Bradoriids from the middle Cambrian ‘thin’ Stephen Formation at Odaray Mountain, Canadian Rocky Mountains

Hanna Andersson

Two new species of Cambrian bradoriid arthropods have been found in the ‘thin’ Stephen Formation, Odaray Mountain, Canada; the hipponicharionid *Flumenoglacies michaeli* n. sp. and the comptalutid *Phasoia stephenensis* n. sp. This paper includes the description and illustrations of these species as well as two undetermined species from the same locality. *Phasoia stephenensis* n. sp. is the first *Phasoia* reported from Laurentia and *Flumenoglacies michaeli* n. sp. belongs to the new genus *Flumenoglacies* recently described by Peel & Streng (in press) from Greenland.

Uppsala universitet, Institutionen för geovetenskaper
Kandidatexamen i Geovetenskap, 180 hp
Självständigt arbete i geovetenskap, 15 hp
Tryckt hos Institutionen för geovetenskaper
Geotryckeriet, Uppsala universitet, Uppsala, 2014.

Självständigt arbete Nr 93

Bradoriids from the middle Cambrian ‘thin’ Stephen Formation at Odaray Mountain, Canadian Rocky Mountains

Hanna Andersson

Självständigt arbete Nr 93

Bradoriids from the middle Cambrian ‘thin’ Stephen Formation at Odaray Mountain, Canadian Rocky Mountains

Hanna Andersson

Handledare: Michael Streng

Abstract

Two new species of Cambrian bradoriid arthropods have been found in the ‘thin’ Stephen Formation, Odaray Mountain, Canada; the hipponicharionid *Flumenoglacies michaeli* n. sp. and the comptalutid *Phasoia stephenensis* n. sp. This paper includes the description and illustrations of these species as well as two undetermined species from the same locality. *Phasoia stephenensis* n. sp. is the first *Phasoia* reported from Laurentia and *Flumenoglacies michaeli* n. sp. belongs to the new genus *Flumenoglacies* recently described by Peel & Streng (in press) from Greenland.

In the discussion previous reports of the genus *Phasoia* are ordered chronologically and a migration path from Gondwana to Laurentia is suggested. However, more information on the stratigraphic and regional distribution of this taxon is needed to support this theory since *Phasoia* is so far only known from Australia, South China and now North America.

The ornamentation of *Phasoia stephenensis* n. sp. and *Flumenoglacies michaeli* n. sp. is discussed and compared with the ornamentation of the hipponicharion *Pseudobeyrichona longquanxiensis* (Cui 1987), the svealutid *Tsunyiella* Zhang (1974) and the cambriid *Petrianna fulmenata* Siveter (1995). It is suggested that it might be remnants of a respiratory system.

Sammanfattning

Två arter av den kambriska artropoden *Bradoriida* har hittats i ”the ’thin’ Stephen Formation”, Odaray Mountain, Kanada; hipponicharioniden *Flumenoglacies michaeli* n. sp. och comptalutiden *Phasoia stephenensis* n. sp. I den här rapporten beskrivs och illustreras de nämnda arterna samt två andra exemplar av *Bradoriida* från samma lokal vars arttillhörighet inte fastslås här. *Phasoia stephenensis* n. sp. är den första arten av genuset *Phasoia* som har raporterats från Laurentia och *Flumenoglacies michaeli* n. sp. hör till det nya genuset *Flumenoglacies* som har upprättats av Peel & Streng (i tryck) från Grönland.

I diskussionen ordnas tidigare rapporter av genuset *Phasoia* kronologiskt och en migrationsväg från Gondwana till Laurentia föreslås. Men för att kunna styrka denna hypotes behöver fler exemplar av detta genus studeras globalt eftersom det hittills endast har rapporterats från Australien, södra Kina och nu Nordamerika.

Ornamentet hos *Phasoia stephenensis* n. sp. och *Flumenoglacies michaeli* n. sp. diskuteras och jämförs med ornamentet hos hipponicharioniden *Pseudobeyrichona longquanxiensis* (Cui 1987), svealutiden *Tsunyiella* Zhang (1974) och cambriiden *Petrianna fulmenata* Siveter (1995). Det föreslås att ornamentet kan vara en kvarlämning av ett andningssystem.

Table of content

Introduction

Bradoriids are a group of arthropods that were most abundant in the early Cambrian seas and disappeared later during the early Ordovician (e.g., Shu & Chen, 1994; Shu *et al.*, 1999; Vannier *et al.*, 2005; Williams *et al.*, 2007). There are several known families of bradoriids of which most belong to Bradoriida sensu stricto; the Cambriidae, Kunmingellidae, Hipponicharionidae, Beyrichonidae, Bradoriidae, Comptalutidae and Svealutidae. The head shields of these families have some features in common and may therefore represent a monophyletic group. There are also bradoriids that have features that may suggest an ostracod affinity, they are referred to as Bradoriida sensu lato (Williams *et al.*, 2007).

In general bradoriids are very small (length c. 1-17.5 mm) and have a bivalved head shield, the so called carapace, which is commonly composed of phosphate (Siveter & Williams, 1997). Studies have been made on phosphatization in soft tissues (Briggs, 2003; Lin *et al.*, 2011 and references therein; Wilby & Briggs, 1997) but weather the phosphate is a primary or secondary composition of the carapace of bradoriids is still in debate. It has been suggested that it was flexible and therefor un-mineralized during life (Vannier *et al.*, 2005). This is supported by Streng et al. suggesting that the many different shape variations in studied specimens is due to deformation of a flexible material during burial (Streng *et al.*, 2008 and references therein).

In the past the bradoriids were classified as ostracods with a close relation to phosphatocopids, these also being classified as ostracods (Sylvester-Bradley, 1961; Müller, 1964; Jones & McKenzie, 1980). Öpik (1968) questioned this affinity, and more recently it has come to light that even though the bradoriids and phosphatocopids might have some morphological affinities to ostracods, they do not lie on the primitive stem line of Crustacea and are therefore not related to ostracods. This was proposed by Hou *et al.* (1996) when studying preserved soft parts of the bradoriid *Kunmingella* from the lower Cambrian 'Chengjiang' Lagerstätte, which is the only known bradoriid with preserved soft parts. These findings also led Hou *et al.* to the conclusion that there is no close relation between bradoriids and phosphatocopids, but that the phosphatocopids might lie close to the crown-group Crustaecea. Soft parts of phosphatocopids have been studied further strengthening the idea that bradoriids and phosphatocopids are not closely related to each other (e.g., Maas & Waloszek, 2005). This question is still very much in debate, the exact affinity of bradoriids is not completely determined.

The bradoriids were widely distributed almost all over the world during the Cambrian. Figure 1 shows a map of the paleocontinents during the Cambrian. Reports have been made from many areas. To name a few, bradoriids have been found in North America (e.g., Siveter & Williams, 1997) and Greenland (Siveter et al., 1995; Peel & Streng, in press) which both belonged to Laurentia. Also several places in Gondwana; Australia (e.g., Hinz-Schallreuter, 1993a; Topper *et al.*, 2011; Betts *et al.*, 2014), East Antarctica (Rode *et al.*, 2003), Spain (e.g., Gozalo *et al.*, 2004), Morocco (Hinz-Schallreuter, 1993b) and Russia (e.g., Melnikova *et al.*, 1997). In Baltoscandica (e.g., Hinz-Schallreuter, 1993a; Topper *et al.*, 2013) and in China, which during Cambrian was separated into North and South China and situated west of Gondwana (e.g., Guangbi & Yong, 1988; Hou et al., 1996; Hou et al., 2002; Shu, 1990 a, b; Zhang, 1987).

