

SMALL SHELLY FOSSILS AND CARBON ISOTOPES FROM THE EARLY CAMBRIAN (STAGES 3–4) MURAL FORMATION OF WESTERN LAURENTIA

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Abstract: The extraordinary window of phosphatized and phosphatic small shelly fossils (SSF) during the early and middle Cambrian is an important testament to the radiation of biomineralizing metazoans. While SSF are well known from most Cambrian palaeocontinents during this time interval, western Laurentia has relatively few SSF faunas. Here we describe a diverse SSF fauna from the early Cambrian (Stages 3–4) Mural Formation at three localities in Alberta and British Columbia, Canada, complemented by carbon isotope measurements to aid in a potential future bio-chemostratigraphic framework. The fauna expands the recorded SSF assemblage diversity in western Laurentia and includes several brachiopods, four bradoriids, three chancelloriids, two hyoliths, a tomotioid and a helcionellid mollusc as well as echinoderm ossicles and specimens of *Microdictyon*, *Volborthella* and *Hyolithellus*. New taxa include the tomotioid genus *Canadiella* gen. nov., the new bradoriid

species *Hipponicharion perforata* sp. nov. and *Pseudobeyrichona taurata* sp. nov. Compared with contemporaneous faunas from western Laurentia, the fauna is relatively diverse, particularly in taxa with originally phosphatic shells, which appear to be associated with archaeocyathid build-ups. This suggests that the generally low faunal diversity in western Laurentia may be at least partly a consequence of poor sampling of suitable archaeocyathan reef environments. In addition, the tomotioid *Canadiella filigrana* appears to be of biostratigraphical significance in Cambrian Stage 3 strata of western Laurentia, and the unexpected high diversity of bradoriid arthropods in the fauna also suggests that this group may prove useful for biostratigraphical resolution in the region.

Key words: small shelly fossils, Brachiopoda, Bradoriida, biostratigraphy, carbon isotope stratigraphy, Cambrian.

LOWER Cambrian fossils of the Mural Formation have been studied for over 100 years and a rich fauna of trilobites and brachiopods has been documented (Walcott 1913; Fritz & Mountjoy 1975; Fritz 1992; Balthasar 2004, 2007, 2008, 2009). The discovery of exceptionally preserved fossils such as soft-shelled brachiopods (Balthasar & Butterfield 2009), anomalocaridids and other non-mineralized biota (Sperling *et al.* 2018) has also sparked interest in the formation. However, Burgess Shale-type exceptional preservation in the Mural Formation is at best marginal (a Tier 3 deposit), and there is little geochemical evidence for anoxic conditions that might result in more spectacular preservation (Sperling *et al.* 2018). The bulk of the known fauna has been derived from mudstones of the middle part of the Mural Formation. Here, we describe skeletal fossils from both the underlying

carbonate-dominated lower Mural Formation and from carbonate storm beds within the middle Mural Formation.

In the early Cambrian (Terreneuvian and Cambrian Series 2), small shelly fossils (SSF) constitute a significant portion of the total taxonomic diversity of the metazoan fossil record (Maloof *et al.* 2010). SSF share nothing beyond a commonly small size range (typically < 2 mm; which may be taphonomically biased for some taxa; Martí Mus *et al.* 2008) and the fact that the fossils are resistant to digestion of the carbonate host rock in weak acids (fossils are typically either phosphatic by original composition or secondarily phosphatized or silicified calcareous shells). The fossils include various shells, sclerites, spicules and other skeletal elements belonging to a multitude of early animal groups representing stem and crown

members of various phyla across the metazoan tree of life (Budd & Jensen 2000; Kouchinsky *et al.* 2012).

Relatively few SSF faunas have been described from the Cambrian of western Laurentia. From the earliest Cambrian (Fortunian), Conway Morris & Fritz (1980) reported a single protoconodont specimen (probably from the Ingta Formation in the Mackenzie Mountains of north-western Canada; see Aitken 1989), and Pyle *et al.* (2006) described a fauna including possible animal embryos, anabaritids and problematic fossils from the Wernecke Mountains of Yukon, Canada. However, SSF records from Laurentia are more common in the late early Cambrian (Series 2), particularly along the present eastern margin of North America. In western Laurentia, published Series 2 accounts from the Great Basin of the western USA are limited to brachiopods and a handful of generally poorly preserved taxa (Signor & Mount 1986; Skovsted 2006a; Skovsted & Holmer 2006; Wotte & Sundberg 2017; Pruss *et al.* 2019). The same applies to the fauna from the Sekwi Formation of the Mackenzie Mountains of north-western Canada (Voronova *et al.* 1987) and Sonora, Mexico (McMenamin 1984; Devaere *et al.* 2019). In addition, the occurrence of single problematic SSF have been reported from different regions of western North America, i.e. *Salterella* (Fritz & Yochelson 1988), *Volborthella* (Hagadorn & Waggoner 2002), *Microdictyon* (Bengtson *et al.* 1986), and '*Lapworthella*' *filigrana* (Conway Morris & Fritz 1984). Hence, the SSF fossil record from western Laurentia is relatively meagre compared with contemporaneous faunas from eastern Laurentia (Skovsted 2006b; Skovsted & Peel 2007, 2011) and other palaeocontinents (Qian & Bengtson 1989; Bengtson *et al.* 1990; Kouchinsky *et al.* 2012, 2015).

Biostratigraphic subdivision and correlation of Cambrian strata traditionally rests on trilobites (Shergold & Geyer 2003; Zhu *et al.* 2019). However, a significant part of the Cambrian Period is pre-trilobitic (Terreneuvian) and in the overlying unnamed Cambrian Series 2, trilobite faunas have proven to be highly endemic with resulting problems for intercontinental correlation. Carbon isotope stratigraphy has also emerged as a robust correlation method in lower Cambrian strata (e.g. Smith *et al.* 2016) but both patterns of negative/positive excursions and absolute values can be non-unique. Consequently, additional sources of age control are needed. Recently, non-trilobite shelly fossils were used to define a new biostratigraphic subdivision of Cambrian Series 1–2 strata from South Australia (Betts *et al.* 2016, 2017, 2018), and various SSF taxa are currently being considered as index fossils for the boundary between Cambrian Series 1 and 2 (see review in Zhang *et al.* 2017). However, the biostratigraphical control of SSF assemblages from western Laurentia remains to be tested.

The excellent preservation and relatively high taxonomic diversity presented here makes the fauna of the Mural Formation one of the most diverse and best preserved SSF faunas described from the lower Cambrian of western Laurentia. The results highlight that an increased sampling focus on archaeocyathan reefs and associated sediments might increase the known SSF diversity in western Laurentia. Our results suggest that specific SSF taxa such as tommotiids and bradoriid arthropods have a good potential for biostratigraphical resolution in Cambrian Stage 3 of western Laurentia, although further work is required to realize this potential. With the combination of carbon isotope chemostratigraphic data in conjunction with SSF data, as we present here, it may be possible in the future to build an improved bio-chemostratigraphic framework. Ultimately this will be key to placing western Laurentian SSF diversity in the global picture and determining if the observed low diversity is due to sampling, ecology, or taphonomic effects.

GEOLOGICAL SETTING

The Mural Formation is located in the southern Canadian Cordillera and was deposited on the western Laurentian margin, approximately during the rift–drift transition and initial Palaeozoic flooding of North America (Sauk transgression) (Pope *et al.* 2012). The Mural was deposited in a relatively shallow-water environment, with the Laurentian craton to the east and deeper water conditions developing to the west. The Mural Formation itself thins substantially across the Peace River Arch, a major east–north–east–trending structure in northern Alberta and British Columbia (Fig. 1; McMechan 1990). However, the tripartite stratigraphic motif of the Mural is recognized from Mexico to Yukon during the Lower Cambrian (Series 2, Age 3 and 4; Waucoban Series, Montezuman–Dyeran Stages in a North American timescale; *Nevadella–Bonnia–Olenellus* trilobite zones in older literature). This motif consists of a lower carbonate (often archaeocyathan limestone mounds/biostromes and ooid grainstone), a medial shale/siltstone, and an upper carbonate, again often containing archaeocyaths (Pope *et al.* 2012). In most localities, the *Nevadella–Bonnia–Olenellus* boundary, which is also the Montezuman–Dyeran boundary, is located in the medial shale (Fig. 2). Additional data on the geology, sedimentology, and palaeontology of the Mural Formation can be found in Fritz & Mountjoy (1975), Balthasar (2004) and Sperling *et al.* (2018). The Waucoban Series is traditionally divided into a series of trilobite zones: the *Fallotaspis*, *Nevadella* and *Bonnia–Olenellus* Zones in ascending order. This biostratigraphical framework has recently been revised and refined with a number of new trilobite zones (Hollingsworth 2011;

Webster 2011). However, given that the trilobites of the Mural Formation have yet to be re-studied in this biostratigraphical framework, consequently we refer to the older zone names herein.

MATERIAL AND METHOD

The Mural Formation was sampled at three different locations: the type Mumm Peak section in Jasper National Park in western Alberta (sample prefix MP; see Balthasar 2004 and Sperling *et al.* 2018 for locality information); a

new section in a glacial valley to the north-west of Mumm Peak in eastern British Columbia (the informally named Rocky Lake camp, sample prefix RL); and the Dezaiko Range further to the north in British Columbia (sample prefix DR). At Mumm Peak the basal limestone and middle shale units were sampled for SSF while carbon isotope samples were collected from a measured stratigraphic section of the entire formation, including the upper carbonate unit that was heavily dolomitized. At Rocky Lake the basal limestones were sampled for SSF in relative stratigraphic order while the upper carbonate (limestone) was sampled for carbon isotopes from a

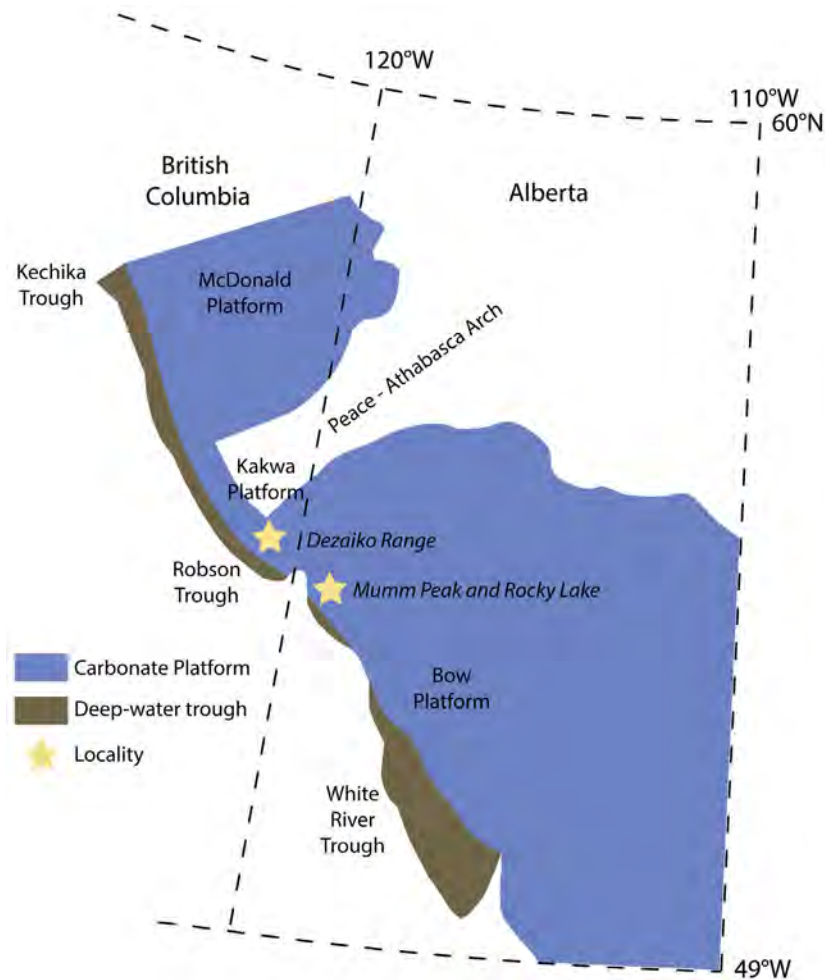


FIG. 1. Locality map of investigated Mural Formation localities in the southern Canadian Cordillera. Map is modified from Norford (2012) and shows the generalized present-day distribution of middle Cambrian – Middle Ordovician rocks from 49°N to Peace River. The transition from the shallow-water platform to deep-water conditions was probably not as sharp in the early Cambrian during deposition of the Mural Formation, but the presence of deep-water slope deposits in the underlying late Neoproterozoic stratigraphy immediately to the west of our study sites (Ross & Arnott 2007) suggests that a westward-deepening basin had been established for some time prior to Mural Formation deposition. Our collection sites in the Dezaiko Range, Mumm Peak, and Rocky Lake sit on the southern edge of the Peace–Athabasca Arch (McMechan, 1990). The Mural Formation thins across the Arch, but stratigraphic equivalents to the Mural Formation deposited during the *Nevadella*–*Bonnia*–*Olenellus* zones can be recognized from Mexico to Yukon (Pope *et al.* 2012). For detailed locality information see text or locality map in Sperling *et al.* (2018).

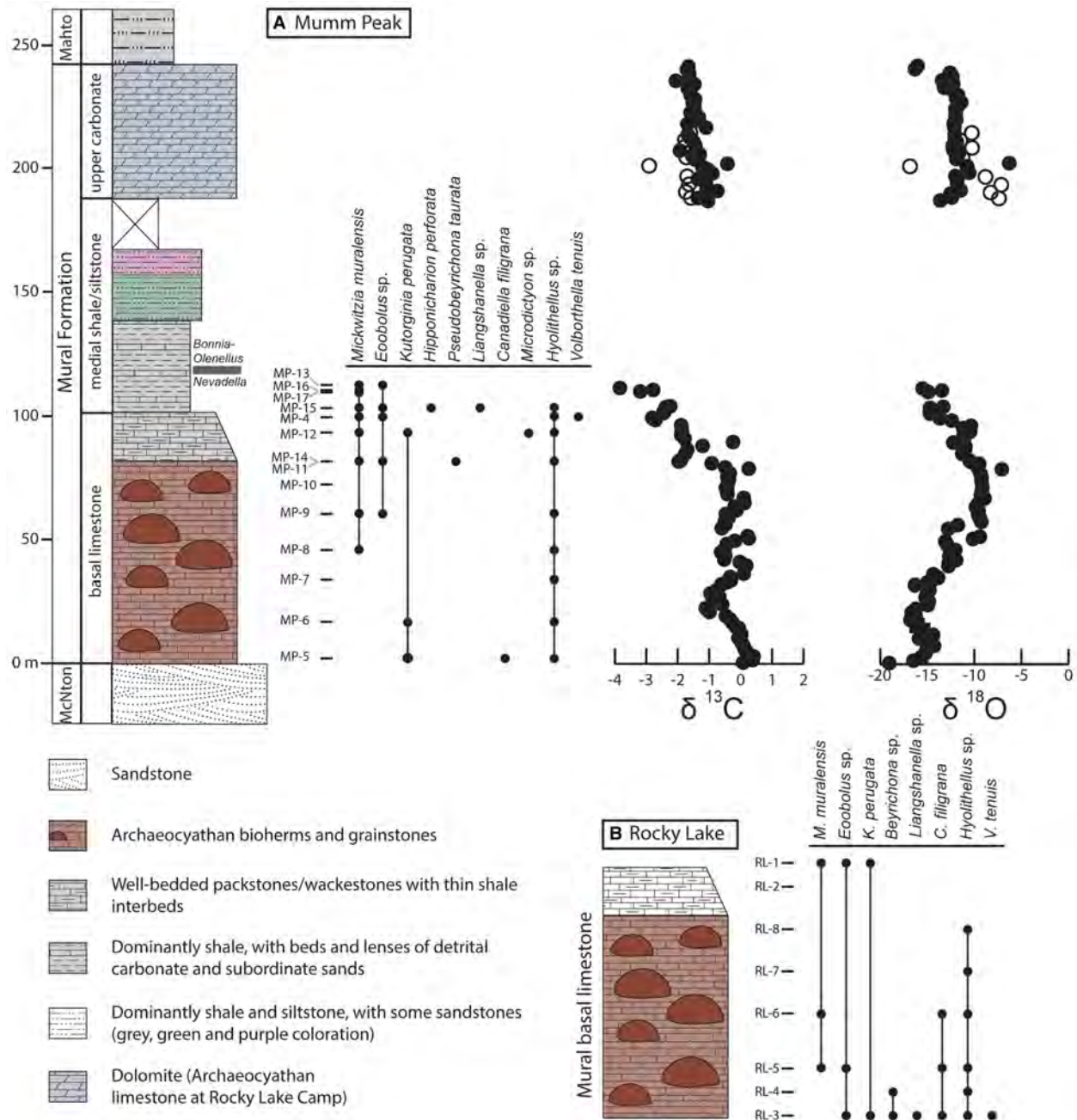


FIG. 2. Measured stratigraphic sections through the Mural Formation. A, section at Mumm Peak (MP), modified from Sperling *et al.* (2018). B, section at Rocky Lake (RL). For both sections sampled fossil horizons are indicated, including stratigraphic ranges of selected fossils as well as stable carbon and oxygen isotope data. All isotope data from the basal limestone are from Mumm Peak. Carbon and oxygen isotope data from heavily dolomitized samples in the upper carbonate at Mumm Peak are shown as open circles. Solid circles represent limestone samples from the Rocky Lake camp, with samples correlated based on a datum at the base of the upper carbonate.

measured section. In the Dezaiko Range, two samples, probably derived from the middle shale unit, were collected from local float (Fig. 1). Lithological descriptions with stratigraphic position for all samples are reported in Skovsted *et al.* (2020, appendix S1). All samples and

recovered microfossils as well as associated macro fossils are deposited in the Royal BC Museum in Victoria (RBCM). Coordinates for the base of all studied sections and most individual samples are available from the curators at RBCM.

