal muscle scars transversely suboval in outline. Length of the cardinal muscle scar field averaging 27% of maximum length of valve, width of cardinal muscle scar field averaging 48% of maximum width of valve.

Well developed, thickened median buttress. Low triangular median ridge (Fig. 13F) anterior of the median buttress on all but very juvenile specimens. Median ridge very pronounced on mature and gerontic specimens, may be slightly thickened along its ventral edge, nearly forming a septum on gerontic specimens. Median ridge extending to about 58% of length of the valve.

Measurements. See Table 7.

Discussion. This species has a higher subconical ventral valve than most species of *Quadrisonia*, and is much higher than that of the type species, *Q. minor* Rowell & Henderson, 1978. The only comparable previously named species

of *Quadrisonia* is *Q. lavadamensis* Popov *et al.*, 2002, but that species differs in having a catacline to anacline ventral pseudointerarea. Grant (1965) described *Angulotreta vescula* from approximately coeval strata in Wyoming. This species may be a species of *Quadrisonia* and is catacline, but it differs in lacking a well developed median ridge. It also appears to be much lower in height than any of the new species described from the Hellnmaria Member, based on illustrated material (Grant 1965, pl. 13, fig. 11).

Quadrisonia swaseyensis is similar to *Q. rattlesnakensis* in having a high subconical ventral valve, but it differs from that species in being somewhat lower, with slightly flatter dorsal valves which have a prominent median ridge and distinctively shaped propareas.

Ventral valves of *Q. swaseyensis* are distinguished from co-occurring *Q. congerensis* by the steeply procline to nearly catacline pseudointerarea, greater height relative to width, more robust appearance, more strongly developed apical pits and apical process, and lack of distinctive ornamentation. The dorsal valves of *Q. swaseyensis* are also more robust than those of *Q. congerensis*, have a better developed median ridge, and different shaped propareas.

The median ridge of *Q. swaseyensis* is prominent on all but the most juvenile specimens but does not form a true median septum.

Acrotretidae gen. et sp. indet. (Fig. 3A)

Locality. Upper Cambrian (Sunwaptan) Hellnmaria Member of the Notch Peak Formation, Tule Valley, Millard County, western Utah. The specimen was collected 0.9 m above the base of the Hellnmaria Member in the ESB section, 278.3 m below the base of the *Proconodontus tenuiserratus* Zone.

Material. One dorsal valve, USNM 543034.

Description. Gently inflated dorsal valve with orthocline pseudointerarea. Pseudointerarea apparently less than half width of valve, subdivided by wide median groove. Cardinal muscle scars closely set. Prominent median septum arising from median buttress and extending towards anterior. Other details unknown.

Discussion. This fragmentary dorsal valve exhibits a prominent median septum which is a characteristic of many different acrotretid genera, but not *Quadrisonia*, which is the only other acrotretid in these collections. It is in the stratigraphically lowest collection, at 0.9 m above the base of the Hellnmaria Member.

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