Until 2007 no findings had been made in the sub-Saharan Africa, India, the Middle East and South America (Williams *et al.*, 2007). Though, more recently, bradoriids have been found in both India (Collette *et al.*, 2011) and in the Middle East i.e., Jordan (Elicki, 2012) and Iran (Ghobadi-Pour *et al.*, 2007).

Since the bradoriids were so dispersed they might have occupied areas in South America and sub-Saharan Africa as well but more research needs to be done in these areas. Shu & Chen (1994) suggested that the paleocontinents were divided in to two realms; the cold-to-cool-water European realm that was located near the South Pole (Baltica, North Africa and Avalonia) and the low latitude warm-water realm (Asia, Australia, North America and Antarctica). In their interpretation, South Africa and South America are not part of either of these realms (for further discussion see Shu & Chen, 1994). The study of the specimens from the 'thin' Stephen Formation in this report strengthens that North America was part of the warm-water realm since one of the found genera hasn't been reported in North America before but in other localities of this realm.

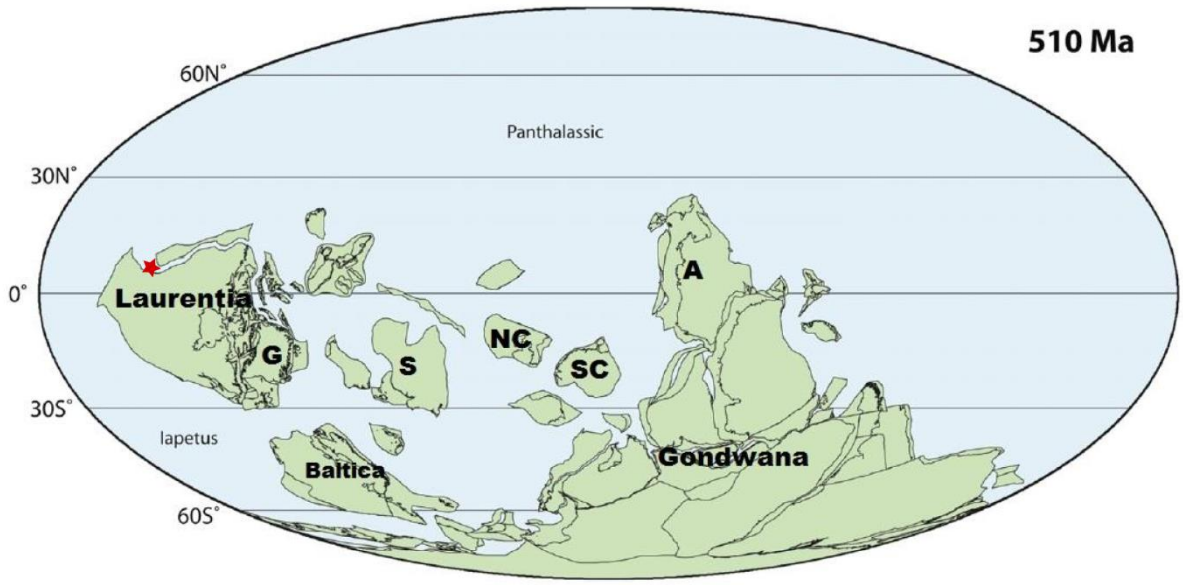

Figure 1. The location of the paleocontinents during the middle Cambrian, 510 Ma. The red star is the location of the study area, the Stephen formation, at this point in time. G; Greenland, S; Siberia, NC; North China, SC; South China, A; Australia. Map modified after Torsvik and Cocks, 2013 fig. 2.8. For more details on locations of individual countries, see Torsvik and Cocks 2013.

The large variety of carapace morphologies suggests that the bradoriids occupied a wide range of ecological niches, they could have been anything from benthic to pelagic (Shu *et al.*, 1999; Williams *et al.*, 2007). The carapace is often preserved with the valves closed, or more commonly, only a single valve is found. There are rare cases when the valves have been found open in a so called 'butterfly position', e.g., the kunmingellids of the Chengjiang fauna. From this, conclusions have been made that this may have been the life attitude of many bradoriids (Shu *et al.*, 1999). The study of the kunmingellids have also strengthened the view that bradoriids probably were detritus feeders or micro-scavengers of small, non-mineralized animals in the water-sediment interface (Williams *et al.*, 2007). In turn the bradoriids themselves were most likely a food source for other larger animals, which coprolite evidence suggests (Vannier & Chen, 2005).

For a long time, only a single species of Bradoriida was known from the Stephen Formation; *Liangshanella burgessensis* from the Burgess Shale (Siveter & Williams, 1997 plate 8, fig. 3-5). Until recently. In 2010, Caron *et al.* illustrated a potential new species of Bradoriida from the 'thin' Stephen Formation at Stanley Glacier (Caron et al., 2010, suppl. fig. DR3L). In 2014 Caron et al. illustrated a new specimen in their supplementary information (suppl. fig. 6:o, q) from the 'thick' Stephen Formation at Marble Canyon. Up to this point the specimens were only illustrated and not described and assigned to a genus or species. But Peel and Streng (in press) then described a new genus, *Flumenoglacies*, based on specimens found on Greenland. They compared them with the specimen illustrated from the Stephen Formation at Marble Canyon. They assigned it to *Flumenoglacies* but at the time only named it *Flumenoglacies* n. sp. (Peel & Streng, in press).

The specimens from Odaray Mountain described in this paper will increase the diversity of middle Cambrian bradoriids within the Stephen Formation. They will also elucidate further the affinity of the specimens from Marble Canyon (Caron et al., 2014; Peel & Streng, in press).

The resulting bradoriid fauna of the Stephen Formation can be compared with faunas from other paleocontinents and might elucidate previously unrecognized geographic relationships of Laurentia.

Study area

The specimens in this study were collected from the 'thin' Stephen Formation in the Canadian Rocky Mountains, c. 1.7 km south of Odaray Mountain (approx. 51° 20.7'N 116° 22.8'W, Fig.2), middle Cambrian, Cambrian Stage 5, *Ehmaniella* Biozone.

The Stephen Formation is part of the Sauk megasequence which was deposited on the western margin of Laurentia during the Cambrian. Generally speaking, the Stephen Formation is distinguished in to the 'thin' and the 'thick' Stephen Formation. This distinction is due to a faulting event, which is known as the Cathedral Megatruncation. This created a big submarine cliff, the so called Cathedral escarpment. This cliff allowed a calm environment at the base of the cliff where thick argillaceous deposits and deep-water limestones dominate. At the top of the cliff there was a wide, tropical platform where there was a shallow-marine environment leading to a thinner deposit of alternating carbonates and shale. The alternating of carbonates and shale is due to past fluctuations in sea level; when there was a

transgression argillaceous sediments were deposited on the platform since a deeper, calmer environment prevailed even here during these periods (Collom *et al.*, 2009).