Carbonate samples (600–1700 g; for details see Skovsted *et al.* 2020, appendix S1) were digested in buffered, 10% acetic acid at the Microfossil Laboratory at Lund University, Sweden, following protocols established for conodont extraction (Jeppsson *et al.* 1999). The resulting residues were scanned for fossils under a stereo microscope and selected specimens were gold-coated and pictured using the Hitachi scanning electron microscope at the Swedish Museum of Natural History in Stockholm, Sweden.

For carbon and oxygen isotope analyses, only samples of pure carbonates were analysed. Hand samples were cut at Stanford University perpendicular to bedding and individual laminae were drilled for powder, avoiding veins or obvious alteration. Samples were then analysed at Yale University using a Thermo Scientific Kiel IV Carbonate Device connected to a Thermo Finnegan MAT 253 mass spectrometer. Long-term precision on a marble reference material was ± 0.05 per mil (‰) for $\delta^{13}\text{C}$ and ± 0.06 ‰ for $\delta^{18}\text{O}$. All measured isotope data are reported in Skovsted *et al.* (2020, appendix S2).

FAUNA OF THE MURAL FORMATION

The fossil assemblage of the Mural Formation was originally described by Walcott (1913) and represents a moderately diverse early Cambrian (Cambrian Stages 3–4) fauna including trilobites (Fritz & Mountjoy 1975; Fritz 1992; Ortega-Hernández *et al.* 2013), brachiopods (Balthasar 2004, 2007, 2008, 2009) and exceptionally preserved compression fossils (Balthasar & Butterfield 2009; Sperling *et al.* 2018). Our investigation of acid-resistant residues of the basal limestone and middle shale units has revealed a well-preserved fauna of SSF. Brachiopods are common in the new collections, being represented by at least four species, three of which are known from previous publications (*Mickwitzia muralensis* Walcott, 1913, *Mummpikia nuda* (Walcott, 1913) and *Eoobolus* cf. *triparilis* (Matthew, 1902)) while the fourth species is reported from the Formation for the first time (*Kutorgina perugata* Walcott, 1905). Other taxa of the Mural Formation include four bradoriid arthropods (*Hipponicharion perforata* sp. nov., *Pseudobeyrichona taurata* sp. nov., *Beyrichona* sp., *Liangshanella* sp.), three types of chancelloriid sclerites (*Chancelloria* sp., *Archiasterella* sp., *Allonnia* sp.), at least two hyoliths (*Cupithecina* sp. and indeterminate hyolithids), one helcionelloid mollusc, the tommotiid *Canadiella filigrana* (Conway Morris & Fritz, 1984), the tubular problematicum *Hyalithellus* sp., sclerites of the lobopod *Microdictyon* sp. and the agmatan *Volborthella tenuis* Schmidt, 1888. Many samples also include trilobite and archaeocyathid debris (not illustrated) and well preserved echinoderm ossicles as previously shown by Dickson (2002).

The fauna includes a high proportion of taxa with presumed original (Malooof *et al.* 2010; Kouchinsky *et al.* 2012) organophosphatic composition (53% of all species; *Eoobolus*, *Mickwitzia*, *Canadiella*, *Hyalithellus*, *Microdictyon* and bradoriid arthropods). These taxa are usually well-preserved, often revealing fine surface details, even in fragmentary specimens, while taxa with originally calcareous shells (42% of all species) are often preserved as internal moulds (hyoliths, chancelloriids), partly silicified shells (helcionelloid mollusc) or rarely as secondarily phosphatized shells (rare chancelloriid sclerites, echinoderm ossicles, *Kutorgina*). A single species (5%; the agmatan *Volborthella tenuis*) is represented by cone-shaped, agglutinated deposits.

AGE AND CORRELATION OF THE MURAL FORMATION

The recovered SSF fauna of the Mural Formation (Fig. 2; Table 1) includes some elements that are known from roughly coeval strata in western Laurentia such as *Canadiella filigrana*. This tommotiid species was originally described from the Cassiar Mountains in northern British Columbia (Conway Morris & Fritz 1984) and is also found in Sonora, Mexico (McMenamin 1984, 1988, 2001) and eastern California (Signor & Mount 1986). The brachiopod *Kutorgina perugata* is also known to occur in Nevada and eastern California (Walcott 1912; Signor & Mount 1986). *Microdictyon* sp. from the Mural fauna is closely comparable to specimens reported as *Microdictyon* cf. *rhomboidale* from the Mackenzie Mountains of Northwest Territories (Bengtson *et al.* 1986) and from the Great Basin (Wotte & Sundberg 2017). *Volborthella tenuis* is another widespread taxon in the Great Basin and the Canadian Rocky Mountains (Fritz & Yochelson 1988; Hagadorn & Waggoner 2002). However, in general the non-trilobite fauna from strata of Cambrian Series 2 in western Laurentia is extremely poorly known and many of the fossil taxa reported here from the Mural Formation have not been reported from the region before.

Although the reported SSF fauna from the Mural Formation is of limited value for biostratigraphical correlation within Laurentia due to the present poor state of knowledge of Laurentian SSF faunas, we note that several taxa appear to be both geographically widespread and have a restricted stratigraphic range in western Laurentia. Particularly, this applies to *Canadiella filigrana*, with a demonstrated range in the Motezuman from northern British Columbia to Mexico. The geographic and stratigraphic distribution of the brachiopods *Kutorgina perugata* and *Mickwitzia muralensis* (see McMenamin 1992) and the problematic *Volborthella tenuis* is similar, although these species have not been reported from

TABLE 1. List of SSF samples from Mumm Peak, Rocky Lake and Dezaiko Range with sample number, absolute or approximate height above base of formation, and fossil content.

Sample	Height/ Species	Archaeocyathid fragm.	Trilobite spines	<i>Mickwitzia muralensis</i>	<i>Eoobolus cf. tripar- ilis</i>	<i>Mummipikia nuda</i>	<i>Kutorgina perugata</i>	<i>Microdictyon sp.</i>	<i>Canadiella filigrana</i>	<i>Hipponicharion perforata</i>	<i>Pseudobeyrichona taurata</i>
MP-13	~113		x	x	x	x					
MP-16	110.7			x							
MP-17	110.1			x							
MP-15	103.7			x	x				30		
MP-4	100		x	x	x						
MP-12	93.6	x		x			x	1			
MP-14	82.1		x	x		x					
MP-11	82		x	x	x	x					27
MP-10	72.7										
MP-9	60.5			x	x						
MP-8	45.9			x		x					
MP-7	33.8		x								
MP-6	16.8						1				
MP-5	1.9						2		14		
MP-3	~80		x	x	x	x		3			
MP-2	~70										
MP-1	~60	x		x	x						
RL-1	~61			x	x		x				
RL-2	~55	x	x			x					
RL-8	~45	x									
RL-7	~35										
RL-6	~25			x					18		
RL-5	~12			x	x				19		
RL-4	~6	x				x					
RL-3	~0.15				x		5		33		
DR-1	??		x	x		x					
DR-3	??	x	x	x							
SUM							8	4	84	30	27

Sample	<i>Beyrichona sp.</i>	<i>Liangshanella sp.</i>	<i>Hyalolithellus sp.</i>	Helcionelloid mollusc	<i>Cupithecra sp.</i>	Hyalolithid sp. Indet	Echinoderm ossicles	<i>Chancelloria sp.</i>	<i>Allonnia sp.</i>	<i>Archiasterella sp.</i>	<i>Volborthella tenuis</i>
MP-13					2						
MP-16					34	4	4		21		
MP-17					7		10	9			
MP-15		1	3		39	21	7	10	51		
MP-4			32			3		4			4
MP-12			12								
MP-14						2	19				
MP-11			8							4	
MP-10											
MP-9			20				5				
MP-8			3		14		12	1			
MP-7			10		4						
MP-6			2								
MP-5			10								
MP-3			3		2	1	1	45		99	
MP-2					7		43				1

(continued)

TABLE 1. (Continued)

Sample	<i>Beyrichona</i> sp.	<i>Liangshanella</i> sp.	<i>Hyolithellus</i> sp.	Helcionelloid mollusc	<i>Cupithec</i> sp.	Hyolithid sp. Indet	Echinoderm ossicles	<i>Chancelloria</i> sp.	<i>Allonnia</i> sp.	<i>Archiasterella</i> sp.	<i>Volborthella</i> <i>tenuis</i>
Mp-1			9					9			
RL-1					14	3		2			
RL-2				1		4		2			
RL-8			16			1					
RL-7			12				163				
RL-6			34	18			114				
RL-5			110	4	2		116	8			
RL-4	2		5					1			
RL-3	18	1	99								16
DR-1						5	5	5			
DR-3					9	6	57	5			
SUM	20	2	388	23	134	50	556	101	72	103	21

For samples MP-1, MP-2, MP-3, MP-4, MP-13 and all samples from Rocky Lake section (RL-1–8) only approximate measurements of stratigraphic position are available. The stratigraphic position of both samples from Dezaiko Range (DR-1 and DR-3) is unknown (see discussion in text). For trilobites, brachiopods (except *Kutorgina perugata*) and archaeocyathan fragments, presence is indicated by ‘x’ because these taxa were not specifically studied. DR, Dezaiko Range; MP, Mumm Peak section; RL, Rocky Lake section; SSF, small shelly fossils.

localities further north in Canada. Other co-occurring taxa such as *Microdictyon*, *Hyolithellus* and various hyoliths and chancelloriids may have similar distributions, but taxonomic identification of species in these genera is difficult and their importance for biostratigraphical resolution is currently uncertain. However, we note that the new data from the lower Mural Formation clearly reinforce the trilobite-based biostratigraphy (*Nevadella* Zone; Fritz & Mountjoy 1975; Fritz 1992) and suggest that non-trilobite species may have an important role to play in future biostratigraphical correlation in western Laurentia. It is pertinent that the kennardiid tomotioid *C. filigrana* appears to represent a biostratigraphical signal in western Laurentia, given that related tomotioids (species of *Dailyatia*) were recently used as a basis for the revised shelly fossil biostratigraphy of south Australia (Betts *et al.* 2016, 2017, 2018).

The new fauna from the Mural Formation further indicates that bradoriid arthropods could be of particular interest for resolving biostratigraphical correlation in western Laurentia based on SSF studies. Bradoriid faunas from the early Cambrian (Terreneuvian & Series 2) of Laurentia are currently relatively poorly known. Siveter & Williams (1997) summarized more than 100 years of research on specimens from crack-out collections by recognizing four lower Cambrian species known from the entire palaeocontinent at that time (Siveter & Williams 1997, text-fig. 7). Since then, reports of bradoriids from SSF faunas from North-East and North Greenland have been published (Skovsted 2006b; Peel 2017a), effectively doubling the taxonomic

diversity of this fossil group in Laurentia during the early Cambrian. On other palaeocontinents, however, bradoriids constitute a major part of the taxonomic diversity of Cambrian Stages 3–4 marine faunas. This particularly applies to Avalonia (Siveter & Williams 1997; Williams & Siveter 1998), South China (Shu 1990; Hou *et al.* 2002; Zhang 2007), Australia (Fleming 1973; Skovsted *et al.* 2006; Topper *et al.* 2007, 2011a; Betts *et al.* 2014) and different areas of peri-Gondwana (Hinz-Schallreuter 1993; Gozalo & Hinz-Schallreuter 2002; Gozalo *et al.* 2004). Furthermore, Betts *et al.* (2017) showed in a recent analysis of the biostratigraphy of the lower Cambrian sequence of South Australia that bradoriids hold great potential for regional correlation within Australia and for intercontinental correlation between Australia and particularly South China, Antarctica and Siberia.

Four different bradoriids were discovered in the acid-resistant residues from the Mural Formation: *Hipponicharion perforata* sp. nov.; *Pseudobeyrichona taurata* sp. nov.; *Beyrichona* sp.; and *Liangshanella?* sp. In most cases only fragmentary or poorly preserved valves are present, precluding definite species assignment, but two samples yielded more complete material, allowing the characterization of two new species. In light of the demonstrated global high taxonomic diversity and wide palaeogeographic distribution of bradoriids in the early Cambrian, the low diversity of contemporaneous bradoriid faunas from Laurentia is likely to reflect insufficient sampling rather than lower original diversity. The fact that the fauna of the Mural Formation documented here

includes four new bradoriid species seems to lend support to this interpretation. Even more strikingly, the new species represents some of the first bradoriids from Cambrian Stages 3–4 strata of western Laurentia known to date (Siveter & Williams 1997). In addition, Devaere *et al.* (2019) recently reported a bradoriid from the Puerto Blanco Formation, in Sonora, Mexico, which may belong to *P. taurata*. It is anticipated that future investigations will reveal a much larger bradoriid diversity in this region.

Carbon isotope stratigraphy

To aid in current and future correlations we also generated carbonate carbon isotope data from our sections. $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ are plotted in Figure 2, with samples from Mumm Peak in closed circles in the basal limestone and middle shale. Heavily dolomitized values from the upper carbonate at Mumm Peak are plotted as open circles whereas the closed circles represent limestones from Rocky Lake, with samples correlated on the base of the upper carbonate. $\delta^{18}\text{O}$ averages -12.4‰ at Mumm Peak and -12.1‰ at Rocky Lake, below general cut-offs for alteration of a sample's carbon isotope composition (e.g. Knoll *et al.* 1995). Given that no other diagenetic evaluation was conducted in this study, these carbon isotope results should be considered with this caveat in mind. $\delta^{13}\text{C}$ values at Mumm Peak start around 0‰ and then undergo a series of *c.* 1‰ oscillations through the archaeocyathan biohermal limestones. At the transition to interbedded packstones/wackestones and shales, in the *Nevadella* Zone, values decrease from *c.* 0‰ to *c.* -3‰ . The only other Laurentian formation in this time interval to have received comprehensive carbon isotope study is the Sekwi Formation, studied in the Mackenzie Mountains, Northwest Territories by Dilliard *et al.* (2007). There, the Montezuman–Dyeran (*Nevadella*–*Bonnia*–*Olenellus*) transition interval is marked by an unconformity and a period of clastic deposition. The stratigraphically highest *Nevadella* samples in the Sekwi Formation do show negative carbon isotope trends, although these excursions start from more positive values than in the Mural and do not reach values as low as -3‰ . Several possibilities exist to explain the discrepant carbon isotope curves from the two formations: (1) the basal limestone in the Mural Formation records carbonate deposition not present in the Sekwi Formation (either time lost in the unconformity or during clastic intervals); (2) the Mural Formation negative carbon isotope excursion represents negative excursion D in the Sekwi Formation (which occurs there in the basal part of the *Bonnia*–*Olenellus* zone); implying time-transgressive trilobite zones; or (3) the negative excursion in the Mural Formation is

artefactual and represents progressive loss of carbonate buffering capacity in the transition from the basal limestone to the middle shale. $\delta^{13}\text{C}$ from the upper carbonate at Rocky Lake is between *c.* -0.5 and -2.0‰ and trends slightly more negatively upsection. Dolomitized samples from the upper carbonate at Mumm Peak are similar but slightly more negative than at Rocky Lake. These results are consistent with results from the Sekwi Formation *Bonnia*–*Olenellus* zone, but given that there are no carbon isotopic excursions in this interval the correlations are non-unique.

SSF OF WESTERN LAURENTIA

The poorly known SSF assemblages from western Laurentia stand in stark contrast to faunas of much higher taxonomic diversity from eastern Laurentia and from other continental blocks, primarily Siberia (Missarzhevsky 1989; Kouchinsky *et al.* 2011, 2015), Australia (Bengtson *et al.* 1990; Gravestock *et al.* 2001; Betts *et al.* 2016, 2017, 2018); South China (Qian & Bengtson 1989; Yang *et al.* 2015) and North China (Li *et al.* 2019; Pan *et al.* 2019). The most diverse SSF faunas reported from Cambrian strata in Laurentia are derived from relatively deep water settings along the present eastern margin of North America, in a region stretching from North (Peel & Willman 2018) and North-East Greenland (summarized in Skovsted 2006b) through western Newfoundland (Skovsted & Peel 2007; Skovsted *et al.* 2017), Quebec (Landing *et al.* 2002), the Taconic allochthons of New York State and Vermont (Lochman 1956; Landing & Bartowski 1996) and into Pennsylvania (Skovsted & Peel 2010). All these faunas are derived from strata assigned to the North American Dyeran Stage (*Bonnia*–*Olenellus* trilobite Zone, provisional Cambrian Stage 4) and are thus younger than the fauna of the Mural Formation described here, which stems from the older Montezuman Stage (*Nevadella* Trilobite Zone, Cambrian Stage 3).

