

## WHAT IS THE BIOSTRATIGRAPHIC VALUE OF THE ICHNOFOSSIL *OLDHAMIA* FOR THE CAMBRIAN: A REVIEW \*

Alain HERBOSCH<sup>1</sup> & Jacques VERNIERS<sup>2</sup>

(3 figures)

<sup>1</sup>Département des Sciences de la Terre et de l'Environnement, Université Libre de Bruxelles, Belgium, herbosch@ulb.ac.be

<sup>2</sup>Department of Geology and Soil Science, Ghent University, Belgium, jacques.verniers@ugent.be

\* This paper is dedicated in memory of Michel Vanguetaine, professor at the Université de Liège, passed away too early, for his outstanding contribution to the biostratigraphy with acritarchs of the Caledonian basement of Belgium.

**ABSTRACT.** We have undertaken an exhaustive review of the literature to check if the ichnogenus *Oldhamia* could be used as a biostratigraphical tool in the Cambrian. On the 19 occurrences observed worldwide and positioned in the recent global chronostratigraphy of the Cambrian, only 16 have a time range sufficiently precise to constrain the stratigraphic interval during which the organisms producing *Oldhamia* lived in the Cambrian. They are clearly distributed in two age groups: a “younger” group of 14 occurrences shows a very well constrained time range from the base of Stage 3 to the three quarter of Stage 5 and an “older” group of 2 occurrences shows a poorly constrained time range which seems restricted to the Fortunian. With this contrasting situation we propose two alternative interpretations: in the first we accept all the results and in the second, more restrictive, we reject the age of the “older” group as scientifically insufficiently substantiated. *Oldhamia* can only be used as a stratigraphic tool in the second interpretation: it appears in the upper part of Stage 2, shows an acme in Stage 3 and 4 and rapidly disappears during Stage 5. This rapid disappearance could be interpreted as the arrival of the Cambrian agronomic revolution in the deep marine setting. The overview also shows that this ichnogenus has a cosmopolitan distribution.

**KEYWORDS:** Biostratigraphy, Cambrian agronomic revolution, palaeogeography, Avalonia, Gondwana.

### 1. Introduction

This review is made in the framework of a long-term stratigraphical study over the last 20 years on the Lower Palaeozoic of the Brabant Massif in Belgium (Herbosch & Verniers, 2002; Herbosch et al., 2008; Maletz & Servais, 1996; Vanguetaine, 1991, 1992; Vanmeirhaeghe et al., 2005; Verniers et al., 2001, 2002a, b). In a recent synthesis by Seilacher et al. (2005) on the palaeoecology of ichnofossils around the Ediacaran-Cambrian boundary, they also revise the taxonomy of the ichnogenus *Oldhamia*. It appeared that this ichnogenus has been observed in more than 15 localities worldwide. This offered the possibility to use this ichnofossil as a biostratigraphical tool, in particular in the Brabant Massif, where it is observed in the two lowest occurring Cambrian formations, which can only tentatively be dated due to the absence of any other fossil (Mortelmans, 1977; Verniers & Devos, 1995; Verniers et al., 2001).

It also appeared that *Oldhamia*, described since the second half of the XIX century in the Caledonian basement in Belgium never were the subject of a description except by Aceñolaza & Durand (1984). Hence, the Belgian occurrences are often ignored or poorly referenced in the international literature dealing with trace fossils. However they have been observed in many places: first in the Lower Palaeozoic inliers of the Ardennes and later in the Brabant Massif. In these two areas the stratigraphy is rather well

known (see overview in Verniers et al., 2001) and for most units the dating is well established due to the palynological studies with acritarchs by Vanguetaine (see his syntheses in 1986, 1992). Furthermore, the revision of the different ichnospecies of *Oldhamia* from Belgium present in various collections is now underway (Herbosch, in prep.).

The main goal of this paper is to check if *Oldhamia* can be used as a stratigraphical tool. Therefore an exhaustive and critical review of the literature and especially the age of the strata in which they are observed, is highly needed. Indeed, the palaeoecology and the systematic of this ichnogenus has been the object of several recent articles (Aceñolaza, 2003; Aceñolaza & Aceñolaza, 2007; Buatois & Mangano, 2003b, 2004; Seilacher et al., 2005), but on the contrary the topic of its age has only rarely been discussed (Lindhölm & Casey, 1990).