These platform deposits are what make up the 'thin' Stephen Formation, from where the specimens described herein are collected. It consists of two members, the lower Narao Member and the upper Waputik Member (Aitken, 1997).

The thick clay dominated deposits at the base of the cliff represent the 'thick' Stephen Formation. It includes the famous lagerstätte Burgess Shale.

Figure 1. A map displaying the area west of Calgary, Canada. The red arrow points to the star which is the location of the Stephen Formation at Odaray Mountain. The map covers a distance of 394 km in east-west direction. (Source: Google maps)

Material and methods

23 bradoriid specimens were obtained by the dissolution of limestone samples in 10% formic acid and subsequent picking of the residue under a binocular microscope. The specimens derive from three carbonate levels in the upper part of the formation, i.e., level 18.45 m, 21.10 m, and 25.55 m.

The 'thin' Stephen Formation at Odaray Mountain is 30 m thick where the specimens were collected and consists of five parasequences of shale and wackestones.

The specimens were examined with SEM (scanning electron microscope) and out of the 23 specimens, 17 were sufficiently preserved to study in detail.

Systematic paleontology

Phylum ARTHROPODA Siebold and Stannius 1845

Order BRADORIIDA Raymond 1935 [nom corr. Ivanova 1960]

Family HIPPONICHARIONIDAE Sylvester-Bradley 1961

Diagnosis: See Siveter & Williams (1997)

Discussion: *Hipponicharionidae* show close resemblance to *Beyrichonidae* Ulrich and Bassler (1931). They are both postplete, about the same size, are trilobate and have a sub-triangular outline. But the lobes in *Beyrichonidae* are not as inflated and ventrally the lobes are not as extended anteriorly and posteriorly.

Genus FLUMENOGLACIES Peel & Streng in press

Type species: *Flumenoglacies groenlandica* Peel & Streng in press, from the Ekspedition Bræ Formation (middle Cambrian; Cambrian Series 3, Drumian Stage), Peary Land, North Greenland.

Diagnosis: A slightly to strongly postplete carapace with a straight hingeline. The greatest length of the carapace is at about two thirds of the height. It has an anterior and a posterior lobe that has coalesced, forming a continuous lobe on the carapace. The lobe is more elevated posteriorly and anteriorly and in the latter area it may culminate in a spine. The presence of a central, wide lobe results in two sulci between the continuous and central lobe in the anterior and posterior area respectively. Along the entire free margin there is a marginal brim from where a shallow to steep ramp runs up to the lobe. The ornamentation is wavy-striated and encircles the lobe and ramp. The brim is smooth and the area on the central lobe is wrinkled or smooth. (Modified after Peel and Streng in press.)

Discussion: *Flumenoglacies* differs from *Neokunmingella* in having less inflated lobes and a ramp between the marginal brim and the continuous lobe. In *Neokunmingella* the lobe is directly adjacent to the marginal brim. *Flumenoglacies* also shows close resemblance to *Beyrichona* Matthew (1895), but the lobes in *Flumenoglacies* are more confluent and are not as inflated and broad as in *Beyrichona*. In general the ventral outline is more triangular in *Beyrichona* than in both *Neokunmingella* and *Flumenoglacies*.

Taxa included: *Flumenoglacies groenlandica* Peel and Streng in press; *Flumenoglacies*? sp. of Peel and Streng in press *and Flumenoglacies michaeli* n. sp.

FLUMENOGLACIES michaeli n. sp.

Fig. 3

Etymology: After Michael Streng, the person who together with John Peel erected the genus *Flumenoglacies*.

Synonymy:

Flumenoglacies n. sp., Peel & Streng in press, fig. 3.1-3.2.

Bradoriid, n. gen. n. sp.; Caron et al. 2014, suppl. fig. 6 o, q.

Holotype: Specimen illustrated in Fig. 3A-C. From a level of 18.45 m above the base of the 'thin' Stephen Formation as exposed c. 1.7 km south of Odaray Mountain, British Columbia, Canadian Rocky Mountains. Age is middle Cambrian, Cambrian Stage 5, *Ehmaniella* biozone.

Material: Eleven individual valves and one fragmentary, ventrally conjoined carapace. Seven are left valves and three are right valves. Five of the individual valves are abraded and not complete. One of the specimens is too fragmented to say if it's a right or left valve.

Age and occurrence: The specimens are from the 'thin' Stephen Formation at a level of 18.45 m and 25.55 m in the Canadian Rocky Mountains, British Columbia, c. 1.7 km south of Odaray Mountain. Middle Cambrian, Cambrian Stage 5, *Ehmaniella* biozone.

Diagnosis: Species of *Flumenoglacies* lacking a spine on the anterior lobe.

Description: A slightly to strongly postplete bradoriid, small in size (length varies between 0.78 and 1.27 mm, n=9), straight hingeline and with a well-developed, narrow, pointed lobe that entire the free margin. The pointy character could be primary but it might also have been caused by diagenetic processes. From the comarginal lobe there is a ramp down to a marginal brim which is separated from the ramp by a shallow groove. The lobe is more pronounced in the anterior and posterior area respectively. The middle of the lobe, in the ventral area, is not as elevated and distinct. In the posterior and ventral area the lobe is situated further from the margin whilst gradually closer to the margin as you move towards the anterior area. In the middle of the valve there is a central lobe that is more elevated and broad in the ventral area, becoming less elevated and broad in the dorsal area. This creates two sulci on either side of the central lobe which is most prominent in ventral profile. The ornamentation is a wavy striation which parallels and encircles the outer part of the lobe and the ramp. The striation lines are in general parallel and in some places they bifurcate (see Fig. 3:**I**). The striation results in small, anastomosing ridges. The groove and marginal brim is smooth, in the sulci and on the central lobe it is somewhat wrinkled.

Discussion: The specimen described as *Flumenoglacies* n. sp. of Peel & Streng (in press) is considered to be conspecific with *Flumenoglacies michaeli* n. sp.

Flumenoglacies groenlandica has a spine on the anterior part of the lobe which is not present in *Flumenoglacies michaeli* n. sp. and *Flumenoglacies*? sp. of Peel and Streng (in press). Additionally, in the specimens described herein the lobe is situated closer to the free margin than in *F. groenlandica* and *Flumenoglacies*? sp. According to Peel and Streng (in press), one of the characteristics of *Flumenoglacies michaeli* n. sp. is that the anterior part of the lobe is more elevated relative to the posterior part. This is based on one specimen and might actually be a diagenetic feature. This observation is in reference to the specimen in fig. 3.1-3.2 of Peel and Streng (in press). The elevation of the anterior part of the lobe is most visible in lateral profile, fig. 3.2, where one also can see that the anterior part of the lobe is narrower and that there is a fracture on the top. It is therefore hard to determine whether the elevation is a primary characteristic of this specimen or if it is caused by compression of the carapace. In the specimens studied herein the anterior part of the lobe appears to be a bit stronger developed but this is not a prominent feature. To erect a new species based on solely this characteristic, more specimens would need to be examined.