In contrast, in western Laurentia knowledge of SSF assemblages is limited to a handful of isolated faunas representing different time intervals (Terreneuvian–Wuliuan) and to localities distributed over an immense distance from Mexico (McMenamin 1984, 1985; Devaere *et al.* 2019) in the South through the Great Basin of western USA (Signor & Mount 1986, Skovsted 2006a; Skovsted & Holmer 2006; Wotte & Sundberg 2017; Moore *et al.* 2019; Pruss *et al.* 2019), the Canadian Rocky Mountains (Conway Morris & Fritz 1984; Bengtson *et al.* 1986; Fritz & Yochelson 1988; herein) to north-western Canada (Conway Morris & Fritz 1980; Voronova *et al.* 1987; Pyle *et al.* 2006). Further, many of these reports are either of limited scope taxonomically or are poorly documented. For instance, an apparently diverse fossil assemblage was

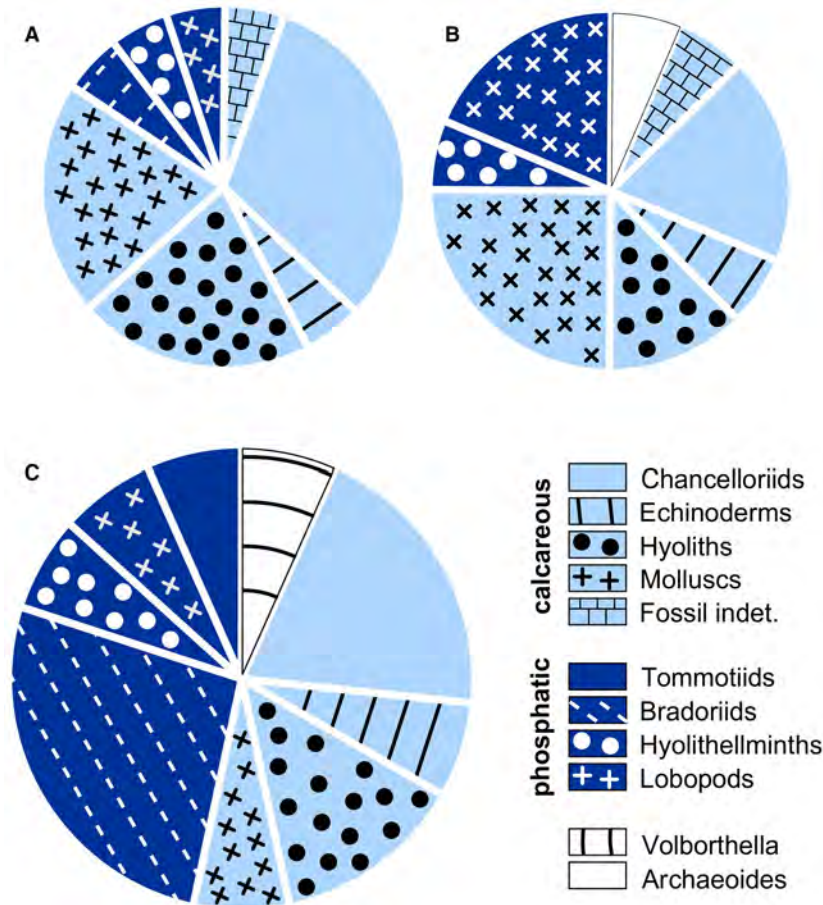


FIG. 3. Comparison of shell mineralogy and relative abundance of small shelly fossil (SSF) taxa (excluding brachiopods, trilobites and archaeocyathans) reported from: A, the Great Basin (Wotte & Sundberg 2017); B, Sonora, Mexico (Devaere *et al.* 2019); and C, the Mural Formation (herein). Bradoriids, tommotiids, lobopod sclerites and hyolithelminth tubes are considered to have originally phosphatic shells (darker shades). Chancelloriids, molluscs, hyoliths, echinoderm ossicles and the net-like Fossil indet. from both Great Basin and Sonora (see discussion in Devaere *et al.* 2019, p. 47) are regarded as originally calcareous (lighter shades). The original shell mineralogy of *Archaeoides* reported from the Great Basin is considered to be uncertain while *Volborthella* from the Mural Formation is agglutinating. Multiple species of *Microdictyon* from the Great Basin are entered as reported by Wotte & Sundberg (2017) despite the taxonomic uncertainty of these species as discussed herein.

reported by Signor & Mount (1986; their fig. 2) from the White–Inyo region of eastern California, but the listed fossils were compiled from a host of older papers and unpublished theses and were not illustrated. This assemblage is in dire need of taxonomic revision before its importance and true taxonomic diversity can be assessed. The same applies to the fauna from the Mackenzie Mountains of the Northwest Territories described by Voronova *et al.* (1987).

In two recent publications, SSF assemblages from the Great Basin and Sonora were described in greater detail than ever before. Wotte & Sundberg (2017) investigated material from nine different stratigraphic sections in the Great Basin, derived from four formations spanning outer to inner shelf environments in the Montezuman–Delamaran time interval (Cambrian Stage 3–Wuliuan). The

reported fauna is composed of four molluscs, two hyoliths, three chancelloriids, three nominal species of *Microdictyon* (probably synonymous, see discussion below) and three problematic taxa in addition to echinoderm ossicles and trilobite debris; no brachiopods were reported. The total diversity of this fauna (15 nominal species, not counting trilobite remains) is of similar richness as the fauna from the two sections of the lower Mural Formation reported herein (15 species, excluding brachiopods, archaeocyathans and trilobites; Fig. 3), despite representing both a longer time interval and a much wider sampling of Cambrian shelf environments (Wotte & Sundberg 2017, fig. 2). The low diversity of the Great Basin SSF fauna reported by Wotte & Sundberg (2017) mirrors results from previous investigations of material from the Great Basin (Skovsted 2006a; Skovsted & Holmer 2006).

Devaere *et al.* (2019) recently described an SSF fauna from the Puerto Blanco Formation at Cerro Rajón of Sonora, Mexico. The sampled section is 700 m thick and spans a significant portion of the early Cambrian (Stages 2–4) with fossils preserved in dispersed carbonate layers in an otherwise clastic-dominated sequence (Devaere *et al.* 2019, their fig. 2). The reported fauna is also of similar taxonomic richness as the fauna of the Mural Formation (18 taxa, excluding brachiopods, archaeocyaths and trilobites) but is dominated by four molluscs, six chancelloriids and four hyoliths with a single species of bradoriid, *Microdictyon* and two other problematic taxa as minor parts of the fauna. Trilobite, archaeocyath and echinoderm debris was also reported as well as two brachiopod species (Devaere *et al.* 2019).

The underlying reasons behind low taxonomic diversity of SSF assemblages in western Laurentia are speculative, but Wotte & Sundberg (2017) suggested that the preservation of originally calcareous shells by secondary phosphatization is rare in this region. This hypothesis seems to explain why molluscs, hyoliths, chancelloriids and echinoderms are preserved only in a few of the investigated sections and samples from the Great Basin, given that all of these taxa are known to have calcareous shells that are not readily recovered in SSF assemblages in the absence of diagenetic mineralization. This observation dovetails nicely with recent investigations into the secondary phosphatization of calcareous shells, which is shown to be highly facies dependent and is tied to sediment starvation and the development of hardgrounds (Pruss *et al.* 2018; Freeman *et al.* 2019; Jacquet *et al.* 2019). It is noteworthy that the fauna of the Mural Formation is also poor in taxonomic diversity of these calcareous fossil groups, although some of the investigated samples yielded a large number of specimens of particular taxa (mainly chancelloriid sclerites or hyoliths; Table 1). However, the suggested hypothesis fails to explain the low diversity of originally phosphatic fossils in the Great Basin compared with the Mural Formation, in particular given that organophosphatic brachiopods are known to be common in the same formations in the Great Basin (brachiopods were not reported by Wotte & Sundberg but see Rowell 1966, 1977; Skovsted & Holmer 2006; Butler *et al.* 2015). Of the taxa reported from the Great Basin by Wotte & Sundberg (2017), four are phosphatic in original composition (25%; Fig. 3A). However, three of these are nominal, co-occurring species of *Microdictyon* that are likely to be synonymous (see Systematic Palaeontology below and discussion in Devaere *et al.* 2019) while seven species from the Mural Formation had phosphatic shells by original composition (48%; Fig. 3C). The fauna from Sonora (Devaere *et al.* 2019) is also to a large extent dominated by secondarily phosphatized calcareous shells while originally

phosphatic shells are represented only by three taxa (15%; Fig. 3B). The fauna is largely derived from three stratigraphically narrow intervals, which reinforces the impression that secondary phosphatization of calcareous shells is rare in western Laurentian sections, perhaps coinciding with generally higher sedimentation rates precluding the development of hardgrounds.

We note that in our material from the Mural Formation, the highest total taxonomic diversity is in samples from storm beds in the middle shale unit, although bioclastic limestones associated with archaeocyathid reefs in the basal limestone unit collectively yielded a higher number of species (Table 1). If only originally phosphatic species are counted, the taxonomic diversity is highest in samples from the basal limestone unit. This pattern indicates that although secondary phosphatization is important for the diversity of recovered SSF assemblages, the distribution of originally phosphatic shells may be more strongly controlled by the environmental preferences of the organisms that secreted the shells. The direct association of a number of the taxa recovered from the Mural Formation with archaeocyathan build-ups mirrors previously reported patterns of distribution of tommotiids and other SSF in and around archaeocyathan build-ups in South Australia (Holmer *et al.* 2008; Skovsted *et al.* 2011, 2015; Betts *et al.* 2016, 2017, 2018). A similar pattern was also reported from the early Cambrian of Mexico and California (McMenamin 1984; Signor & Mount 1986), but not in the recent investigation of SSF faunas from Sonora, Mexico, where samples from archaeocyathid reefs yielded only a low diversity fauna (Devaere *et al.* 2019, fig. 2). However, Pruss *et al.* (2019) recently reported abundant SSF from archaeocyathan build-ups in the Harkless Formation (Dyeran, Cambrian Stage 4) in Nevada, although the fossils were not described in detail. The examples from the Harkless and Mural Formations suggest that specifically targeting sediments associated with archaeocyathan build-ups can increase the sampled taxonomic diversity in lower Cambrian deposits. This has the potential to provide crucial new insights into the evolution of early Cambrian life and new biostratigraphical data to enhance correlation of strata in this time interval.

The SSF fauna from the Mural Formation described here is one of the richest faunas ever discovered in the Cambrian successions of western Laurentia, particularly when its limited stratigraphic range is taken into account. The excellent preservation of many taxa in the fauna reveals new taxonomic and palaeobiological details and further increases its importance. In addition, the discovery that originally organophosphatic fossils such as tommotiids and bradoriids were associated with archaeocyathid reefs may be useful for biostratigraphical resolution in western Laurentia.

Institutional abbreviations. GSC, Geological Survey of Canada, Ottawa; RBCM, Royal BC Museum in Victoria, British Columbia, Canada.

(1997) and Zhang (2007). For other taxa, the terminology largely follows Bengtson *et al.* (1990), Popov & Williams (2000) and Skovsted *et al.* (2017).

SYSTEMATIC PALAEOONTOLOGY

Terminology used in describing the tommotiid *Canadiella filigrana* follows Skovsted *et al.* (2015), while terminology used in descriptions of bradoriid arthropods follows Siveter & Williams

Phylum BRACHIOPODA Duméril, 1806

Remarks. As previously reported (Walcott 1913; Balthasar 2004, 2007, 2008, 2009; Balthasar & Butterfield 2009), brachiopods are common in the Mural Formation, being represented by the problematic taxon *Mickwitzia muralensis* Walcott, 1913, the

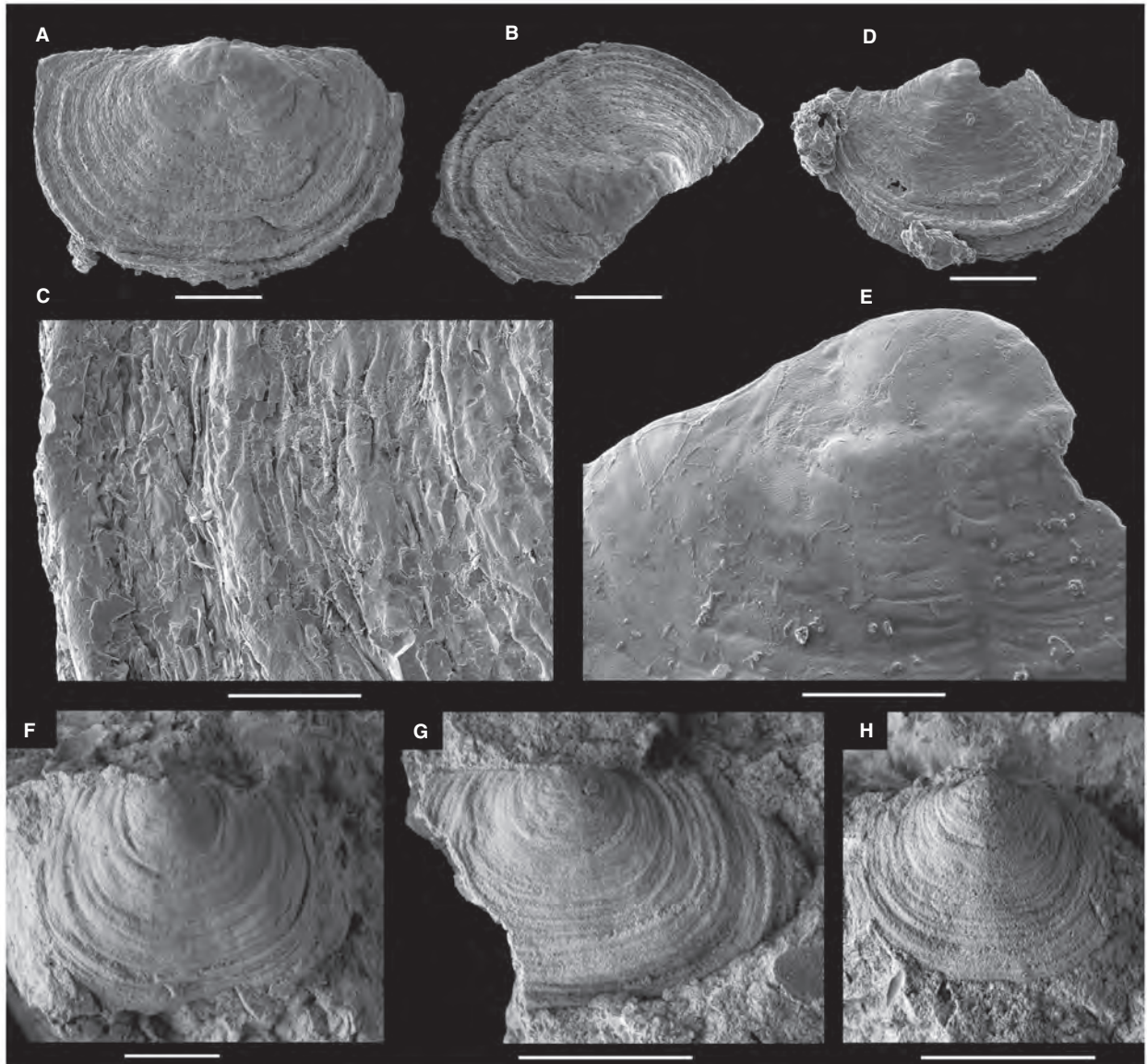


FIG. 4. *Kutorgina perugata* Walcott, 1905 from the lower carbonate unit of the Mural Formation. A–C, complete, phosphatized dorsal valve RBCM P1327 from sample RL-3, Rocky Lake: A, dorsal view; B, oblique anterior view; C, detail of shell ornament. D–E, partial, phosphatized ventral valve RBCM P1328 from sample RL-3, Rocky Lake: D, ventral view; E, detail of partial larval shell. F, dorsal valve in matrix RBCM P1465 from same stratigraphic level as sample MP-12, Mumm Peak. G, dorsal valve in matrix RBCM P1466 from same stratigraphic level as sample MP-12, Mumm Peak. H, ventral valve in matrix RBCM P1464 from same stratigraphic level as sample MP-12, Mumm Peak. Scale bars represent: 250 μ m (A, B, D); 50 μ m (C, E); 5 mm (F–H).

linguliforms *Eoobolus* cf. *triparilis* and *Kyrshabaktella* sp., the obolellid *Mummpikia nuda* (Walcott, 1913) and the problematic soft-shelled *Lingulosacculus nuda* Balthasar & Butterfield, 2009. In the current study, fragmentary specimens of *Mickwitzia muralensis*, *Mummpikia nuda* and *Eoobolus* cf. *triparilis* were found to occur in both the basal limestone member and in the middle shale member of the Mural Formation of both the Mumm Peak and the Rocky Lake sections. In addition, the rynchonelliform *Kutorgina perugata* Walcott, 1905, described below, was found during the present investigation, both as macroscopic specimens in the field and as rare phosphatized specimens in samples from the basal limestone member at both investigated sections.