#### ***1.1. Ichnofauna of the deeper seas at the Ediacaran - Cambrian transition and the onset of the Cambrian agronomic revolution***

Benthic animals started to colonize the deeper sea floor in the Ediacaran (Seilacher, 1999; Narbonne & Aitken, 1990; Crimes, 2001; Orr, 2001; Buatois & Mangano, 2003b, 2004; Seilacher et al., 2005; Jensen et al., 2006), but the diversity of behaviour and life style remained very low. In

recent years it became more evident that the Ediacaran was rich in problematic structures, often mistaken for trace fossils (Droser et al., 2005; Seilacher et al., 2005; Jensen et al., 2006). For Seilacher et al. (2005 p. 352, fig. 7, 20) the ichnofauna is dominated by grazing traces, weakly specialized and not diagnostic, which can also be observed in shallow water environments of the same age. *Oldhamia recta* would be the only distinctive ichnospecies present. It consists of traces in the form of straight tunnels observed in the Ediacaran of Carolina (USA: Gibbison, 1989; Seilacher & Pflüger, 1992), of Argentina (Omarini et al., 1999) and of Australia (Jensen et al., 2006). However, Jensen et al. (2006 p. 143) expressed their reservation for the attribution of these traces to the ichnogenus *Oldhamia* and, indeed later, Tacker et al. (2008, 2010) could prove that they were not traces, but instead body fossils of a rod-like organism.

The Puncoviscana Formation of NW Argentina shows an overview of the ecology of the deep ecosystems in the lowermost Palaeozoic. Its rich trace fossil assemblage has been described in the seventies (Aceñolaza & Durand, 1973) and its ecological importance for the deep ecosystems of the early Cambrian has been emphasized in several publications (Aceñolaza, 2003, 2004; Aceñolaza et al., 2009; Buatois & Mangano, 2003a, 2003b, 2004; Seilacher et al., 2005). The assemblage is dominated by the ichnogenus *Oldhamia* and several other grazing traces present in the uppermost millimetres of a relatively firm substratum, indicating the presence of microbial mats. The benthic communities developed two strategies in direct association with the microbial substratum: grazing and undermat mining (Buatois & Mangano, 2003b).

The ichnogenus *Oldhamia* is mostly described from deep marine environments of the lower Cambrian and more rarely the middle Cambrian, in many folded stratigraphical succession. The ichnocoenoses of the deep seas seem to experience an explosion in diversity of behaviour in the early Cambrian (Seilacher et al., 2005), which at first is limited to a radiation of *Oldhamia*. The changes in burrowing behaviour can be seen by the appearance of different ichnospecies seemingly succeeding each other in time (Lindholm & Casey, 1990; Buatois & Mangano, 2003b; MacNaughton et al., 2005). For Buatois & Mangano (2003b) this diversification reaches its climax at the base of the Cambrian. The different *Oldhamia* traces would be caused by animals differing from each other at species level. Indeed, the behaviours are too distinct from each other to be induced by the environment only. In addition, the different ichnospecies are very rarely co-occurring on the same bedding plane.

For Seilacher et al. (2005) *Oldhamia* represents an ecological association (called an ecologic guild), which would become rare after the Cambrian agronomic revolution (Seilacher & Pflüger, 1994; Bottjer et al., 2000). This revolution becomes apparent in the destruction of the firm microbial mats by bioturbation, which on its turn affects all the benthic ecosystems. While this revolution in the substrata of the shallow marine environments start to happen in the Tommotian-

Atdabanian (part of Cambrian Stages 2 and 3, Peng & Babcock, 2008 fig. 4.5), it is still uncertain when this event reaches the deeper environments. Indeed, the age of strata containing *Oldhamia* is poorly constrained, not allowing determining a precise time range of this ichnogenus. According to Seilacher et al. (2005) and Mangano & Buatois (2007), the *Oldhamia* associations extended into the deeper environments probably between the earliest Cambrian and the middle Cambrian, the later age is suggested by the occurrences in Canada (Hoffman et al., 1994) and Morocco (El Hassani & Willefert, 1990). Recently Buatois et al. (2009) presented new arguments to place this event near the base of the Ordovician.