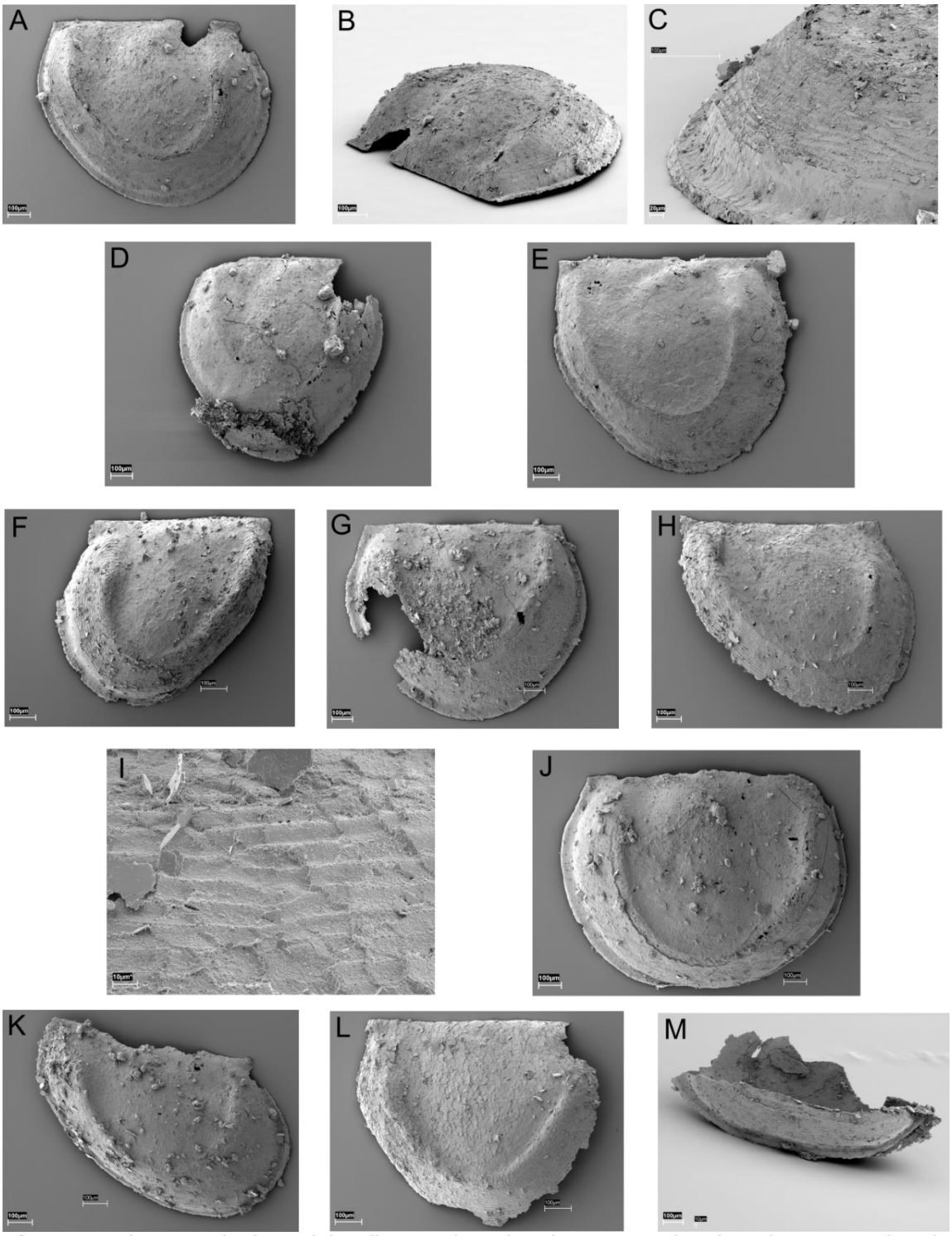

Figure 3. *Flumenoglacies michaeli* n. sp. from levels 18.45 m (A-E) and 25.55 m (F-M) of the 'thin' Stephen Formation south of Odaray Mountain; middle Cambrian (*Ehmaniella* Biozone). **A-C**: left valve (holotype); A, lateral view; B, oblique anterodorsal view; C, close-up of ornamentation on comarginal ramp. **D**: exfoliated left valve. **E**: exfoliated left valve with well preserved cardinal corners. **F**: right valve with distinct ornamentation. **G**: left valve. **H-I**: left valve; H, lateral view with anterior part of marginal brim eroded; I, close-up of ornamentation on comarginal ramp; note bifurcating ridges. **J**: almost symmetrical right valve. **K**: strongly postplete left valve. **L**: left valve with corroded free margin. **M**: fragmented ventrally conjoined carapace showing ornamented ramp and remnants of comarginal lobe. Scale bars represent 100 µm for entire views of specimens or 10 µm for close-ups.

Family COMPTALUTIDAE Öpik 1968

Diagnosis: See Öpik, 1968 and Hou et al., 2002.

Genus PHASOIA Hinz-Schallreuter 1993

non 1943 *Ophiosema*; Romieux (=Lepidoptera).
1968 *Ophiosema* nov.; Öpik, p.27.
1993a *Phasoia* n. g. n. sp.; Hinz-Schallreuter, p.321.

Type species: *Ophiosema spicatum* Öpik 1968, p.27 and pl. 3; fig.1 and fig.2, from shales in the Yelvertoft beds, locality M426, Mount Isa Sheet area (Australia). Ordian (middle Cambrian).

Diagnosis: See Öpik 1968 (*Ophiosema*).

Discussion: This is the first report of *Phasoia* from Laurentia. Previously described specimens of this genus have been found in Australia and South China, and they don't seem to have the same ornamentation as those from the Stephen Formation.

Remarks: Hinz-Schallreuter erected the new genus name *Phasoia* because the name *Ophiosema* is a homonym of Romieux 1943 (Lepidoptera).

PHASOIA stephenensis n. sp.

Fig. 4

Holotype: Specimen A-B in Fig. 4. A left valve with a length of c. 0.8 mm. From a level of 21.1 m above the base of the 'thin' Stephen Formation as exposed c. 1.7 km south of Odaray Mountain, British Columbia, Canadian Rocky Mountains. Age is middle Cambrian, Cambrian Stage 5, *Ehmaniella* biozone.

Material: Three individual valves, two are right valves and one is a left valve. Two of the specimens are somewhat fragmented. The specimens are from a level of 21.1 m above the base of the 'thin' Stephen Formation as exposed c. 1.7 km south of Odaray Mountain, British Columbia, Canadian Rocky Mountains. Age is middle Cambrian, Cambrian Stage 5, *Ehmaniella* biozone.

Diagnosis: Species of *Phasoia* with weakly convex valves, bearing a continuous, looped lobe. Outer valve surface ornamented with conspicuous longitudinal wavy striation. No subdorsal node or spicate extremities developed.

Description: A postplete bradoriid, small in size (length varies from 0.65 to 0.81 mm, n=3). There is a well-developed narrow lobe running from the anterior area, along the free margin up to the posterior cardinal corner where it curves and follows the dorsal margin and then loops inwards and terminates in the sub-anterior area. This creates a depression in the valve surrounded by the lobe and a sub-triangular sulcus in the

anterodorsal area. The lobe is more elevated in the posterior area, becoming less elevated in the anterior area. From the lobal area there is a gently dipping ramp towards the free margin terminating in a brim. This was probably present around the whole free margin but the specimens are not perfectly preserved so it is hard to say for certain. (Brim is only visible in the specimen illustrated in A and B, Fig. 4.) There is a lateral, wavy striated ornamentation on the entire valve except on the brim (E in Fig. 4 show a close-up of the ornamentation). In general the lines are parallel but on some places they bifurcate. This striation results in small anastomosing ridges.