Subphylum RHYNCHONELLIFORMEA Williams *et al.*, 1996

Class KUTORGINATA Williams *et al.*, 1996

Order KUTORGINIDA Kuhn, 1949

Superfamily KUTORGINOIDEA Schuchert, 1893

Family KUTORGINIDAE Schuchert, 1893

Genus KUTORGINA Billings, 1861

Kutorgina perugata Walcott, 1905

Figure 4

1905 *Kutorgina perugata* Walcott; p. 310.

1912 *Kutorgina perugata* Walcott; Walcott; p. 583, pl. 5, fig. 3a–e.

1977 *Kutorgina perugata* Walcott; Rowell, p. 79, pl. 2, figs 1–3.

?2017 *Kutorgina* cf. *K. perugata* Walcott; Saxén, figs 5.2–5.6.

Material. 15 dorsal and 8 ventral valves in hand specimens from the upper part of the basal limestone unit of the Mural Formation at Mumm Peak section (Sample MP-12), 8 phosphatized valves (7 dorsal and 1 ventral) from the basal part of the basal limestone unit of the Mural Formation at Mumm Peak and Rocky Lake sections (Table 1).

Description. Kutorginid brachiopod with ventribiconvex shell; transversely ovate to sub-rectangular in outline with almost straight posterior margin and marginal apex in both valves. Ventral valve convex with weakly developed fold (Fig 4D, H); apex slightly overhanging the posterior margin; greatest height slightly anterior of apex (Fig. 4H). Dorsal valve almost flat or gently convex with a broad, weakly developed sulcus (Fig. 4A, F, G). External ornament in both valves of concentric rugae of variable amplitude (Fig. 4F–H), often inconsistently developed and sometimes interrupted by prominent nickpoints (Fig. 4D). Micro-ornament of elongate or rhomboidal elevations separated by narrow furrows (Fig. 4C). Ventral larval shell smooth (Fig. 4D). Dorsal larval shell bilobed, c. 280 µm wide (Fig. 4A).

Remarks. The kutorginid shells from the Mural Formation are variable in morphology but appear to be closely comparable to *Kutorgina perugata* Walcott, 1905, which is known from Nevada

(Walcott 1912; Rowell 1977; Saxén 2017). The convex ventral valve is similar in morphology with the highest height just anterior of the apex and a similar ornament of inconsistently developed concentric rugae. The relatively poorly preserved micro-ornament is preserved in one juvenile shell, and appears to be similar to the rhombic elevations described by Rowell from specimens from Nevada (Rowell 1977), although the individual units are more elongate than in the material from Nevada. The material differs from the type species, *K. cingulata* (Billings, 1861), which is known from slightly younger rocks across Laurentia (Cambrian Stage 4 of Nevada, North Greenland, Labrador, Quebec, Vermont; Walcott 1912; Rowell 1977; Popov *et al.* 1997), by the less pronounced concentric ornament, and from *K. reticulata* Poulsen, 1932 from North and North-East Greenland (Cambrian Stage 4; Poulsen 1932; Skovsted & Holmer 2005) by the much less strongly developed median sulcus and fold.

The stratigraphic position of the type material of *Kutorgina perugata* from Nevada is uncertain, but Rowell (1977) suggested that it was probably derived from the *Nevadella* Trilobite Zone of the Middle Poleta Formation. In an unpublished Masters thesis, Saxén (2017) reported similar brachiopod shells (identified as *K. cf. perugata*) from the slightly older Campito Formation (*Fritzaspis* and *Fallotaspis* Zones) at other locations in Nevada. The finding of *K. perugata* in the *Nevadella* Zone of the lower Mural Formation seems to suggest that this species may have been widely distributed in western Laurentia in Cambrian Stage 3.

Occurrence. Barrel Springs section (USNM locality 1v *sensu* Walcott 1912, p. 161), Nevada (probably Middle Poleta Formation; Rowell 1977) and possibly other localities in Esmeralda County (Saxén 2017), as well as the lower Mural Formation at Mumm Peak and Rocky Lake in eastern British Columbia.

Phylum & Class UNCERTAIN

Order TOMMOTIIDA Missarzhevsky, 1970 emend. Matthews, 1973

Family KENNARDIIDAE Laurie, 1986

Genus CANADIELLA nov.

LSID. urn:lsid:zoobank.org:act:D999AE6F-34DF-4EA7-9AB0-EC0CEF6BE5C6

Derivation of name. From Canada, where the fossils have been discovered.

Type species. *Lapworthella filigrana* Conway Morris & Fritz, 1984, monotypic.

Diagnosis. Kennardiid tommotiid with three distinct sclerite types (A, B, C); A sclerites bilaterally symmetrical pyramidal; B sclerites asymmetrical pyramidal with rectangular cross-section; C sclerites laterally compressed cone-shaped with crescentic cross-section; initial shell and first 2–3 growth increments of B and C sclerites narrow, spine shaped with ornament of pustules of two size ranges; adult shell with clear differentiation of co-

marginal ribs and inter-rib grooves and radial plicae concentrated to specific sclerite regions; adult ornament of spine-shaped pustules with superimposed reticulate network in inter-rib grooves; larger, radially arranged pustules on co-marginal ribs form pseudo plicae.

Remarks. Conway Morris & Fritz (1984) described *Lapworthella filigrana*, based on material from the Cassiar Mountains of northern British Columbia. Additional specimens from Mexico and Nevada have also been reported in unpublished PhD theses (Tynan 1981; McMenamin 1984) and illustrated in several other publications (McMenamin 1988, 2001; McMenamin & McMenamin 1990; McMenamin *et al.* 1994). The tommotiid material from the Mural Formation described herein exhibits identical sclerite morphology and shell ornament and clearly belongs to the same species. However, this species differs in important characteristics from the genus *Lapworthella* and is referred here to a new genus, *Canadiella*. These characters include: (1) the development of three distinct sclerite types, one bilaterally symmetrical A sclerite, one asymmetrical B sclerite with rectangular cross-section and one asymmetrical C sclerite with a crescent-shaped cross-section; (2) the presence of lateral plicae on the dorsal surface of C sclerites; and (3) the development of pseudoplicae (formed by radially arranged swellings on co-marginal ribs) in all sclerite types. All these characteristics instead suggest that the new genus belongs to the family Kennardiidae Laurie, 1986, hitherto only known from two genera, *Dailyatia* Bischoff, 1976 and *Kennardia* Laurie, 1986, exclusively occurring in Australia and Antarctica (Bischoff 1976; Laurie 1986; Evans & Rowell 1990; Wrona 2004; Skovsted *et al.* 2015; Betts *et al.* 2019).

The new genus differs from *Kennardia* by the presence of radial plicae and from both *Kennardia* and *Dailyatia* by the presence of minute spine-like pustules in inter-rib grooves as well as the development of the apical spine (elongated sclerite tips) in B and C sclerites, formed by the initial shell and the first 2–3 growth increments. In terms of ornamentation *Canadiella* is most similar to species of *Dailyatia* with subdued radial plicae and clear pseudoplicae (i.e. *D. bacata* Skovsted, Betts, Topper & Brock, 2015 and *D. odyseii* Evans & Rowell, 1990). However, the differences in morphology and shell ornament outlined above clearly distinguish the new genus. Unfortunately, too few complete sclerites are known to be able to determine sclerite variability in general or if specific sclerite subtypes exist. In particular, the A sclerite is poorly represented in the current material, and more complete material will be needed to clearly outline its morphology.

Devaere & Skovsted (2017) recently redescribed *Lapworthella schodackensis* (Lochman, 1956) based on collections from North-East Greenland and noted the presence of tubercles in inter-rib grooves with a superimposed reticulate network that makes this species more similar to *Canadiella* than other species of *Lapworthella*. In addition, the most common sclerite type in *L. schodackensis* is a pyramidal sclerite with a rectangular cross-section (B sclerites), which is comparable to the B sclerites of *Canadiella*. However, *L. schodackensis* lacks sclerites with a crescentic cross-section (C sclerites) as well as radial plicae and pseudoplicae and also exhibits sections of shell with co-marginal striations representing regular intervals of small-scale incremental

growth, which lack counterparts in *Canadiella* or other kennardiids where the external surface was formed by a succession of growth sets (composed of one co-marginal rib and one inter-rib groove formed by a single shell lamina; see description of shell structure and sclerite formation in *Dailyatia* in Skovsted *et al.* 2015, p. 67).

Even though Devaere & Skovsted (2017) demonstrated the presence of distinct sclerite types in *Lapworthella schodackensis* (Lochman, 1956) from Greenland, the genus *Lapworthella* remains one of the least poorly understood of all camenellan tommotiids, despite its apparently global distribution. Widely differing species concepts have been applied to lapworthellids in the past and combined with a high degree of variability in sclerite shape and ornament, this has led to much confusion (Devaere & Skovsted 2017). We anticipate that renewed study of lapworthellid assemblages in the future will lead to significant taxonomic refinement of this problematic fossil group, as exemplified by the present discovery of the kennardiid affinity of '*Lapworthella filigrana*'.

Occurrence. Late early Cambrian (Series 2, Montezuman Stage, *Nevadella* Trilobite Zone) of western Laurentia; northern and eastern British Columbia and western Alberta (Canada), Sonora (Mexico) and possibly eastern California (USA).

Canadiella filigrana (Conway Morris & Fritz, 1984) Figures 5–6

- 1984 *Lapworthella filigrana* Conway Morris & Fritz; p. 199, figs 1–3.
1988 *Lapworthella filigrana* Conway Morris & Fritz; McMenamin, fig. 1.
1990 *Lapworthella filigrana* Conway Morris & Fritz; McMenamin & McMenamin, fig. 4.8.
1994 *Lapworthella filigrana* Conway Morris & Fritz; McMenamin *et al.*, pl. 1, fig. 6.
2001 *Lapworthella filigrana* Conway Morris & Fritz; McMenamin, p.62, pl. 10, figs 1–6, pl. 11, figs 1–5.

Holotype. C sclerite GSC 45356 (Conway Morris & Fritz 1984, fig. 1a–f) from the Rosella Formation (*Nevadella* Zone) of the Cassiar Mountains, northern British Columbia, Canada.

Material. 3 A sclerites, 4 B sclerites, 10 C sclerites and 67 juvenile or fragmentary specimens of uncertain sclerite type. All specimens from the lower part of the basal limestone unit of the Mural Formation at Mumm Peak and Rocky Lake (Table 1).

Diagnosis. As for genus (monotypic).

Description. Kennardiid tommotiid with three distinct sclerite types: bilaterally symmetrical A sclerites (Fig. 5A–E), asymmetrical B sclerites with rectangular cross-section (Fig. 5F–I), and asymmetrical C sclerites with crescentic cross-section (Fig. 6). Apical area of all sclerite types with differentiated growth regimen and ornamentation compared with the adult shell.

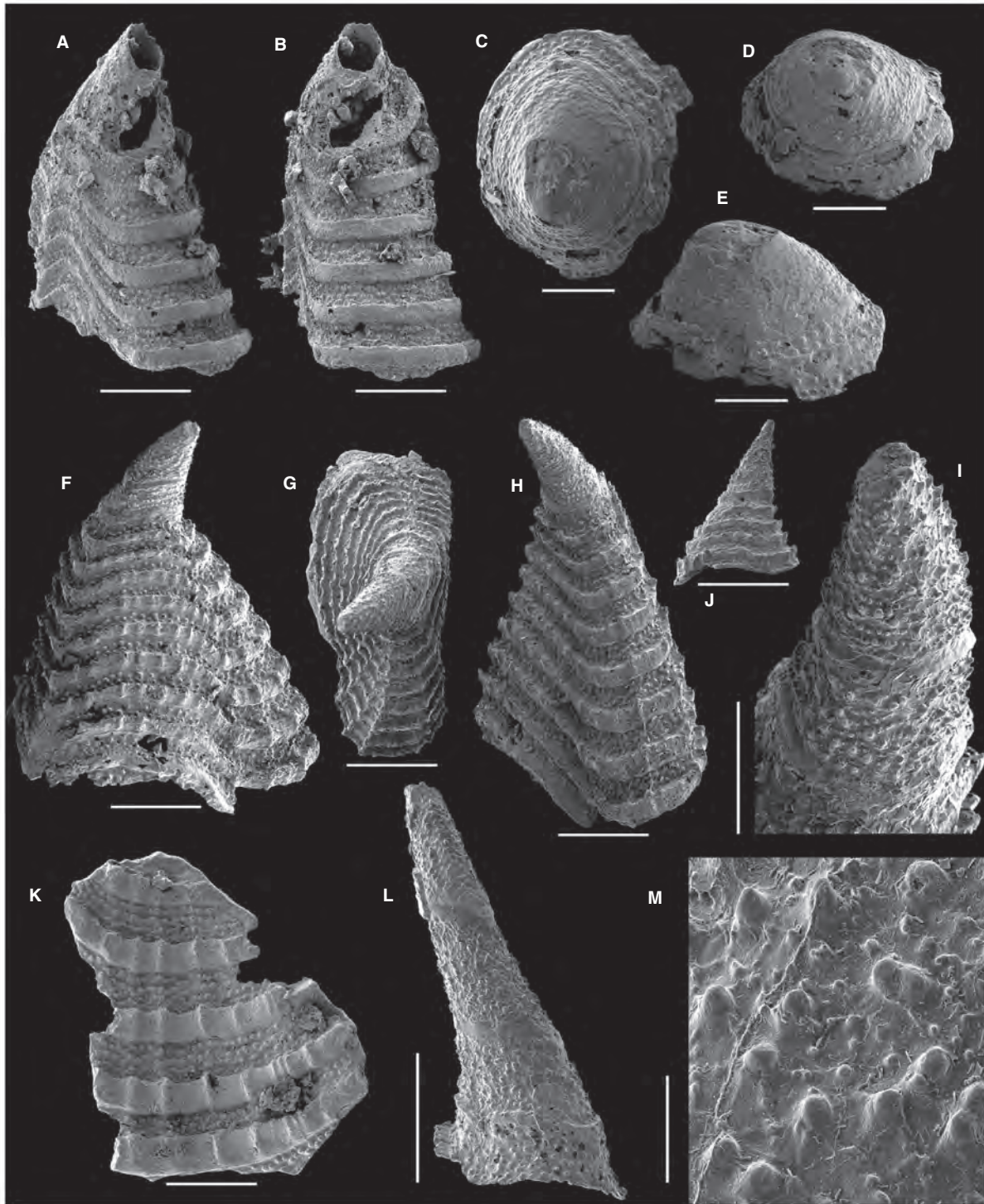


FIG. 5. *Canadiella filigrana* (Conway Morris & Fritz, 1984) from sample RL-3 of the basal limestone unit of the Mural Formation at Rocky Lake; A and B sclerites and shell ornament. A–B, partial A sclerite RBCM P1321: A, oblique posterior view; B, posterior view. C–E, juvenile, cap-shaped sclerite RBCM P1372, possible A sclerite: C, apical view; D, posterior view; E, right lateral view. F–I, complete B sclerite RBCM P1345: F, lateral view of sub-apical field; G, apical view; H, oblique posterior view; I, detail of apical part with ornament. J, complete juvenile B(?) sclerite RBCM P1347 in lateral view. K, shell fragment (uncertain sclerite type) RBCM P1322 showing adult ornament with pustulose inter-rib areas and co-marginal ribs with elongate pustules forming pseudoplicae. L–M, juvenile, tube-shaped specimen (uncertain sclerite type) RBCM P1348: L, lateral view; M, detail of juvenile ornament with pustules in two size ranges. Scale bars represent: 500 μm (A–B, F–K); 100 μm (C–E, I); 200 μm (L); 20 μm (M).