### 1.2. Taxonomy of *Oldhamia* and its evolution

Seilacher et al. (2005) revised the taxonomy of all ichnospecies of *Oldhamia*, which we follow in our study and to which we refer for more details. In the later work they retained for the Cambrian only six ichnospecies: *O. antiqua* Kinahan, 1858; *O. radiata* Kinahan, 1858; *O. flabellata* Aceñolaza & Durand, 1973; *O. curvata* Lindholm & Casey, 1990; *O. geniculata* Seilacher, Buatois & Mangano, 2005 and *O. alata* Seilacher, Buatois & Mangano, 2005. They also accept the presence of one species in the Ediacaran: *O. recta*, one species in the Ordovician: *O. pinnata* and one in the Carboniferous *O. fimbriata*.

Seilacher (1974) was the first to suggest an evolutionary scheme for the trace fossil *Oldhamia*, observing radial or dendroid forms in the Cambrian to pinnate forms in the Ordovician. Lindholm & Casey (1990) emphasize that this concept of evolution in the burrowing form of this ichnogenus represents an evolutionary tendency, corresponding to an optimization of the exploitable surface. If this concept can be accepted, one could use the different *Oldhamia* species to refine biostratigraphically the Cambrian. The latter authors tried to implement this in the Blow Me Down Brook Formation (cf. § 2.15) where radial forms are observed stratigraphically below dendritic forms. MacNaughton et al. (2005) observed the same evolutionary tendency of traces in the Selwyns Mountains (cf. § 2.16). However afterwards (MacNaughton, pers. comm.), they could only be sure of two trace fossil associations, making the suggested evolutionary trend less convincing.

## 2. Review of the stratigraphy of *Oldhamia* occurrences in the Cambrian

As mentioned above, it is generally accepted now that the *Oldhamia* ichnofossils are the traces of worm-like undermat miners (Seilacher et al., 2005), living probably between the earliest Cambrian and the middle Cambrian mostly in deep oceanic environments and more rarely in shallow ones. Because of that age and the very deep environment the strata containing *Oldhamia* are often devoid of macrofossils and hence poorly dated. In this paper we want to show that is not always the case and that recent progress in the chronostratigraphy and the

biostratigraphy of the Cambrian, has changed this shortcoming.

First, we will list up the stratigraphical constraints of all known occurrences of Cambrian *Oldhamia* in the literature. We exclude from this review *O. recta*, because of its controversial presence in the Ediacaran (Jensen et al., 2006; Tacker et al., 2010) as well as the post-Cambrian species. The occurrences will be described successively in function of their palaeogeographic position in the Cambrian (Cockx & Torsvik, 2002; Scotese, 2007). We begin with the locations on West Gondwana (future Avalonia microplate) with the Bray Group where historically the ichnogenus was first described and continue with the major palaeoplates Gondwana, Baltica and Laurentia. The biostratigraphical constraints are synthesized from the most recent data in the literature and also with the help of several researchers who responded to our questions. We positioned these data in the new global chronostratigraphical scale of the Cambrian (Gradstein et al., 2008; Ogg et al., 2008 fig. 1.1). Although still incomplete, it allowed dating rather precisely the *Oldhamia* occurrences, using several correlation charts between regional and global biostratigraphy (Geyer & Shergold, 2000 Table 1; Babcock & Peng, 2007 fig. 2; Peng & Babcock, 2008 fig. 4.4 and 4.5). It is important to underline that these correlations are delicate to perform and sometimes not very precise especially in the lower Cambrian, where most GSSP's are not yet defined. For these correlations we have always used the broadest possible time ranges. The new global scale has the advantage over the earlier scales by using a more elaborate time-scale calibration. The former lower Cambrian is now divided into two series and four stages, acknowledging much longer time duration (about 32 Ma) than previously assumed. The sedimentology and the environment of deposition of the succession with *Oldhamia*, important data for the palaeoecology, are also given whenever available.