Discussion: *Phasoia stephenensis* n. sp. shows typical features of the type species *Ophiosema spicatum*; it has the postplete valve with the very distinctive looped lobe. The ornamentation of taxa assigned to *Phasoia* is not always described and hard to see on illustrations, but for the type species a pustulose ornamentation is mentioned. A summary of bradoriids from China by Hou *et al.* (2002) describes the ornamentation of *Phasoia* as smooth, reticulate or punctuate. So this wavy striation that results in small anastomosing ridges is something unique for the new species of *Phasoia*. Earlier descriptions of *Phasoia* don't mention the convexity of the valve in the descriptions and diagnoses, but when pictures of specimens have been studied in Hinz-Schallreuter (1993a; 1999) and Öpik (1968) it has been found that those show a much higher convexity than *Phasoia stephenensis* n. sp. These mentioned different characters, and the lack of nodes and spicate dorsal extremities, are therefore considered enough to erect a new species.

The ornament of the *P. stephenensis* n. sp. is almost the same as in *Flumenoglacies michaeli* n. sp. found at the same locality. In *P. stephenensis* the small ridges that are a result of the striation are a bit more pronounced than in *F. michaeli*.

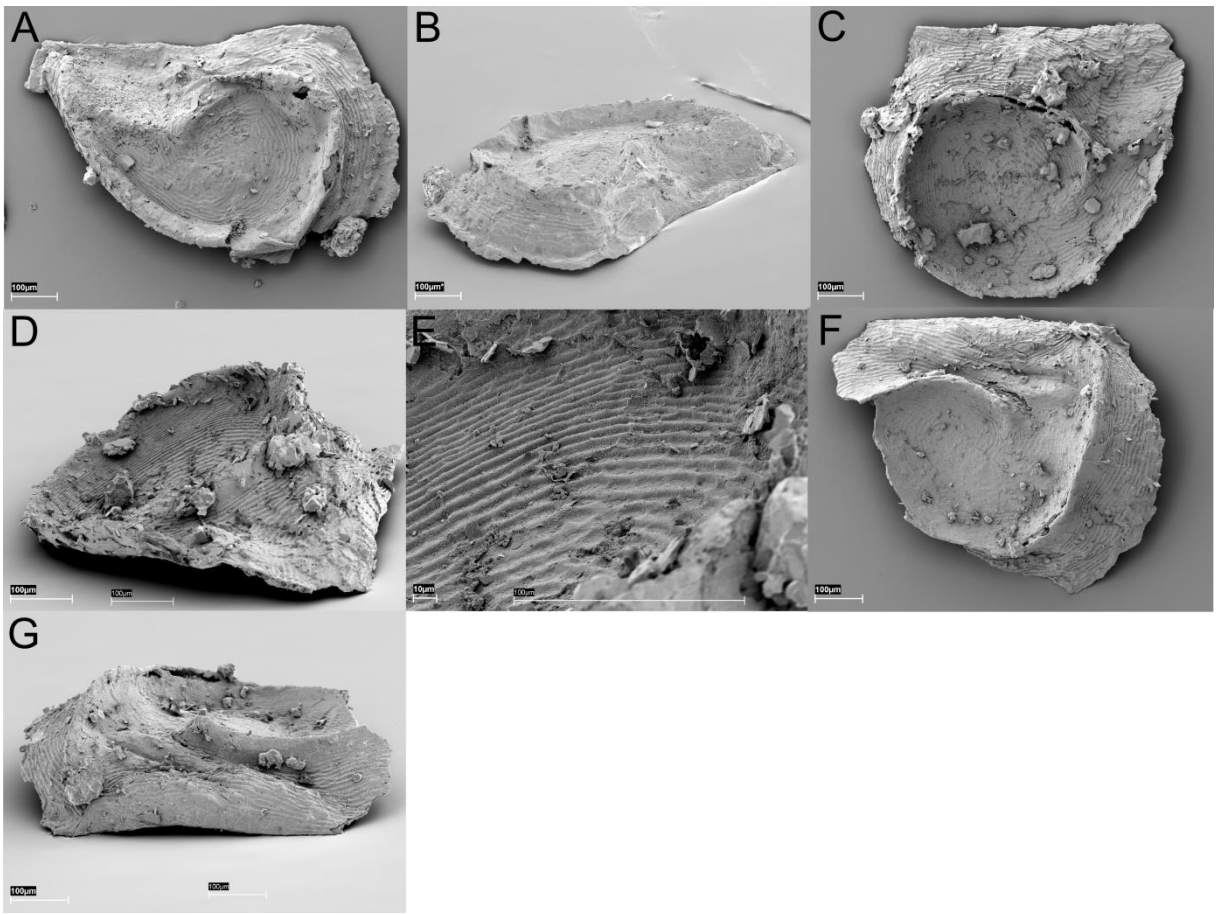

Figure 4. *Phasioa stephenensis* n. sp. from a level of 21.1 m of the 'thin' Stephen Formation south of Odaray Mountain; middle Cambrian (*Ehmaniella* Biozone). **A-B** Left valve (Holotype); A, lateral view; B, oblique posterodorsal view; **C-E** Right valve; C, lateral view; D, oblique anterodorsal view; E, close-up of ornamentation on the inner part of the lobe; **F-G** Right valve with damaged posterodorsal area; F, lateral view; G, oblique dorsal view. Scale bars represent 100 µm for entire views of specimens and in the close-ups they represent 10 µm.

Family UNKNOWN

Genus and species undet. A

Fig. 5 A-C

Material: One valve (left or right can't be determined) from a level of 25.55 m in the 'thin' Stephen Formation in the Canadian Rocky Mountains, British Columbia, c. 1.7 km south of Odaray Mountain. Middle Cambrian, Cambrian Stage 5, *Ehmaniella* biozone.

Description: A small, somewhat elongated (length of valve c. 1.26 mm), neither postplete or preplete bradoriid. Maximum height is at mid-length. The valve is evenly convex with no nodation or lobation, and with a well-developed, flattened marginal brim that's separated from the convex valve by a furrow. Approaching the furrow, the inclination of the valve surface is steepening, making an almost vertical, inward plunge down to the furrow. This is most prominent in the anterior and posterior areas. The straightness of the hingeline can't be determined since it's not intact. There is some anastomosing ornamentation visible on the valve but mostly you see a punctured ornamentation (Fig. 5:B). The punctures look like small, upraised craters which are c. 4 µm in diameter, evenly distributed on the valve, roughly 5-15 µm apart. This might be pore-channels that have been exposed by exfoliation of the valve since remnants of a smooth, outer layer is visible in some areas of the valve.

Discussion: The anastomosing ornamentation is not sufficiently preserved to be fairly compared with the ornamentation of the other specimens from the same locality previously described herein. But one can speculate that it in fact might be the same ornamentation.