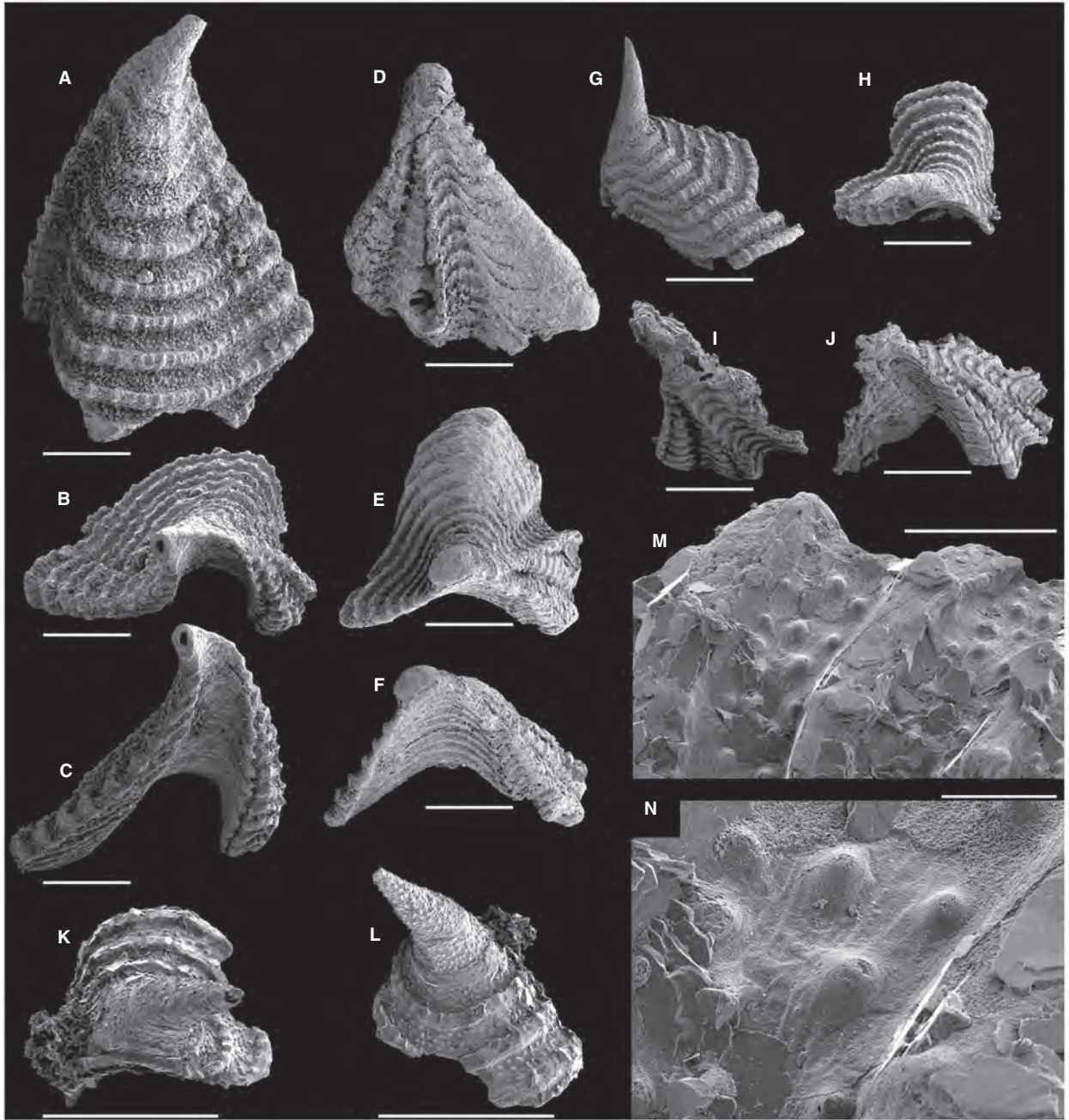


FIG. 6. *Canadiella filigrana* (Conway Morris & Fritz, 1984) the basal limestone unit of the Mural Formation at Rocky Lake; C sclerites and shell ornament. A–C, large dextral C sclerite RBCM P1352 from sample RL-3: A, dorsal surface; B, apical view; C, ventral surface. D–F, large dextral C sclerite RBCM P1320 from sample RL-3: D, lateral view of dorsal surface; E, apical view; F, ventral surface. G–H, small dextral C sclerite RBCM P1341 from sample RL-6: G, oblique dorsal view; H, apical view. I–J, small dextral C sclerite RBCM P1343 from sample RL-6 with multiple radial plicae: I, oblique dorsal view; J, ventral surface. K–N, small sinistral C sclerite RBCM P1346 from sample RL-3: K, apical view; L, oblique dorsal view; M, detail of shell ornament with pustulose inter-rib grooves and smooth co-marginal ribs; N, detail of shell ornament showing subdued reticulate micro-ornament superimposed on pustules in inter-rib grooves. Scale bars represent: 500 μm (A–L); 100 μm (M); 25 μm (N).

The A sclerite is represented only by one fragmentary sclerite preserving mainly the posterior and left lateral fields (Fig. 5A, B) in addition to two possible small specimens representing early growth stages (Fig. 5C–E). The larger specimen has a rectangular cross-section, elongated along the anterior–posterior axis and appears to be bilaterally symmetrical although the first 2–3 growth increments are slightly displaced compared with later growth along the posterior margin (Fig. 5B). The apex is missing but appears to have been slightly inclined over the posterior field, which is developed into a gently domed deltoid (Fig. 5A). No clearly defined posterolateral plications are present but the lateral field is delimited anteriorly by a well-developed anterolateral plication (Fig. 5B). The co-marginal ribs on the lateral field exhibit a distinct apical bend. The apex of the small specimens is a dome-shaped structure with an oval outline, elongated along the anterior–posterior axis and the first two co-marginal ribs replicate this shape (Fig. 5C).

The B sclerite is represented by several well-preserved specimens representing different growth stages. The sclerites are pyramidal with an elongate rectangular cross-section and a moderate helical twist with the apex inclined over one of the wide lateral fields (Fig. 5G). The anterior and posterior fields are narrow and bounded by weakly expressed radial plicae (Fig. 5G). The sub-apical lateral field is divided into two regions by a median fold: a concave posterolateral sector with several radial plicae and a convex anterolateral sector with only pseudoplicae (Fig. 5F). The supra-apical lateral field is straight or gently convex and with only pseudoplicae (Fig. 5H).

The asymmetrical C sclerites are more numerous than the A and B sclerites and exhibit a pyramidal shape with a crescentic cross-section (Fig. 6B, E, H, K). The inflated dorsal surface is divided into a central, strongly convex zone and two narrow lateral zones by weakly expressed folds (Fig. 6A, E, H). The central zone is typically ornamented by multiple pseudoplicae, increasing in number with sclerite size (Fig. 6A, H). The proximal zone (over which the apex curves) has weakly expressed pseudoplicae (Fig. 6B). The distal zone is characterized by 2–5, strongly developed and closely set radial plicae (Fig. 6E, J). Co-marginal ribs in the folds between plicae are curved towards the apex. The ventral surface is moderately to strongly concave with co-marginal ribs curved towards the apex but without radial ornament (Fig. 6C, F, J).

Both B and C sclerites exhibit distinct apical spines, elongated spine-shaped structures consisting of a tubular initial shell and the 2–3 first co-marginal growth sets (Figs 5F, J, L, 6A, G, L). After the formation of this apical spine the rate of expansion increases dramatically to initiate the adult morphology (sometimes with a single growth set of intermediate expansion; Fig. 5L).

The shell ornament consists of growth sets of a deeply concave inter-rib groove and a convex, flat-topped rib (Figs 5A, K, 6M). Growth sets are separated by a narrow slit at the base of the ad-apertural slope of the rib (Fig. 6N). The surface of inter-rib grooves is ornamented by irregularly distributed rounded pustules with a weakly expressed superimposed reticulate pattern (Fig. 6M, N). Co-marginal ribs are smooth or with large pustules, elongated in the direction of growth and aligned across successive growth sets to form pseudoplicae (Fig. 5K). The initial shell and first growth sets of B and C sclerites are

ornamented by two orders of pustules: large pustules conforming in size and arrangement with the pustules of inter-ribs of the adult shell, and a second set of smaller pustules that are more or less irregularly arranged on, and between the larger pustules (Fig. 5I, L, M). The ornament of the initial shell of A sclerites has a single order of densely set pustules but adult ornament conforms closely with the adult ornament of B and C sclerites.

Remarks. The sclerite morphology and ornamentation of the tomotioid sclerites from the Mural Formation is essentially identical to that of sclerites from the Cassiar Mountains described as *Lapworthella filigrana* by Conway Morris & Fritz (1984), and the respective specimens are considered conspecific. The only notable difference is the more regular hexagonal pattern formed by the smaller pustules on the initial shell in the Cassiar Mountain specimens (compare Fig. 5I, M to Conway Morris & Fritz 1984, figs 2g, 3a). Closely comparable specimens from the Puerto Blanco Formation of Sonora, Mexico were also described and illustrated in an unpublished PhD thesis by McMenamin (1984, pp. 85–86, pls 10–11) and were later refigured by McMenamin and coworkers in a series of publications (McMenamin 1988, 2001; McMenamin & McMenamin 1990; McMenamin *et al.* 1994). Possibly conspecific specimens from the White–Inyo Mountains of California were illustrated under the name ‘Genus I, sp. A’ in a previous, unpublished PhD thesis by Tynan (1981; pp. 123–125, pl. 6, figs 12, 13, 17) and the species was included in a list of taxa recovered from the lower part of the Poleta Formation in this area by Signor & Mount (1986). The specimens from California were reportedly silicified (Tynan 1981, p. 124) but the illustrations are poor and it has not been possible to confirm their association with *Canadiella filigrana*. The material from both Mexico and California was recovered from strata of the *Nevadella* Zone (McMenamin 1984; Signor & Mount 1986; McMenamin *et al.* 1994). Consequently, it appears that *Canadiella filigrana* is a widespread tomotioid taxon in Cambrian Stage 3 strata of western Laurentia (Montezuma) with a distribution from northern Mexico to northern British Columbia.

Conway Morris & Fritz (1984) recognized two sclerite types in *Canadiella filigrana* from the Cassiar Mountain: one ‘A’ sclerite with polygonal cross-section and one ‘B’ sclerite with rapidly expanding aperture and a central ‘saddle’, and McMenamin (1984, 2001) followed this sclerite designation. According to our interpretation, the ‘A’ sclerite of Conway Morris & Fritz (1984) is equivalent to the B sclerites in kennardiids (Laurie 1986; Skovsted *et al.* 2015), and sclerites of this morphology are consequently referred to as B sclerites herein. The ‘B’ sclerite of Conway Morris & Fritz (1984) is equivalent to the kennardiid C sclerites and this designation is followed herein. In addition to these sclerite types we also recognize a bilaterally symmetrical sclerite morph in *C. filigrana*, equivalent to the A sclerites of kennardiids. The material of the A sclerite is, however, limited to fragmentary specimens and its morphology is uncertain. The smaller possible A-type sclerites in the collection represent a low dome-shaped initial shell and this contrasts with the spiniform initial shell of the associated B and C sclerites. A similar difference in initial shell morphology between A and B + C sclerites was documented in *Dailyatia* (Skovsted *et al.* 2015, figs 56–58).

In the Mural Formation, *Canadiella filigrana* occurs in shallow carbonate facies associated with archaeocyathan reefs and a similar sedimentological setting is likely for the occurrence of the species in the Cassiar Mountains (Conway Morris & Fritz 1984; Kobluk 1984). In the White–Inyo Mountains of California the taxon is also reported from strata that yielded a rich archaeocyathan fauna (Signor & Mount 1986, fig. 2) and the same applies to the specimens from Mexico (subunit 3 of the Puerto Blanco Formation; McMenamin 1984, 2001). The association of *Canadiella* with archaeocyaths in shallow water carbonates throughout its range in western Laurentia mirrors the distribution of the best known kennardiid tommotiid, *Dailyatia*, in the Arrowie and Stansbury Basins of South Australia (Skovsted *et al.* 2015). In South Australia, *Dailyatia* is present in a wide range of carbonate environments but is most common in direct association with archaeocyathans and the genus is notably absent from siliciclastic rocks of the same basins, including the exceptionally preserved Emu Bay biota (Skovsted *et al.* 2015).

Occurrence. Lower Mural Formation at Mumm Peak, Alberta, and Rocky Lake in eastern British Columbia, the Lower Rosella Formation of the Cassiar Mountains of northern British Columbia, the Puerto Blanco Formation of Sonora, Mexico and possibly the lower Poleta Formation of the White–Inyo region, California.

Phylum EUARTHROPODA Lankester, 1904

Class UNCERTAIN

Order BRADORIIDA Raymond, 1935

Family HIPPONICHARIONIDAE Sylvester-Bradley, 1961

Genus HIPPONICHARION Matthew, 1886

Hipponicharion perforata sp. nov.

Figure 7

LSID. urn:lsid:zoobank.org:act:42FE344A-1A84-4F8D-AEBC-5E3DF07AD6F9

Derivation of name. From *perforare* (Latin) in reference to the finely perforate or pitted shell surface.

Holotype. Articulated valve RBCM P1411 (Fig. 7C) from sample MP15, lower part of middle shale unit, Mural Formation, Mumm Peak Section, Alberta, Canada.

Material. Holotype and 29 additional specimens, including valve fragments from sample MP15, lower part of middle shale unit, Mural Formation, Mumm Peak Section (Table 1).

Diagnosis. Species of *Hipponicharion* with elongate, postplete subtriangular shell with strongly marked angular anterodorsal curve; three strongly developed and clearly separated lobes; anterior and posterior lobes long, high and narrow; well developed, transversely elongate central lobe located close to dorsal margin; ornament of fine, circular perforations or pits separated by low nodular ridges.

Description. Equivalved, rounded triangular shell, postplete in lateral outline with length greater than height. Greatest length coincides with anterodorsal curve and crest of anterior lobe (Fig. 7A, F). Hinge line almost straight. Three distinct and well developed nodes: anterior lobe straight, strongly elevated, reaching from anterodorsal corner to close to the ventral margin at about mid-valve, separated from flattened lateral margin by a clearly demarcated furrow (Fig. 7A, C, F); posterior lobe straight, strongly elevated and slightly shorter than anterior lobe, reaching from posterolateral corner to close to the ventral margin but clearly separated from anterior lobe (Fig. 7A, C, F); central lobe transversely elongated oval in outline, located close to dorsal margin, with greatest width roughly parallel to the margin (Fig. 7C, D, F). Anterodorsal curve strongly marked and angular, well separated from anterior lobe (Fig. 7A, C). Shell ornament of fine pits or perforations separated by uneven, nodular ribs, which may be developed as discrete pustules on the anterior and posterior nodes (Fig. 7D, E). A well-defined circular area situated between anterior and central lobes lacking perforations, exhibits much finer, anastomosing ridges forming a fingerprint-like pattern (Fig. 7E).

A single articulated specimen (Fig. 7G, H) with the left valve partly broken away, exhibits internal structures in the form of a sheet-like inner lamella, partly covering the internal cavities of the prominent anterior and posterior nodes and an elongate, tapering and posteriorly curving and structure emanating from the anterocentral part of the right-hand shell. These structures are partly covered by an anastomosing network of filamentous structures.

Remarks. *Hipponicharion perforata* differs from the type species, *H. eos* from Avalonia and Baltica by the more strongly postplete valve outline, the widely separated anterior and posterior lobes and the transverse elongation of the central node, as well as in the pitted ornament (Siveter & Williams 1997; Dies Álvarez *et al.* 2008). The new species is similar to *H. geyeri* Hinz-Schallreuter, 1993 from Morocco in the punctate ornament of the shell. However, the pits of *H. geyeri* are much larger and more widely dispersed on an otherwise smooth shell surface (Hinz-Schallreuter 1993, pl. 12, fig. 1), which is different from the ornament of fine pits separated by nodular ridges in *H. perforata* (Fig. 7E). The species also differs from *H. geyeri* in the marked anterodorsal curve and the much longer posterior lobe. *Hipponicharion perforata* also differs from *H. australis* Topper *et al.*, 2007 from South Australia in the higher anterior and posterior lobes, the presence of a well-defined central lobe and the clearly marked anterolateral curve as well as in the pitted surface ornament. The new species differs from *H. skovstedii* Peel, 2017a from North Greenland in the longer valve profile (length greater than width) and the more equally developed anterior and posterior nodes. The species also differs from three morphologically similar and possibly synonymous species (*H. hispanicum*, *H. taidalensis* and *H. elickii*) reported from the lower Cambrian of Morocco, Spain and Germany by Gozalo & Hinz-Schallreuter (2002) in the subtriangular valve outline with marked anterodorsal curve and the dorsal position of the strongly developed central node.