### 2.1. Bray Head Formation, Bray Group, SE Ireland (West Gondwana)

It is in the Bray Head Formation of the Bray-Wicklow Unit that Forbes (1849) and later Kinahan (1858, 1859) described for the first time *Oldhamia* on samples discovered by T. Oldham where the ichnospecies *O. radiata* and *O. antiqua* occur. The Bray Group is observed in several different places (the units of Howth & Ireland's Eye, of Bray-Wicklow, and of Wexford) in SE Ireland (Gardiner & Vanguetaine, 1971; Bruck & Reeves, 1976; Bruck et al., 1979). *Oldhamia* has been observed in all these outcrop areas, but it is in the Bray-Wicklow Unit that the assemblages of traces are the most diverse: *Oldhamia*, *Arenicolites didymus*, *A. sparsus*, *Skolithos* sp., *Haughtonia poecila*, *Histioderma hibernicum*, *Ichnium watsii* and *Monocraterion* (Bruck & Reeves, 1976). The Bray Group in the Bray-Wicklow Unit forms a succession more than 4500 m thick, which starts with the Devil's Glen Formation, covered by the Bray Head Formation in which the *Oldhamia* can be observed. Green

and red greywacke of different grain-size and more rarely light coloured sandstones are interpreted as a thick relatively proximal turbiditic sequence (Vanguetaine et al., 2002).

Biostratigraphically, the acritarchs in the base of the sequence in the Ireland's Eye Unit allow to attribute an age of mid early to early middle Cambrian for these samples (Gardiner & Vanguetaine, 1971). Smith (1977) proposes an age of the middle part of the lower Cambrian for the Gaskin's Leap Formation in the Howth Unit. More recently, Vanguetaine et al. (2002) could narrow the age to the mid-late early Cambrian and link the acritarch assemblage to an interval comprising the undifferentiated Olenellid and the Protolenid-Strenuellid trilobite zones of Avalonia (Vanguetaine et al., 2002 p. 68 et fig. 5). The acritarch samples were taken in the upper part of the Bray Head Formation of the Bray-Wicklow Unit where *Oldhamia* was described for the first time (see above).

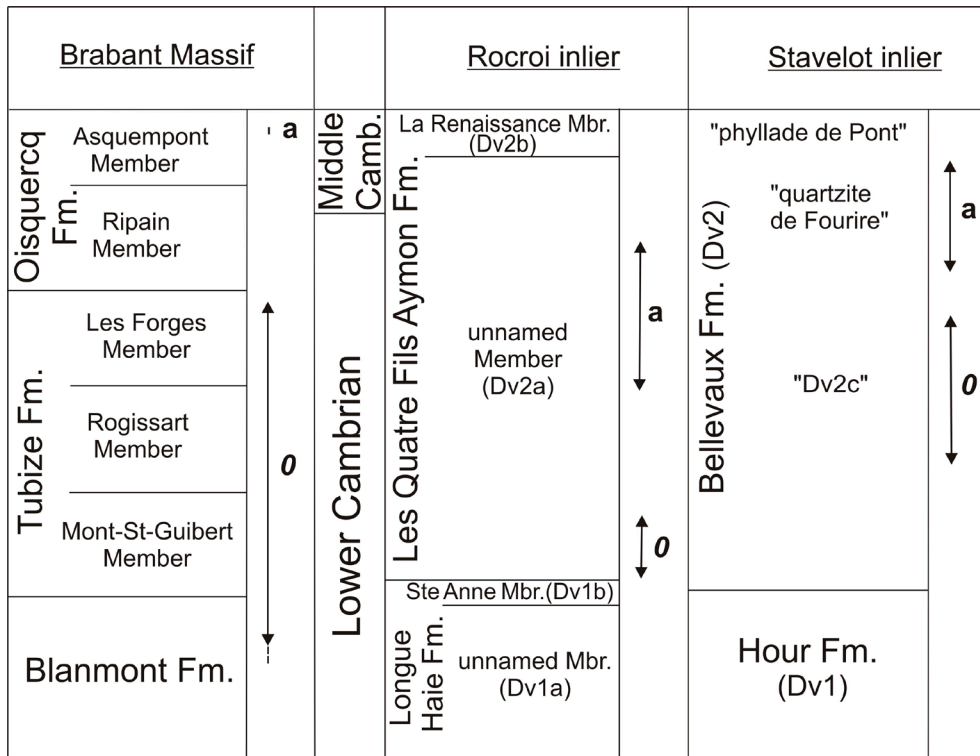
The acritarchs are located in the same formation as *Oldhamia*. Hence we can conclude that the *Oldhamia* of the Bray Head Formation belong to the trilobite zones Olenellid to Protolenid-Strenuellid, which in W Avalonia are situated in the Branchian Series (Geyer & Shergold, 2000 Table 1). In the global chronostratigraphy of the Cambrian (Peng & Babcock, 2008 fig. 4.5) the Branchian Series correspond to the interval from the upper third of Stage 3 to the top of Stage 4 (Fig. 2). The deep marine environment of deposition is dominated by turbidites (Woodcock, 2000 p. 145). The Bray Group is situated on West Gondwana, more precisely on the NW side of the future Avalonia microplate (Fig. 3).