Affinity with a family or genus can't be determined, but it has closest resemblance to *Indiana* (Matthew 1902) since it is rounded, and shows no lobation or nodation. But it does have marginal structures, which is not typical for Indiana. It could thus be compared with *Indiana labiosa*, a species described by Ulrich and Bassler 1931, which was based on two specimens found in the Stephen Formation that possess a marginal structure. But these are bigger in size (c.5.8 mm) and since the specimen illustrated and described herein is not intact further comparison with hinge line, cardinal angles etc. can't be made to determine a relationship.

Family UNKNOWN

Genus and species undet. B

Fig. 5 D-F

Material: One left? valve from a level of 25.55 m in the 'thin' Stephen Formation in the Canadian Rocky Mountains, British Columbia, c. 1.7 km south of Odaray Mountain. Middle Cambrian, Cambrian Stage 5, *Ehmaniella* biozone.

Description: The specimen is one poorly preserved valve, presumably a left valve. The valve is small, c. 1.13 mm, slightly asymmetric, and there is no visible nodation

or lobation. There is a u-shaped area on the valve that is more corroded then the rest of the valve. Outside this area the valve is more ramp-like towards the margin and inside the area it is more flat but still a bit convex. Along the margin there are some remains of what might have been a marginal brim. There is only a small remain of what might have been the hingeline (c. 0.16 mm long). On the valve, in the area enclosed by the u-shaped area, there's nested pustulation (Fig.5:E) and outside the u-shaped area there are small, evenly distributed holes in a wave-like pattern (Fig. 5:F) These are best visible in the posterodorsal corner and might have been pustules that have corroded away.

Discussion: Most bradoriids are postplete, it is therefore suggested that the specimen is a left valve. The u-shaped area on the valve might be remains of a lobe, or there might have been a larger node on the center of the valve. If it would have been a confluent lobe, like on a *Flumenoglacies*, the center wouldn't probably be flat/convex but more like a depression. And since the ornamentation is not similar, affinity with *Flumenoglacies* is probably not in question.

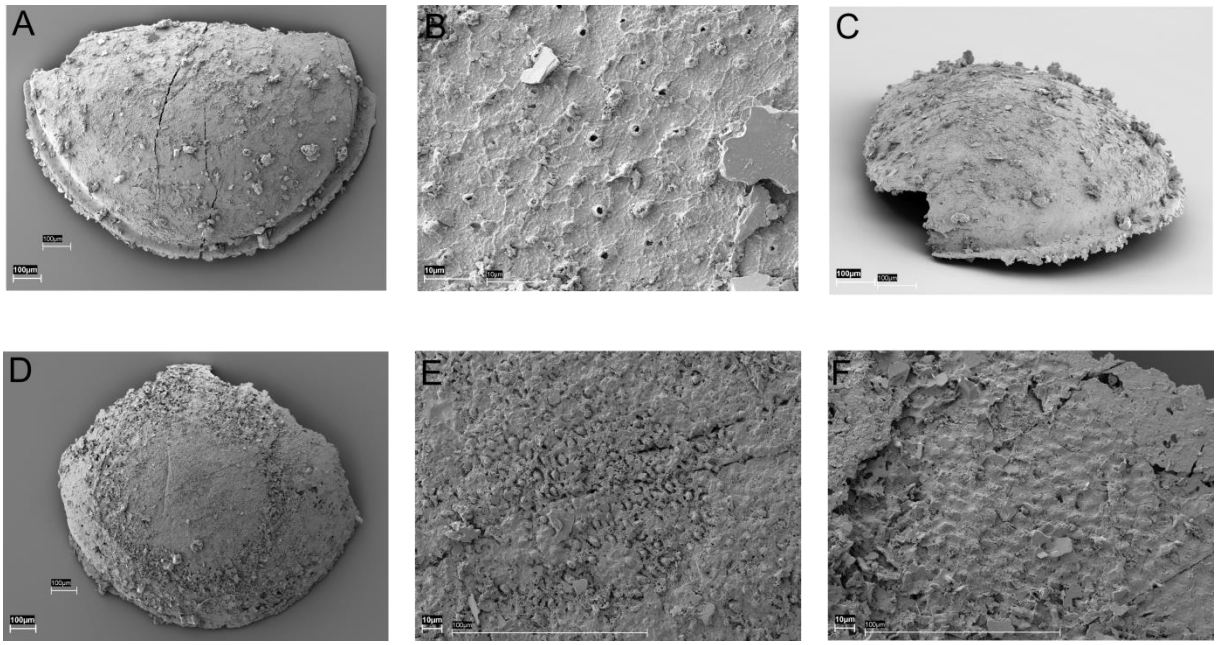

Figure 5
Bradoriid specimens of undetermined affinity from a level of 25.55 m of the 'thin' Stephen Formation south of Odaray Mountain; middle Cambrian (*Ehmaniella* Biozone)..
A-C Valve of family and genus undetermined A; A, lateral view; B, close-up of the ornamentation; C, oblique view; **D-E** Valve of family and species undetermined B; D, oblique view; E, close-up of the ornamentation inside the u-shaped area; F, close-up of the ornamentation close to the margin. Scale bars represent 100 µm for entire views of specimens and in the close-ups they represent 10 µm.

Discussion

The most interesting find in the 'thin' Stephen Formation is the new species of *Phasoia* as the genus hasn't been reported from the paleocontinent of Laurentia before. So from where and from which ages has the genus *Phasoia* been reported so far?

The age of the sediments in the Stephen Formation, where *Phasoia stephenensis* n. sp. was found, is middle Cambrian, Series 3, Stage 5 and belongs to the *Ehmaniella* biozone. This biozone is almost coeval with the *Ptychagnostus gibbus* Biozone (Peng *et al.*, 2012) from which Hinz-Schallreuter (1993a) described a new species of *Phasoia* at Rogers ridge in Australia; *Phasoia rogerensis*.

The first species of *Phasoia*, which is also the type species of the genus, was described by Öpik (1968) as *Ophiosema spicatum* from Australia. The genus name was subsequently changed to *Phasoia* by Hinz-Schallreuter (1993) as *Ophiosema* Öpik was a junior homonym of *Ophiosema* Romieux. *Ophiosema spicatum* is from a bit older sediments than the *Ehmaniella* and *Ptychagnostus gibbus* biozone- Öpik reported it to be from the Ordian Stage. This stage was defined by Öpik based on the presence of the *Redlichia chinensis* fauna (Peng *et al.*, 2012). There has been much debate about the age of the Ordian Stage (see Babcock & Peng, 2007; Kruse *et al.*, 2009; Peng *et al.*, 2012 and references therein). It has traditionally been said that the Ordian is the base of the Middle Cambrian in Australia, but it correlates with zones in North China and Siberia, which are there considered to be late Early Cambrian (Peng *et al.*, 2012). It has recently been suggested that the Ordian might be equivalent to Stage 4 of Series 2, i.e., the uppermost traditional Early Cambrian (Kruse *et al.*, 2009). So it is hard to say exactly how Öpik's species is placed in time relative to *Phasoia stephenensis* n. sp. and *Phasoia rogerensis* but it's at least safe to say that it's older.

Also from Australia, even older specimens of *Phasoia* have been described as *Phasoia* cf*. spicata* (Betts et al., 2014). They originate from a succession in the Flinders Ranges, from a stratigraphic level that belongs to the *Abadiella huoi* zone (Topper pers. com.). That is in Series 2, Stage 3 which is about the middle of the traditional Lower Cambrian.