The marked change in surface ornament from pits separated by nodular ridges to much finer, anastomosing ridges, in a

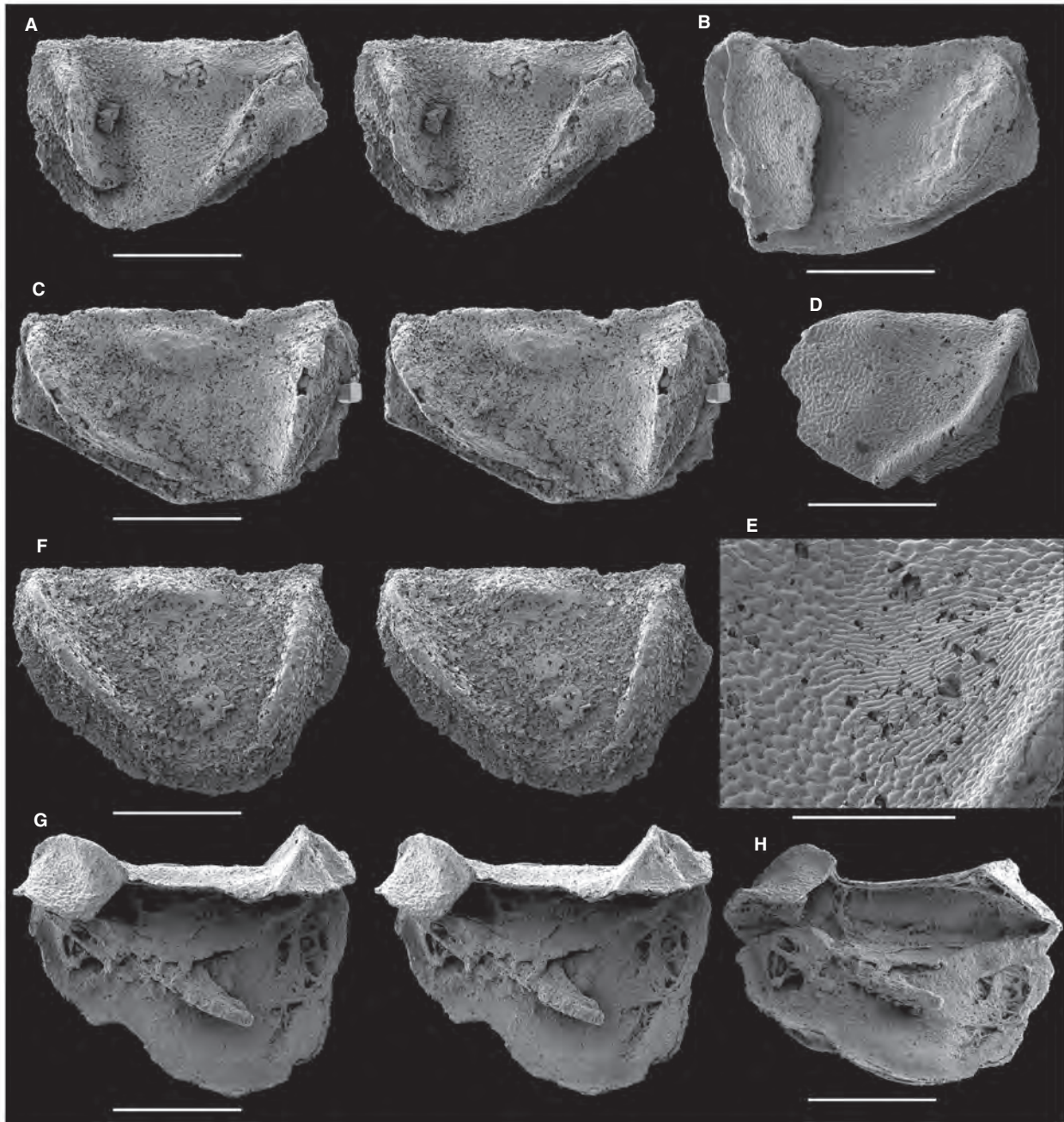


FIG. 7. Bradoriid *Hipponicharion perforata* sp. nov. from sample MP-15 of the middle shale unit of the Mural Formation at Mumm Peak. A, right valve of complete specimen RBCM P1409; stereo image pair. B, right valve of complete specimen RBCM P1417 showing lateral deformation of lobes. C, left valve of complete specimen RBCM P1411 (holotype); stereo image pair. D–E, incomplete right valve RBCM P1418: D, lateral view; E, detail of ornament including possible eye spot close to anterior lobe. F, left valve of complete RBCM P1414, uncompressed specimen; stereo image pair. G–H, complete specimen RBCM P1421 with left valve removed showing bacterial growth and possible remains of soft parts in shell interior: G, lateral view, stereo image pair; H, oblique ventral view. Scale bars represent: 500 μm (A–D, F–H); 200 μm (E).

subcircular zone between the anterior and central nodes (Fig. 7E), mirrors the position of a smooth zone behind the anterior spine in *Pseudobeyrichona taurata* described below (Fig. 8C). Similar anterodorsal zones of reduced or unusual ornaments are present in some other hipponicharionid taxa,

such as *Hipponicharion geyeri* from Morocco (Hinz-Schallreuter 1993, pl. 12, fig. 1), *H. skovstedii* from North Greenland (Peel 2017a, fig. 4G) and *Parahoulongdongella bashanensis* (Shu, 1990) from South China (Zhang 2007, pl. 18, fig. 2). While the function of the zone of unusual ornament in hipponicharionids is

uncertain, we note that the position of the zone close to the anterodorsal corner of the valve is reminiscent of the position of eye spots in recent and fossil ostracods (Tanaka 2005). Shu *et al.* (1999) interpreted the small, rounded anterior (anterodorsal) lobes of the kunmingellid bradoriid *Kunmingella* Huo, 1956 from the Chengjiang Lagerstätte of South China as specific eye lobes. The extensive anterior lobes of hipponicharionid bradoriids do not conform closely with the eye lobes of *Kunmingella*, but the interpretation of the anterodorsal region of unusual ornament as possible eye spots, suggests that these bradoriids also had well-developed eyesight.

The internal structures exposed in a single bivalved specimen with left valve partly broken away (Fig. 7G, H) may represent strongly degraded phosphatized soft parts, including the internal lamella and a large posteriorly projecting limb as well as other unclear structures in the anterior portion of the shell. However, these features are partly covered by filamentous structures presumably representing a phosphatized bacterial cover, which limits biological interpretations. This specimen, together with all other specimens of *Hipponicharion perforata*, were recovered from a limestone layer close to the base of the middle shale unit of the Mural Formation.

Occurrence. Lower part of middle shale unit, Mural Formation at Mumm Peak in eastern British Columbia.

Genus PSEUDOBEYRICHONA Shu, 1990

Remarks. The hipponicharionid genus *Pseudobeyrichona* was proposed by Shu (1990) to accommodate *P. longquanxiensis* (Cui *et al.*, 1987) from the lower Cambrian (Stages 3–4) Shuijingtuo Formation of Chongqing Municipality, South China (see discussion in Zhang 2007 and Streng & Geyer 2019). The genus differs from other hipponicharionid and beyrichonid genera by the strongly developed, spine-like, anterior lobe, the reduced posterior lobe and in lacking a median lobe (Zhang 2007). *Pseudobeyrichona monile* Streng & Geyer, 2019 from Germany was recently reported as the first occurrence of the genus outside China (Streng & Geyer 2019). This occurrence was used as a biogeographic signal, as evidence for a mixed ‘eastern’ and ‘western’ fauna in Germany (Streng & Geyer 2019). However, the occurrence of the new species *P. taurata* in the Mural Formation appears to indicate a more or less cosmopolitan distribution of this genus in Cambrian Stage 2, as already demonstrated for other hipponicharionid genera such as *Hipponicharion* and *Albrunnicola* (Topper *et al.* 2007; Peel 2017a). It is also noteworthy that ‘Bradoriid species 2’ from the Shabakhty Formation of Kazakhstan (Dzik 2003, text-fig. 8B, C) has a prominent anterior node developed into a short spine and may also represent a species of *Pseudobeyrichona*, further extending the range of the genus.

Pseudobeyrichona taurata sp. nov.

Figure 8A–D

?2019 Bradoriid sp.; Devaere *et al.*, p. 41, fig. 20.

LSID. urn:lsid:zoobank.org:act:CDFC4C70-B819-4CB8-9452-73FBFE76F203

Derivation of name. From Latin *Taurus*, bull. In reference to the prominent anterior spine on the valves.

Holotype. Complete left valve RBCM 1375 (Fig. 8A–C) from sample MP-11, upper part of basal limestone unit of the Mural Formation, Mumm Peak section, Alberta, Canada.

Material. Holotype and 26 additional fragmentary specimens from sample MP-11, upper part of basal limestone unit of the Mural Formation, Mumm Peak section (Table 1).

Diagnosis. Equivalved, amplete or weakly postplete hipponicharionid with moderately inflated subtriangular valves; prominent anterior lobe drawn out into an anterodorsally projecting spine with lenticular cross-section; posterior lobe weakly developed; straight hinge line; wide marginal rim; shell ornamented by a network of shallow, circular pits developed into anastomosing furrows on anterior spine.

Description. Equivalved bradoriid with rounded triangular shell, amplete or slightly postplete in lateral outline with straight hinge-line (Fig. 8A). Greatest length coincides with angular anterodorsal curve. Anterior and posterior nodes are confluent with a uniform ventral swelling (Fig. 8B). Anterior node inflated and drawn out in the anterodorsal direction, forming a long, flattened spine (Fig. 8A, D). Posterior node weakly developed and restricted to dorsal half of valve (Fig. 8A). Marginal rim wide, with greatest width posteriorly and slightly narrower on anterior side, separated from valve by a prominent furrow (Fig. 8A, B). Shell ornamented by network of irregularly distributed fine pits developed as anastomosing furrows on anterior spine. A circular region at the base of the anterior lobe lacks pits (Fig. 8C).

Remarks. A single bradoriid valve from the Puerto Blanco Formation of Mexico (Bradoriid sp.; Devaere *et al.* 2019) is closely comparable to *Pseudobeyrichona taurata* in valve shape, spine morphology and the width of the marginal rim and may belong to the same species. However, the described valve ornament of the Mexican specimen differs by the presence of pustules around the anterior spine and, until further material is described, the taxonomic identity is considered questionable. *Pseudobeyrichona taurata* differs from the type species and from *P. monile* Streng & Geyer, 2019 by the less strongly postplete valve profile and the longer, anterodorsally directed spine of the anterior lobe as well as by the weaker posterior lobe (compare Fig. 8A, D with Zhang 2007, pl. 18, figs 9–19 and with Streng & Geyer 2019, fig. 8). From *P. monile* the species is also distinguished by the lack of crenulation on the admarginal ridge. The surface sculpture of fine anastomosing furrows and shallow circular pits also differs from the more effaced sculpture of *P. longquanxiensis*. The new species differs from the otherwise similar ‘Bradoriid species 2’ from the Shabakhty Formation of Kazakhstan (Dzik 2003, text-fig. 8B, C), which may also represent a species of *Pseudobeyrichona*, by the triangular rather than rounded valve profile and the more forward-directed inclination of

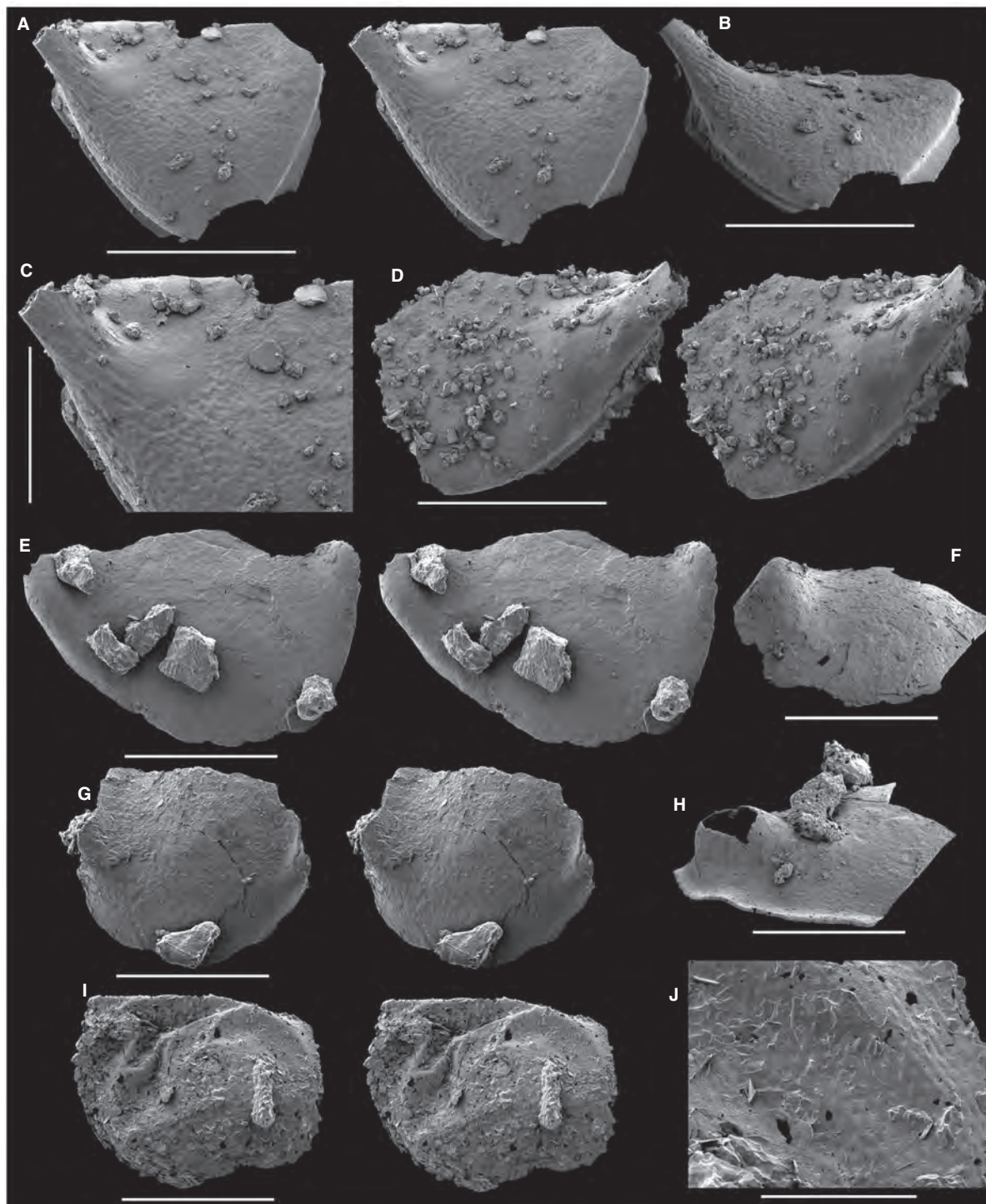


FIG. 8. Bradoriids from the basal limestone unit of the Mural Formation. A–D, *Pseudobeyrichona taurata* sp. nov. A–C, right valve RBCM P1375 (holotype) from sample MP-11, Mumm Peak: A, lateral view, stereo image pair; B, oblique ventral view; C, detail of posterior spine and shell ornament. D, incomplete left(?) valve RBCM P1381 from sample MP-11, Mumm Peak in lateral view, stereo image pair. E–H, *Beyrichona* sp.: E, left valve RBCM P1360 from sample RL-3, Rocky Lake, stereo image pair; F, valve fragment RBCM P1359 from sample RL-3, Rocky Lake, showing low, circular (anterior?) lobe; G, right valve fragment RBCM P1356 from sample RL-3, Rocky Lake, stereo image pair; H, oblique view of valve fragment RBCM P1362 from sample RL-5, Rocky Lake, with circular (anterior?) lobe. I–J, *Liangshanella* sp.: I, left valve of complete, slightly deformed specimen RBCM P1373 from sample RL-3, Rocky Lake: I, stereo image pair; J, detail of shell ornament from posterodorsal surface. Scale bars represent: 1 mm (A, B, D, E, G, I); 500 µm (C, F, H); 100 µm (J).

the anterior spine. *Hipponicharion skovstedii* from Kap Troedsson Formation of North Greenland is a spinose hipponicharionid from the lower Cambrian of Laurentia (Peel 2017a, fig. 4) but *P. taurata* differs from this species by the postplete valve outline, the forwardly directed anterior spine and the weakly developed posterior lobe.

The circular zone lacking the characteristic pitted surface sculpture at the dorsal side of the base of the prominent anterior spine in the best preserved specimen of *Pseudobeyrichona taurata* is reminiscent of the possible eye spot present in *Hipponicharion perforata* described above and may have had a similar function.

Occurrence. Lower Mural Formation at Mumm Peak in eastern British Columbia, possibly the Puerto Blanco Formation of Cerro Rajón, Sonora, Mexico.

Family BEYRICHONIDAE Ulrich & Bassler, 1931

Genus BEYRICHONA Matthew, 1886

Beyrichona sp.

Figure 8E–H

Material. 20 specimens from the base of the basal limestone unit of the Mural Formation, Rocky Lake section (Table 1).

Description. Beyrichonid bradoriid with smooth shell surface. Valve outline uncertain but appear to be elongated subtriangular with evenly inflated valve centre and two relatively small but well-constrained and equally developed anterior and posterior nodes (Fig. 8E, G). The nodes appear to be restricted to dorsal half of the valve (Fig. 8G, H). Marginal rim narrow with poorly defined furrow, slightly uneven, indicating a possible gape adjacent to anterior lobe (Fig. 8H).

Remarks. All available specimens of this species are fragmentary, mainly preserving the central part of the valves but sometimes with the anterior and posterior nodes preserved. However, the specimens are clearly different from the other bradoriid species in the Mural Formation. The nodes appear to be restricted to the upper half of the valves, which differs from the situation in *Hipponicharion perforata* where the nodes extend almost from the dorsal to the ventral edge. The presence of two almost equally developed low, rounded nodes also differs from the spine-like anterior and subdued posterior node of *Pseudobeyrichona taurata* as well as from *Liangshanella* sp., which lack distinct lobes.