### 2.2. Les Quatre Fils Aymon and Bellevaux formations, Deville Group, S Belgium (West Gondwana)

*Oldhamia radiata* and *O. antiqua* were already described at the end of the XIX century (Malaise, 1874, 1876, 1878; Dewalque, 1877) in the Deville Group of the Lower Palaeozoic inliers of the Ardennes. They occur more specifically in the Rocroi Massif at the base of the Lower Member of the Les Quatre Fils Aymon Formation ("Dv2a" *ex litteris*; Beugnies, 1960; Verniers et al., 2001) and in the Stavelot Massif in the middle part of the Bellevaux Formation ("Dv2" *ex litteris*; Corin, 1926; Verniers et al., 2001) (Fig. 1).

The Lower Member of the Les Quatre Fils Aymon Formation is 120-250 m thick and consists of thick beds of more or less coarse quartzite of a pale colour, separated by green or red slate (Beugnies, 1960, 1963). *Oldhamia* is observed in the more clayey lower 20 m of this member in the northern part of the Rocroi Massif (Beugnies, 1963 p. 383). Acritarchs are observed in the middle part of the same member (Vanguetaine, 1992 fig. 2) (Fig. 1). In the absence of any sedimentological study, the general lithology of the sequence and the presence of an important roofing slate interval in the top of the formation (La Renaissance Member, "Dv2b") suggest a deep marine environment of deposition.

The Bellevaux Formation in the Stavelot Massif (Corin, 1926; Geukens, 1999) is 150-300 m thick and