From the same biozone as this Australian lower Cambrian species (*Phasoia* cf. *spicata*), but in the Qiongzhusi Formation, Yunnan, South China, Hou et al. (2002) described and illustrated a specimen as *Phasoia* sp. So this specimen has about the same age as the specimens from Australia described by Betts et al. (2014).

More Chinese specimens have been described from southern-most China. They were reported by Zhang (1986) and he assigned them to various species of *Ophiosema* (=*Phasoia*). These are from the Damao Formation, Maochuan Stage. For the stratigraphy of Southern China no such name appears in the literature. The stage that Zhang might have referred to is a stage that is recognized for northern China called the Maochuangian stage, which is at the base of the traditional Middle Cambrian (Peng 2003). Unfortunately, Zhang didn't indicate a biozone so the exact age of these taxa is uncertain. They might be from early traditional Middle Cambrian.

As far as this study goes, the conclusion is that the oldest specimens of *Phasoia* reported (Cambrian Stage 3) come from Australia (*Phasoia* cf*. spicata* of Betts et al., 2014) and South China (*Phasoia* sp*.* of Hou et al., 2002), and the

youngest (Cambrian Stage 5) are from Canada (*Phasoia stephenensis* n. sp.) and Australia (*Phasoia rogerensis* of Hinz-Schallreuter, 1993a). Based on this, one could imagine that the genus migrated from Gondwana (Australia and South China) and then reached Laurentia. But to confirm a migration path more research would need to be done in the entire Cambrian strata, i.e., not only Stage 3 and 5. This would be needed to be able to either include or exclude *Phasoia* from the Cambrian fauna of all past paleocontinents. Concerning Laurentia, there hasn't been much research on the small shelly fauna so far. What is to say one wouldn't find *Phasoia* in sediments from for example Cambrian Stage 3 or 4 if one started looking for it?

The genus *Flumenoglacies* was described recently and the only place it has been found so far, except in Canada, is on Greenland. The specimens of *Flumenoglacies* found there are from the Drumian Stage, which is above Stage 5 in Series 3, so they are also from the middle Cambrian but slightly younger than the ones found in the Stephen Formation. Since very few specimens of this genus have been found so far it's hard to discuss their distribution and migration pattern.

The ornamentation of the *Flumenoglacies michaeli* n. sp. and *Phasoia stephenensis* n. sp., the anastomosing ridges, have been found in more species previously described. If it is exactly the same ornamentation, and precisely how many other species there are that show this characteristic, is hard to say. This has partly to do with the vast amount of bradoriids described and that the descriptions are not always complete due to abraded or incomplete specimens. The illustrations are also often very poor, it is therefore sometimes hard to see details such as ornamentation. But at last it seems as this ornamentation is something that is recurrent in different families.

Flumenoglacies belongs to the family *Hipponicharionidae,* and another bradoriid of that family which shows something that could be anastomosing ridges is *Pseudobeyrichona longquanxiensis* (Cui 1987). The diagnosis describes the ornamentation as 'partially wrinkled' (Zhang, 2007), which could insinuate that it is a result of compression during diagenesis. Looking at the illustrations of the *Pseudobeyrichona* it actually looks more 'wrinkled' than in the specimens of *Flumenoglacies* and *Phasoia* described in this paper, but it's still similar.

A few specimens of the svealutid genus *Tsunyiella* Zhang (1974) are described to have "…remains of a fine network of anastomosing ridges…" (Hou *et al.*, 2002: p. 397). This is unfortunately not visible in the illustrations so its resemblance with the ornamentation of *F. michaeli* and *P. stephenensis* is difficult to discuss further.

One idea is that this ornamentation is a feature acquired after burial and therefore had no practical function during life. It could also be a pattern that is a result of how the carapace was structured and composed chemically. It can be seen on abraded specimens that the carapace seem to have been built up by layers. Maybe the layers grew in a way that created these small ridges while the outer surface was actually smooth or had some other ornamentation.

Bradoriids have in the past conventionally, as mentioned in the introduction, been closely associated with ostracods. This has led to that features of the two groups often have been compared. Vannier *et al.* (1997) published research about the circulatory system in crustaceans and evidence on different crustacean fossils, mainly ostracods. In this publication they describe the network of anastomosing ridges in the cambriid bradoriid *Petrianna fulmenata* Siveter *et al.*, 1995 and suggest that this area might be the place where the hemolymph is reoxygenated (Vannier *et al.*, 1997).

The anastomosing ridges in *Petrianna fulmenata* are perpendicular relative to the ridges on *F. michaeli* and *P. stephenensis*, they radiate outwards from the central nodes on the valve out to the free margin. The ridges are also fewer and broader in *P. fulmenata*. Even though there are differences in the ornamentation it doesn't exclude the possibility of the ridges in *F. michalei* and *P. stephenensis* to be remnants of a slightly different respiratory system compared to *P. fulmenata*.

Acknowledgements

I would like to give my greatest gratitude to my supervisor Michael Streng who has been a truly amazing support throughout this whole process. Both by being generous with his time and helping me along the way with advise, inspiration and material.

I also want to thank Uppsala University for the access to the Scanning Electron Microscope at the Evolutionary Biology Center in Uppsala.

Reference list

Aitken, J. . (1997). Stratigraphy of the Middle Cambrian platformal succession, southern Rocky Mountains. *Geological Survey of Canada Bulletin* 398, 1–322.

Babcock, L. E. & Peng, S. (2007). Cambrian chronostratigraphy: Current state and future plans. *Palaeogeography, Palaeoclimatology, Palaeoecology* 254(1–2), 62–66 (From Snowball Earth to the Cambrian bioradiation: calibration of Ediacaran-Cambrian history in South China).

Betts, M. J., Topper, T. P., Valentine, J. L., Skovsted, C. B., Paterson, J. R. & Brock, G. A. (2014). A new early Cambrian bradoriid (Arthropoda) assemblage from the northern Flinders Ranges, South Australia. *Gondwana Research* 25(1), 420–437.

Briggs, D. E. G. (2003). The Role of Decay and Mineralization in the Preservation of Soft-Bodied Fossils. *Annual Review of Earth and Planetary Sciences* 31(1), 275–301.

Caron, J.-B., Gaines, R. R., Mángano, M. G., Streng, M. & Daley, A. C. (2010). A new Burgess Shale–type assemblage from the "thin" Stephen Formation of the southern Canadian Rockies. *Geology* 38(9), 811–814.

Collette, J. H., Hughes, N. C. & Peng, S. (2011). The First Report of a Himalayan Bradoriid Arthropod and the Paleogeographic Significance of This Form. *Journal of Paleontology* 85(1), 76–82.

Collom, C. J., Johnston, P. A. & Powell, W. G. (2009). Reinterpretation of 'Middle' Cambrian stratigraphy of the rifted western Laurentian margin: Burgess Shale Formation and contiguous units (Sauk II megasequence), Rocky Mountains, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology* 277(1–2), 63–85 (Paleoenvironments and taphonomy of Cambrian Lagerstätten).