The fragmentary specimens are most similar to the hipponicharionid genus *Albrunnicola* Martinsson, 1979 and the beyrichonid *Beyrichona* Matthew, 1886. *Albrunnicola* is best known from the lower Cambrian of South Australia (Skovsted *et al.* 2006; Topper *et al.* 2011a) and South China (Zhang 2007) but *Albrunnicola* sp. has also been reported from the Bastion Formation of North-East Greenland (Skovsted 2006b; Peel 2017a). However, *Albrunnicola* have typically very reduced lobes, particularly the posterior lobe, and the specimens from the Mural Formation seem to have more strongly pronounced lobes of more or less equal development, which makes them more closely comparable to *Beyrichona*. This genus is common in Avalonia (Siveter & Williams 1997; Williams & Siveter

1998) but also occurs in Baltica (Dies Álvarez *et al.* 2008) as well as Kazakhstan (Melnikova *et al.* 1997). Recently, *Beyrichona avganna* Peel, 2017a was described from the lower Cambrian of North Greenland (Peel 2017a) and this species is similar to the specimens from the Mural Formation in lobation and general outline, suggesting that they may be congeneric. However, the fragmentary nature of the Mural specimens precludes detailed comparison and hence they are consequently left in open nomenclature.

Occurrence. Basal part of the basal limestone unit of the Mural Formation at Rocky Lake (sample RL3), eastern British Columbia, Canada.

Family SVEALUTIDAE Öpik, 1968

Genus LIANGSHANELLA Huo, 1956

Liangshanella sp.

Figure 8I, J

Material. 1 specimen from sample MP-15, lower part of middle shale unit of the Mural Formation, Mumm Peak section. 1 specimen from sample RL-3, basal part of basal limestone unit of the Mural Formation, Mumm Peak section (Table 1).

Description. Two isolated, articulated but partly deformed specimens. Sub-rounded, postplete shell with straight dorsal hinge, a likewise straight posterodorsal margin and obtuse anterodorsal corner with a rounded anterodorsal curve (Fig. 8I). The ventral margin is not well-preserved and the shell is partly compressed with irregular folds in the anterior part. The shell surface preserves a fine reticulate pattern (Fig. 8J).

Remarks. These specimens appear to represent a postplete bradoriid with rounded valves with a distinctive straight posterodorsal margin but without lobes. This morphology resembles the cosmopolitan svealutid genus *Liangshanella* Huo, 1956, particularly the widely dispersed species *Liangshanella sayutinae* (Melnikova, 1988). This species is known from the Trans-Baikal Region in Russia (Melnikova 1988; Melnikova *et al.* 1997), South Australia (Betts *et al.* 2017) and North-East Greenland (Skovsted 2006b). The shells of *L. sayutinae* are usually smooth or ornamented by fine wrinkles (Skovsted 2006b; Betts *et al.* 2017) but reticulate ornaments have been reported in rare specimens from South Australia (Betts *et al.* 2017) and Greenland (Skovsted 2006b). The incomplete nature of the material precludes definite species determination and it is left in open nomenclature.

Occurrence. Lower–middle Mural Formation, Cambrian Stage 3, Alberta and British Columbia, Canada.

Phylum UNCERTAIN

Class HYOLITHA Marek, 1963

Remarks. In the Mural Formation, hyoliths are relatively common in acid residues from both the basal limestone and middle

shale units but are almost exclusively represented by internal moulds of the conical conchs. At least two species are present. Indeterminable hyolithids, represented by internal moulds with a subtriangular cross-section are common throughout the

investigated sections (Fig. 9G–J). Based on differences in rate of expansion of the conchs, more than one species may be represented but better preserved material will be required to confirm this. Gently tapering and curved orthothecid conchs with a

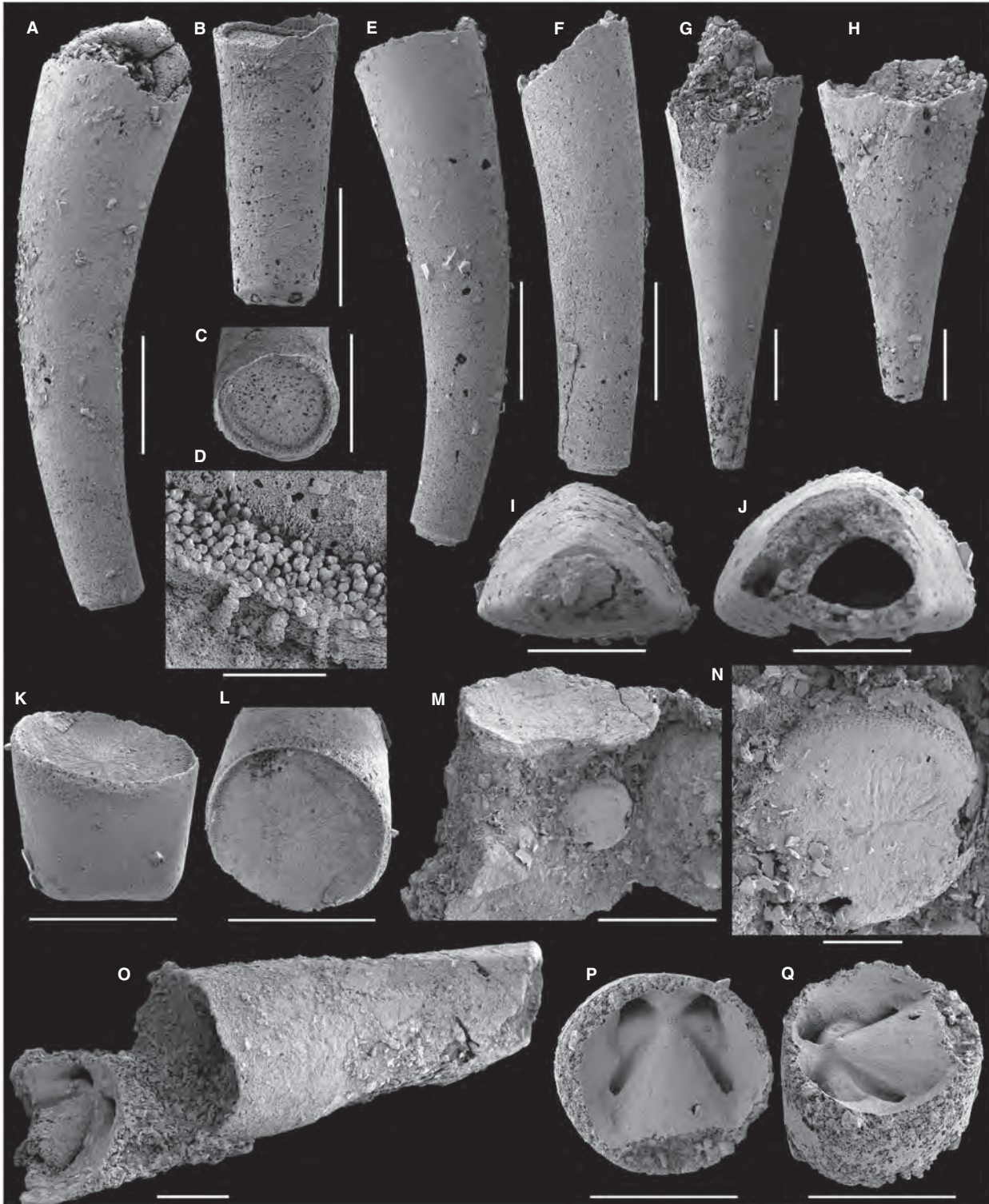


FIG. 9. Hyoliths from the Mural Formation. All specimens except O from the middle shale unit at Mumm Peak. A–F, *Cupitheca* sp.: A, lateral view of internal mould of large conch RBCM P1433 from sample MP-15, with open aperture (with cancelloriid sclerite lodged inside aperture). B–D, internal mould of conch section RBCM P1436 from sample MP-15, bound by septa at either end: B, lateral view; C, oblique view of septum at widest end; D, detail of B showing tubules along margin of septal constriction. E, lateral view of internal mould of large conch RBCM P1432 from sample MP-15, with open aperture. F, lateral view of internal mould of large conch RBCM P1435 from sample MP-15, with open aperture. K–L, internal mould of conch section RBCM P1441 from sample MP-16, bound by two septa: K, lateral view; L, oblique view of widest end showing star-shaped pattern on mould of septum. M–N, external shell of small specimen RBCM P1457 from sample MP-17, adhering to sediment flake: M, overview; N, detail of septum showing tubules along septal constriction and star-shaped pattern on septal wall. O, internal view of large conch RBCM P1422 from sample RL-1, basal limestone unit at Rocky Lake, with obliquely oriented mould of operculum. P–Q, internal mould of conch section and operculum RBCM P1442 from sample MP-16: P, plan view of operculum; Q, oblique lateral view. G–J, Hyolithid sp. indet.: G, internal mould of conch RBCM P1428 from sample MP-15, viewed from dorsum; H, internal mould of conch RBCM P1444 from sample MP-16, viewed from dorsum; I, internal mould of conch RBCM P1446 from sample MP-16, in apical view; J, internal mould of conch RBCM P1431 from sample MP-15, in apical view. Scale bars represent: 500 μm (A–C, E–M, O–Q); 50 μm (D); 100 μm (N).

circular cross-section may also represent more than one species. The majority of specimens are terminated by a convex transverse wall separated from the conch wall by a countersunk rim, suggesting the genus *Cupitheca* as described below. Two internal moulds of a hyolith operculum with circular outline may represent the same taxon.

Order ORTHOTHECIDA Marek, 1966

Family CUPITHECIDAE Duan, 1984

Genus CUPITHECA Duan in Xing *et al.*, 1984

Cupitheca sp.

Figure 9A–E, K–Q

Material. 134 specimens (132 conchs and 2 opercula) from samples spanning the basal limestone and middle shale units of the Mural Formation at Mumm Peak, Rocky Lake and Dezaiko Range sections (Table 1).

Description. Elongate internal moulds of gently curved hyolith conchs with circular cross-section. Specimens are up to 2.5 mm long (Fig. 9A) and rate of expansion is 8° . Many specimens terminated apically by a rounded transverse wall with countersunk rim (Fig. 9A–F). The margins of the rim often ornamented by short, densely spaced tubercles or rod-like units (Fig. 9D). In a single small specimen, almost completely embedded in matrix, the phosphatized shell is preserved with the countersunk rim ornamented by fine circular pits and a well preserved star-like pattern on the transverse wall (Fig. 9M, N). Weakly impressed star-like impressions are also preserved in some internal moulds (Fig. 9K, L).

Internal moulds of subcircular opercula with deep impressions of spine-like cardinal processes with rounded triangular base (Fig. 9O–Q). Inclined, rod-like clavicles inserted behind the cardinal processes and forming an angle of *c.* 80° (Fig. 9P), enclosing the rounded apex and a dome-shaped triangular area. The area of the mould between cardinal processes and clavicles slightly depressed, indicating that this surface was elevated in the original shell (Fig. 9Q). Internal surface ornamented by small pustules, particularly on the rounded apex and the depressed area between cardinal processes and clavicles (Fig. 9Q).

Remarks. The specimens of *Cupitheca* sp. from the Mural Formation are almost exclusively internal moulds of the conch. Only a single small and fragmentary specimen with the outer shell preserved was found. Two internal moulds of opercula were found in direct association with fragmentary conchs, and the circular cross-section indicates that these specimens belong to the same species. Many specimens probably represent the living chamber of the hyolith terminated by the characteristic mould of a convex septum with countersunk rim (Fig. 9A, E, F), while others represent tube segments that were released during the growth of the organism (compare discussion in Bengtson *et al.* 1990). However, some specimens (see Fig. 9B) seem to preserve moulds of septa at both terminal ends and these specimens presumably represent intermediate stages in tube development with multiple septa. Such specimens with multiple septa have previously been described in material of *Cupitheca* cf. *C. mira* from Sonora, Mexico (Devaere *et al.* 2019, fig. 12). Previously, characteristics of the outer surface sculpture of the conch have been used as the base for taxonomy of *Cupitheca* (Bengtson *et al.* 1990; Skovsted *et al.* 2016), although Sun *et al.* (2018) recently suggested that the nature of the operculum may be of greater significance. In either case, the specimens from the Mural Formation are difficult to determine precisely and are left in open nomenclature. However, we note that the perpendicular walls terminating the specimens often preserve an uneven star-shaped impression of fine wrinkles. Such ornaments have previously been described from *C. convexa* Sun, Malinky, Zhu & Huang, 2018 from the Manto Formation of North China (Cambrian Stage 5; Sun *et al.* 2018). It is difficult to compare the morphology of the associated opercula because the preservation of the specimens in the Mantuo Formation (partly compressed specimens on bedding surfaces; Sun *et al.* 2018) is very different from the material described here. However, the presence of short, rod-like clavicles behind the cardinal processes (Fig. 9O–Q) makes the Mural Formation species more similar to *C. convexa* (Sun *et al.* 2018, fig. 6) than to the otherwise better known *C. holocyclata* from South Australia, North China and Greenland, which is known to have cardinal processes but no clavicles (Skovsted *et al.* 2016). Comparison of the Mural specimens to recently described specimens of *Cupitheca* aff. *C. mira* from the Puerto Blanco Formation of Sonora, Mexico (Devaere *et al.* 2019) is

difficult due to differences in preservation and the fact that the operculum is not known in the Mexican material.

Phylum, Class & Order UNCERTAIN
Family CHANCELLORIIDAE Walcott, 1920
Figure 10A–D

Material. 276 sclerites and disarticulated rays (101 specimens referable to *Chancelloria* sp., 103 specimens to *Archiasterella* sp., 72 specimens to *Allonnia* sp.) from samples spanning the basal limestone and middle shale units at Mumm Peak, Rocky Lake and Dezaiko Range sections.

Remarks. Chancelloriid sclerites are among the most common fossils in the investigated material but most specimens are fragmentary internal moulds, often representing single, isolated rays, and are consequently difficult to identify. However, at least three different genera are represented by rare, better-preserved specimens. Star-shaped sclerites with a rosette of lateral rays surrounding a central, vertical ray (6 + 1, 7 + 1) are referable to *Chancelloria* Walcott, 1920 (Fig. 10A). Other sclerites with four rays, one of which is strongly recurved over the rest (4 + 0), represent *Archiasterella* Sdzuy, 1969 (Fig. 10B), while sclerites with four or five sub-equal rays bent away from the basal surface (4 + 0, 5 + 0) are more closely comparable to *Allonnia* Doré & Reid, 1965 (Fig. 10C, D). Although much of chancelloriid taxonomy is based on articulated specimens from Burgess Shale-type Lagerstätten, sclerites of all three genera are common components in SSF assemblages of early and middle Cambrian age worldwide and a number of sclerite-based species of each genus are recognized. The Mural Formation has not yet yielded any articulated chancelloriid specimens and, although recent investigations have shown that it may be possible to correctly classify disarticulated sclerites (given large enough samples; Moore *et al.* 2014, 2019; Devaere *et al.* 2019; Yun *et al.* 2019), we leave the disarticulated sclerites in open nomenclature herein. However, we note that the distribution of sclerites referable to *Allonnia* sp. and *Archiasterella* sp. appear to be stratigraphically controlled, with specimens of *Archiasterella* sp. restricted to the basal limestone unit at Mumm Peak section and specimens of *Allonnia* in the middle shale unit of the Mumm Peak section.

Phylum ECHINODERMATA Bruguière, 1791
INDET. echinoderm ossicles
Figure 10E–H

Material. 556 specimens from samples spanning the basal limestone and middle shale units at Mumm Peak, Rocky Lake and Dezaiko Range sections (Table 1).

Remarks. Disarticulated echinoderm ossicles are common in samples from the basal limestone and middle shale units of the Mural Formation. The majority of specimens are preserved as secondary phosphatic infill of the cavities in the echinoderm stereome structure (Fig. 10F). The morphology of the ossicles varies considerably but most are subcircular or polygonal in outline with smooth or scalloped surfaces (Fig. 10E, G, H). The generalized nature of the majority of specimens precludes identification to any particular echinoderm type.

?Phylum AGMATA Yochelson, 1977
Family SALTERELLIDAE Walcott, 1886

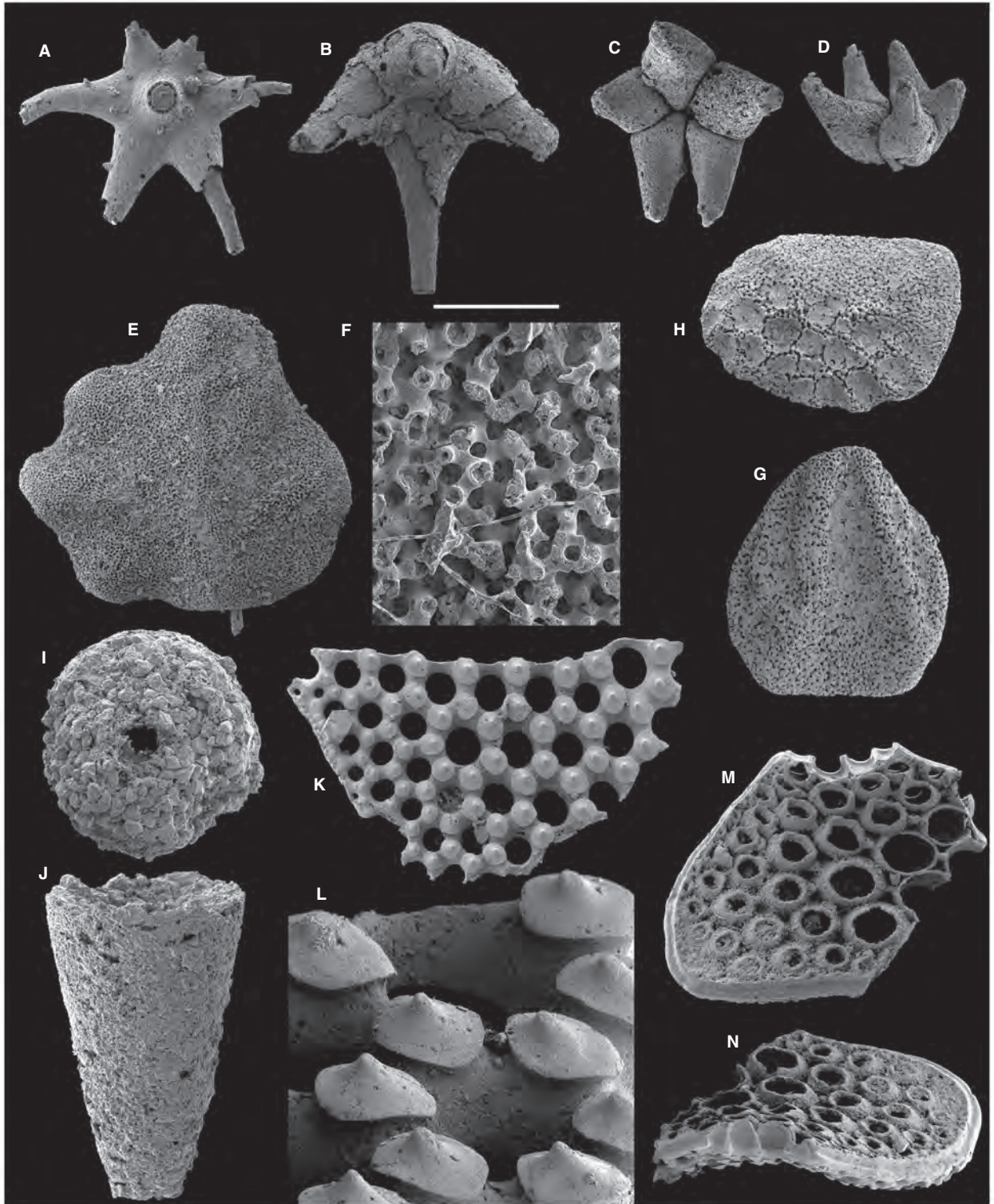
Genus VOLBORTHELLA Schmidt, 1888
Volborthella tenuis Schmidt, 1888
Figure 10I–J

Material. 21 specimens from the basal limestone unit of Mumm Peak and Rocky Lake sections (Table 1).

Remarks. The problematic agmatans (*sensu* Yochelson 1977) *Volborthella* Schmidt, 1888 and *Salterella* Billings, 1861 form cone-shaped structures of agglutinated sediment grains that may be locally common in the early Cambrian of western Laurentia (Fritz & Yochelson 1988; Hagadorn & Waggoner 2002). *Volborthella* and a third genus, *Ellisell* Peel & Berg-Madsen, 1988, also occur in Baltica (Schmidt 1888; Peel & Berg-Madsen 1988). Yochelson (1977) proposed that agmatans are so different from other fossil and extant taxa that they should be classified in a separate phylum. However, agmatans are known only from the Cambrian and the validity of a phylum-level grouping with only extinct members is uncertain.

Agmatan genera are mainly separated from each other by structural differences. In *Salterella* the agglutinated deposits are

FIG. 10. Small shelly fossils from the Mural Formation. All specimens except I–J from Mumm Peak. A, *Chancelloria* sp., partly phosphatized RBCM P1447 from sample MP-16, middle shale unit, star-shaped sclerite (6 + 1). B, *Archiasterella* sp., partly phosphatized sclerite RBCM P1404 from sample MP-15 middle shale unit, with recurved vertical ray (4 + 0). C–D, *Allonnia* sp., internal mould of star-shaped sclerite RBCM P1408 from sample MP-15 middle shale unit, with all rays recurved (5 + 0): C, dorsal view; D, oblique lateral view. E–H, phosphatized echinoderm sclerites. E–F, RBCM P1385 from sample MP-14, basal limestone unit; F, detail of phosphatized stereome microstructure. G, RBCM P1454 from sample MP-16 middle shale unit. H, RBCM P1450 from sample MP-16 middle shale unit. I–J, *Volborthella tenuis* Schmidt, 1888: I, transverse section through agglutinated tube RBCM P1463 from sample RL-2, Rocky Lake, showing central lumen; J, lateral view of semi-complete specimen RBCM P1460 from sample RL-2, Rocky Lake. K–N, *Microdictyon* sp. K–L, partial sclerite RBCM P1391 from sample MP-12, basal limestone unit; K, in external view; L, detail of exterior in oblique view showing morphology of node-crests. M–N, partial sclerite RBCM P1388 from sample MP-3, basal limestone unit: M, interior view; N, oblique lateral view showing inward projections around perforations in sclerite. Scale bars represent: 500 μ m (A–E, G–H, K, M–N); 50 μ m (F); 1 mm (I); 750 μ m (J); 100 μ m (L).



sandwiched between narrow calcareous layers inside a mineralized calcareous shell (Yochelson 1977; Peel & Yochelson 1982; Skovsted 2003; Peel 2017b), while *Volborthella* seems to lack calcareous components (Hagadorn & Waggoner 2002; Yochelson & Kisselev 2003). Agglutinated cone-shaped fossils occur in

samples from both the basal limestone member and in the middle shale member of the Mural Formation (Fig. 10I, J). The fossils have a uniform angle of divergence (c. 30°), a smooth outer surface (Fig. 10J) and a narrow central canal (Fig. 10I). This morphology indicates that the material belongs to the genus

Volborthella given that the outer surface of the agglutinated deposits in *Salterella* typically exhibit uneven furrows representing the insertion of calcareous laminae, even when the outer shell is dissolved (Peel 2017b). Consequently, we identify the material at hand as belonging to *V. tenuis* Schmidt, 1888, the only known species of *Volborthella*. Further support for this identification comes from the stratigraphic position in the *Nevadella* Zone (Montezuman). Fritz & Yochelson (1988) discussed the occurrence of *Salterella* in western Laurentia and ascertained that this genus is restricted to the medial portion of the overlying *Bonnina–Olenellus* Zone (Dyeran), while *V. tenuis* is known to range into much older Cambrian strata (Hagadorn & Waggoner 2002).

Stem group ONYCHOPHORA

Family EOCONCHARIIDAE Hao & Shu, 1987

Genus MICRODICTYON Bengtson *et al.*, 1986

Microdictyon sp.

Figure 10K–N

Material. 4 fragmentary sclerites from the upper part of the basal limestone unit at Mumm Peak section (Table 1).

Remarks. Phosphatic, net-like specimens represent sclerites of the lobopodian *Microdictyon* Bengtson *et al.*, 1986. All recovered specimens are fragmentary (Fig. 10K, M) but preserve the node morphology (Fig. 10L) and the basal structure of the perforations in relatively good detail (Fig. 10N). The specimens match the description of *Microdictyon* cf. *rhomboidale*, described from similarly aged rocks of the Mackenzie Mountains of north-western Canada (Bengtson *et al.* 1986). However, extensive individual and ontogenetic variability has been demonstrated for *Microdictyon* assemblages (Topper *et al.* 2011b; Pan *et al.* 2018), and in view of the fragmentary nature and limited number of specimens, specific determination of the material from the Mural Formation is not possible. Devaere *et al.* (2019, p. 43) recently included fragments from Sonora, Mexico of similar morphology in a species referred to as '*Microdictyon multicavus* (McMenamin, 1984)'. However, given that the original reference (McMenamin 1984) was an unpublished PhD thesis, this name was invalid under the rules of the ICZN until it was reintroduced by McMenamin (2001).

Wotte & Sundberg (2017) reported three different species of *Microdictyon* from the Montezuma Range of Nevada. All three species are represented by one or two fragmentary specimens that occur in a single sample derived from the Montenegro Member of the Campito Formation (*Fallotaspis* trilobite Zone; Wotte & Sundberg 2017). All illustrated specimens are small, abraded and appear to lack clear diagnostic features (Wotte & Sundberg 2017, fig. 8.24–32). In our view all the reported specimens probably belong to a single species and the reported differences probably represent different degrees of abrasion. The specimens are not sufficiently preserved to allow a detailed comparison with the material from western Laurentia illustrated by Bengtson *et al.* (1986) or herein, and should be

referred to *Microdictyon* sp., although Devaere *et al.* (2019) suggested that all the different node morphologies present in these specimens can be accommodated in *M. multicavus*. In addition, strongly corroded perforated fragments were referred by Wotte & Sundberg (2017) to *Microdictyon* sp., but, as noted by Devaere *et al.* (2019), these specimens probably represent phosphatized shell fragments and are better referred to as Fossil indet.

Phylum MOLLUSCA Cuvier, 1797

Class HELCIONELLOIDA Peel, 1991

INDET. helcionelloid mollusc

Figure 11A–D

Material. 23 fragmentary specimens from the basal limestone unit of the Mural Formation at Rocky Lake section (Table 1).

Remarks. Helcionelloid molluscs are represented by a small number of imperfectly preserved silicified shells. The specimens represent a single planispiral (Fig. 11A, D), openly coiled (up to *c.* 180°) and laterally flattened species (Fig. 11C). The specimens exhibit prominent, widely spaced and acutely pointed co-marginal ribs that appear to be continuous across the dorsum (Fig. 11B, C). Areas between the co-marginal ribs are ornamented by fine longitudinal striations (Fig. 11D). In gross morphology the specimens may resemble internal moulds of *Davidonia* Parkhaev, 2017, which are common in sediments from Cambrian Series 2 in Mexico, Greenland and the Taconic allochthons (Landing & Bartowski 1996; Skovsted 2004; Devaere *et al.* 2019), but the corrugated sculpture of these moulds reflects internal ribs in this genus, which are not reflected on the external shell surface (Bengtson *et al.* 1990; Gravestock *et al.* 2001; Skovsted 2004). Instead, the specimens from the Mural Formation are reminiscent of helcionelloid genera such as *Oelandiella* Vostokova, 1962, *Latuocheella*, Cobbold, 1921 and *Capitoconus* Skovsted, 2004, which have external ribs on the shell. However, due to the poor preservation, precise determination is not possible based on the current material.

Phylum & Class UNCERTAIN

Order HYOLITHELMINTHIDA Fisher, 1962

Family HYOLITHELLIDAE Walcott, 1886

Genus HYOLITHELLUS Billings, 1872

Hyalithellus sp.

Figure 11E–H

Material. 388 specimens from samples spanning the basal limestone and middle shale units of the Mural Formation at Mumm Peak and Rocky Lake sections (Table 1).

Remarks. Narrow phosphatic tubes with a circular cross-section and external ornamentation of regular annulations occur in the

basal limestone and middle shale units. The average rate of expansion is 3.1° and on average the tubes exhibit 24 annulations per mm with individual annulations variable from c. 25 to 75 μm in width. The tubes are straight (Fig. 11E) or gently curved (Fig. 11F) and may bend up to 90° (Fig. 11H). The circular cross-section and finely annulate ornament facilitates identification of the material as belonging to the genus *Hyolithellus* Billings, 1872. However, due to the high degree of variability, tubes of *Hyolithellus* are difficult to identify to species based only on the morphology of individual specimens (Skovsted & Peel 2011; Devaere *et al.* 2019). Although the specimens from the Mural Formation are numerous and generally well-preserved, the variability is also great. A number of specimens with an extremely slow rate of expansion and occasional sharp bends or contorted morphologies (Fig. 11H) are comparable to the species *H. filiformis* Bengtson *in* Bengtson *et al.*, 1990, previously known only from South Australia (Bengtson *et al.* 1990). However, straight specimens of otherwise comparable morphology and more rapidly expanding tubes (Fig. 11E), more closely comparable to the common Laurentian taxon *H. micans* Billings, 1872 (Skovsted & Peel 2011) are also present. Consequently, the available material from the Mural

Formation is left under open nomenclature, pending further study.

The narrow end of several specimens exhibits a flaring aperture representing a basal increase in diameter of c. 60% (Fig. 11F–G). This flaring, funnel-shaped base is reminiscent of holdfasts in other fossil and recent mineralized tubes (Vinn 2006), and may suggest that tubes were formed by an epibiont, attaching to hard substrates.

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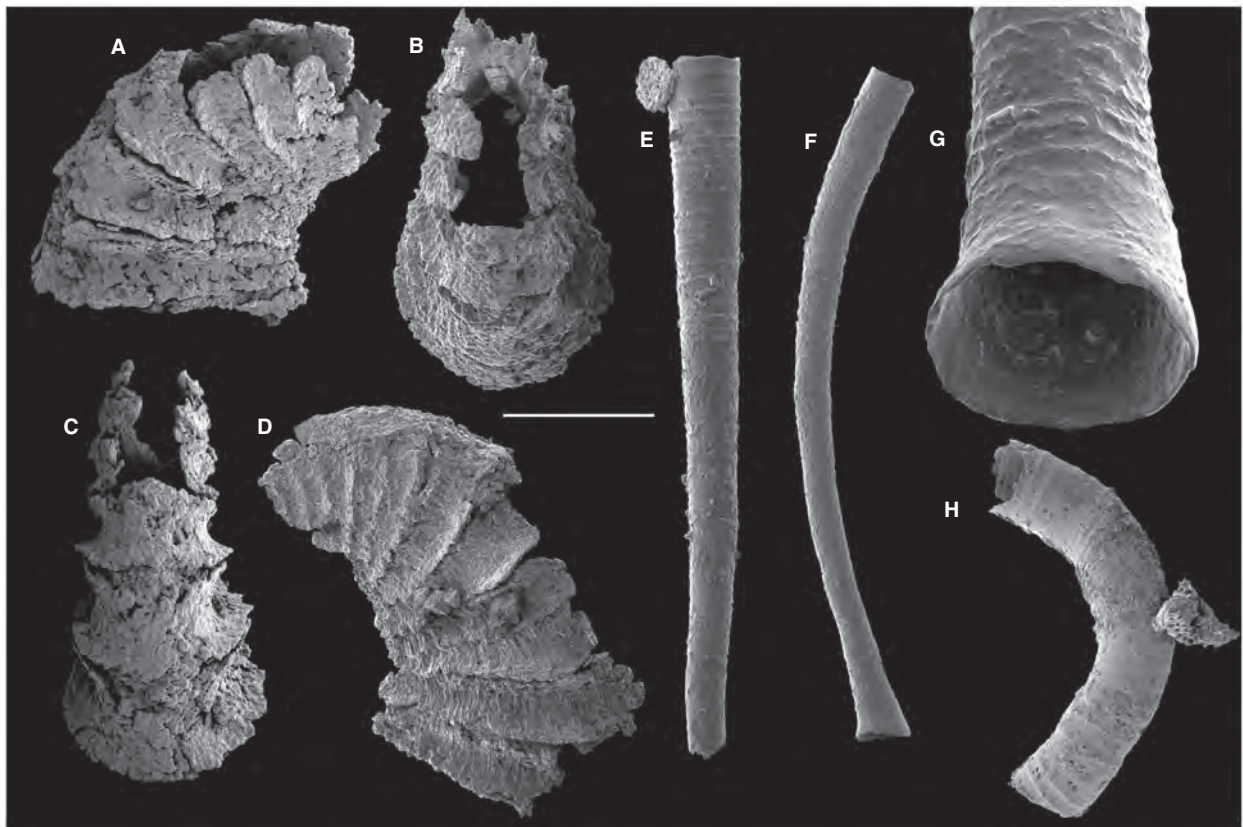


FIG. 11. Small shelly fossils from the basal limestone unit of the Mural Formation at Rocky Lake. A–D, Helcionelloid mollusc. A–C, partially silicified specimen RBCM P1366 from sample RL-6: A, lateral view; B, view from dorsum; C, view from supra-apical side. D, lateral view of partially silicified specimen RBCM P1365 from sample RL-6. E–H, *Hyolithellus* sp. E, lateral view of long, straight specimen RBCM P1329 from sample RL-3, Rocky Lake, with even rate of expansion. F–G, long, bent specimen RBCM P1330 from sample RL-3, with possible holdfast: F, lateral view; G, oblique view of possible holdfast. H, tube fragment RBCM P1333 from sample RL-3, with 90° bend. Scale bar represents: 500 μm (A–F, H); 100 μm (G).

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