Elicki, O. (2012). First skeletal microfauna from the cambrian series 3 of the jordan rift valley (Middle East). *Memoirs of the Association of Australasian Palaeontologists* 1(42), 153–173.
Gozalo, R., Dies, M. E. & Chirivella, J. B. (2004). New occurrence of the family Hipponicharionidae (Bradoriida, Arthropoda), in the lower and middle Cambrian of the Cadenas Ibéricas, Spain. *Geobios* 37(2), 191–197.
Guangbi, T. & Yong, L. (1988). EARLY CAMBRIAN BRADORIIDA OF ZHENBA, SOUTH SHANXI. *Journal of Chengdu University of Technology (Science & Technology Edition)* 1, 001.
Hinz-Schallreuter, I. (1993a). Cambrian ostracodes mainly from Baltoscandia and Morocco. *Archiv für Geschiebekunde* 1, 329–350.
Hinz-Schallreuter, I. (1993b). Ostracodes from the Middle Cambrian of Australia. *Neues Jahrbuch fuer Geologie und Palaeontologie. Abhandlungen* 188(3), 305–326.
Hou, X., Siveter, D. J., Williams, M. & Feng, X. (2002). A monograph of the Bradoriid arthropods from the Lower Cambrian of SW China. *Transactions of the Royal Society of Edinburgh, Eart Sciences* 92, 347–409.
Hou, X., Siveter, D. J., Williams, M., Walossek, D. & Bergström, J. (1996). Appendages of the arthropod Kunmingella from the early Cambrian of China: its bearing on the systematic position of the Bradoriida and the fossil record of Ostracoda. *Philosophical Transactions of the Royal society of London* B351, 1131–1145.
Jones, P. J. & McKenzie, K. G. (1980). Queensland Middle Cambrian Bradoriida (Crustacea): new taxa, palaeobiogeography and biological affinities. *Alcheringa: An Australasian Journal of Palaeontology* 4(3), 203–225.
Kruse, P. D., Jago, J. B. & Laurie, J. R. (2009). Recent developments in Australian Cambrian biostratigraphy. *Journal of Stratigraphy* 33(1), 32–47.
Lin, J.-P., Ivantsov, A. Y. & Briggs, D. E. G. (2011). The cuticle of the enigmatic arthropod Phytophilaspis and biomineralization in Cambrian arthropods: Phosphatic cuticle of Phytophilaspis. *Lethaia* 44(3), 344–349.
Maas, A. & Waloszek, D. (2005). Phosphatocopina – ostracode-like sister group of Eucrustacea. *Hydrobiologia* 538(1-3), 139–152.
Melnikova, L. M., Siveter, D. J. & Williams, M. (1997). Cambrian Bradoriida and Phosphatocopida (Arthropoda) of the former Soviet Union. *Journal of Micropalaeontology* 16(2), 179–191.
Müller, K. J. (1964). Ostracoda (Bradorina) mit phosphatischen Gehäusen aus dem oberkambrium von Schweden. *Neus Jahrbuch für Geologie und Paläontologie, Abhandlungen* 121, 1–46.
Peng, S., Babcock, L. . & Cooper, R. . (2012). The Cambrian period. *The geological time scale 2012*. pp 437–487. Elsevier B.V.
Pour-Ghobadi, M., Williams, M. & Popov, L. E. (2007). A new Middle Ordovician arthropod fauna (Trilobita, Ostracoda, Bradoriida) from the Lashkarak Formation, Eastern Alborz Mountains, northern Iran. *GFF* 129(3), 245–254.
Rode, A. L., Lieberman, B. S. & Rowell, A. J. (2003). A New Early Cambrian Bradoriid (Arthropoda) from East Antarctica. *Journal of Paleontology* 77(4), 691–697.
Shu, D. & Chen, L. (1994). Cambrian paleobiogeography of Bradoriida. *Journal of Southeast Asian Earth Sciences* 9, 289–299.

Shu, D., Vannier, J., Luo, H., Chen, L., Zhang, X. & Hu, S. (1999). Anatomy and lifestyle of Kunmingella (Arthropoda, Bradoriida) from the Chengjiang fossil Lagerstätte (lower Cambrian; Southwest China). *Lethaia* 32(4), 279–298.
Siveter, D. J. & Williams, M. (1997). *Cambrian Bradoriid and Phosphatocopid Arthropods of North America*. London: The Paleontological association. (Special papers in paleontology; 57).
Siveter, D. J., Williams, M., Peel, J. S. & Siveter, D. J. (1995). Bradoriida (Arthropoda) from the early Cambrian of North Greenland. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 86(02), 113–121.
Streng, M., Ebbestad, J. O. R. & Moczydłowska, M. (2008). A Walcottella-like bradoriid (Arthropoda) from the lower Cambrian of Sweden. *GFF* 130(1), 11–19.
Sylvester-Bradley, P. . (1961). Archaeocopida. *Part Q, Arthropoda 3*. pp 100–105. Boulder, Colorado: Geological society of America. (Treatise on Invertebrate Paleontology).
Topper, T. P., Skovsted, C. B., Brock, G. A. & Paterson, J. R. (2011). The oldest bivalved arthropods from the early Cambrian of East Gondwana: Systematics, biostratigraphy and biogeography. *Gondwana Research* 19(1), 310–326.
Topper, T. P., Skovsted, C. B., Harper, D. A. T. & Ahlberg, P. (2013). A bradoriid and brachiopod dominated shelly fauna from the furongian (Cambrian) of Vastergotland, Sweden. *Journal of Paleontology* 87(1), 69–83.
Vannier, J. & Chen, J. (2005). Early Cambrian Food Chain: New Evidence from Fossil Aggregates in the Maotianshan Shale Biota, SW China. *PALAIOS* 20(1), 3–26.
Vannier, J., Williams, M., Alvaro, J. J., VizcaïNo, D., Monceret, S. & Monceret, E. (2005). New Early Cambrian bivalved arthropods from southern France. *Geological Magazine* 142(06), 751.
Vannier, J., Williams, M. & Siveter, D. J. (1997). The Cambrian origin of the circulatory system of crustaceans. *Lethaia* 30(3), 169–184.
Wilby, P., R. & Briggs, D. E. G. (1997). Taxonomic trends in the resolution of detail preserved in fossil phophatized soft tissue. *GEOBIOS* 20, 493–502.
Williams, M., Siveter, D. J., Popov, L. E. & Vannier, J. M. C. (2007). Biogeography and affinities of the bradoriid arthropods: Cosmopolitan microbenthos of the Cambrian seas. *Palaeogeography, Palaeoclimatology, Palaeoecology* 248(1-2), 202–232.
Zhang, X.-G. (1986). A comment on some middle Cambrian bradoriids from Yaxian, Hainan Island, Guangdong. *Acta Palaeontologica Sinica* 25(1).
Zhang, X.-G. (1987). Moult stages and dimorphism of Early Cambrian bradoriids from Xichuan, Henan, China. *Alcheringa: An Australasian Journal of Palaeontology* 11(1), 1–19.
Zhang, X.-G. (2007). Phosphatized Bradoriids (Arthropoda) from the Cambrian of China. *Palaeontographica Abteilung A* 93–173.
Öpik, A. . (1968). Ordian (Cambrian) Crustacea Bradoriida of Australia. *Bulletin of the Bureau of mineral resources, geology and geophysics* 103, 1–46.