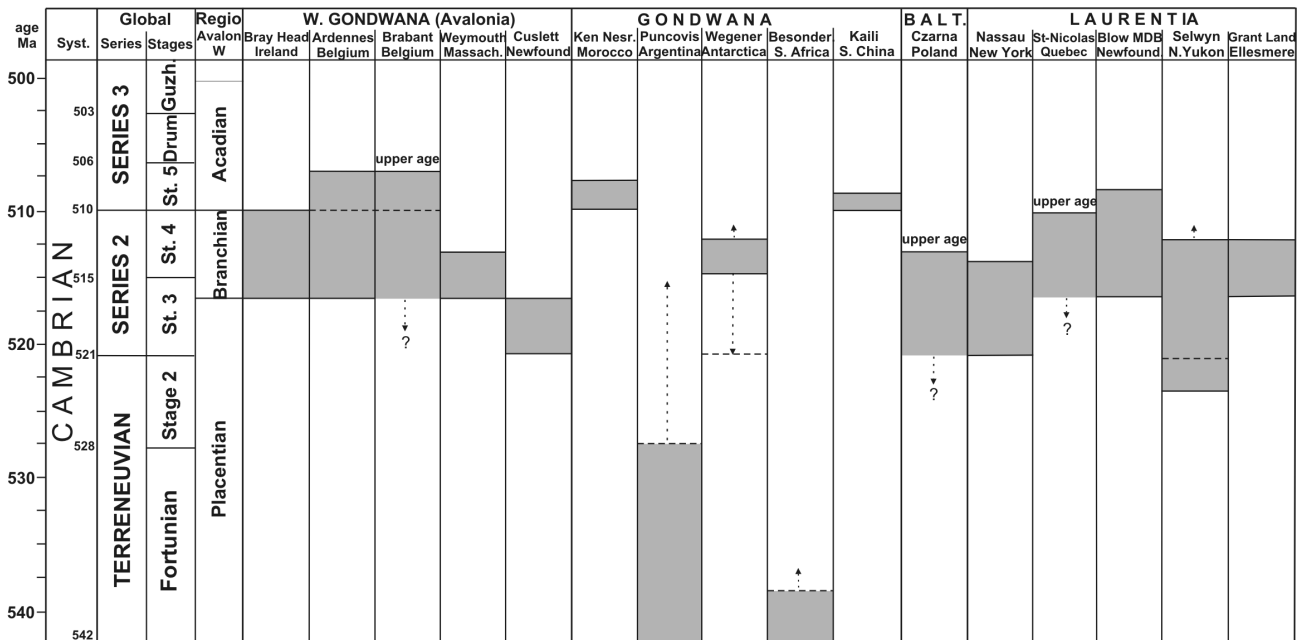


**Figure 1.** The position of levels with *Oldhamia* (O) and with acritarchs (a) in the lithostratigraphy of the Brabant Massif and the Stavelot and Rocroi inliers. The regional correlations proposed between the three areas and a part of the definitions used for the lithostratigraphy are slightly different from those proposed by Verniers et al. (2001). The units «phyllade de Pont» and «quartzite de Fourire» are after Anthoine (1940) and were used by Vanguetaine (1992 fig. 2 and 3), «Dv2c» is used in the sense of Corin (1926).

composed of an alternation of sandstone, siltstone and slate, red at its base and green higher-up. A sedimentological study by Von Hoegen et al. (1985) indicates a rapid transition from a shallow shelf at the base to a deep environment with turbiditic sedimentation higher. The acritarchs samples were taken in the upper part of the

formation in a local unit called “quartzite de Fourire” (Vanguetaine 1986, 1992 fig. 2), while *Oldhamia* is observed in the green slate and siltstone of the middle part of the formation (“Dv2c” *sensu* Corin, 1926) (Fig. 1).

Both formations contain a homogenous and similar acritarch assemblage allowing Vanguetaine (1992 p. 4)



**Figure 2.** Comparative chart with most confident time range, given with grey rectangles, of the *Oldhamia* occurrences from all areas mentioned in the literature and discussed in the text (see chapter 2). Horizontal full lines correspond to well dated lower or upper limits of the time range, horizontal dashed lines to probable limits. Vertical dashed lines with arrows indicate the possible extensions of the time range. For the occurrences where only the age of the covering unit has been established, the words «upper age» are added above the grey rectangle. In this case the upper full line of the grey rectangle corresponds to the upper age limit for the formation with *Oldhamia*. There is no lower line because the real lower limit is unknown and only a dashed line with an arrow pointing down with a question mark is shown. Series and stages, either local or global, and the ages of their limits are after Peng & Babcock (2008 fig. 4.5). Abbreviations: Syst.: Systems; Regio.: Regional; St.: Stage; Drum.: Drumian; Guzhangian.

to give them an age extending from the lower to the middle Cambrian, coeval with the Baltica trilobite zonation from the *Holmia* Superzone up to the *Paradoxides oelandicus* Zone. He adds that the correlation tends to indicate an age more restricted to the *Holmia* and *Protolenus* zones from the lower Cambrian, but without firm proof. This interval correspond in the W Avalonia zonation (Geyer & Shergold, 2000 Table 1) to the Branchian Series plus a part of the Acadian Series between the *Oryctocephalus indicus* Zone, base of Stage 5, and the base of *Ptychagnostus gibbus* Zone (Zhao et al., 2008).

The acritarchs and *Oldhamia* being found in the same formation (Fig. 1), we can conclude that the *Oldhamia* from the Les Quatre Fils Aymon and the Bellevaux formations have a lower to middle Cambrian age. In the new global chronostratigraphy of the Cambrian (Peng & Babcock, 2008 fig. 4.4 and 4.5) it corresponds rather surely with an age interval from the upper third of Stage 3 to the lower three quarters of Stage 5 (Fig. 2). In the Stavelot Massif the depositional environment is deep and of a turbiditic nature, it is probably the same in the Rocroi Massif. The Ardennes inliers belong to West Gondwana, more precisely on the SE side of the future Avalonia microplate (Verniers et al., 2002a).

### 2.3. *Blanmont and Tubize formations, Brabant Massif, N Belgium (West Gondwana)*

Also at the end of the XIX century *Oldhamia radiata* and *O. antiqua* were mentioned in the Blanmont and Tubize formations of the Brabant Massif (Malaise, 1883a, 1883b, 1900; Asselberghs, 1919; de la Vallée Poussin, 1932; Legrand, 1968; Van Tassel, 1986). But they were never described in some detail. The Blanmont Formation is now accepted to be the oldest outcropping formation of the Brabant Massif (Herbosch et al., 2008). It is covered by the Tubize Formation, which on its turn is covered by the Oisquercq Formation. From these three formations only the upper part of the latter (Fig. 1) contained acritarchs and could be dated (Vanguetaine, 1991, 1992). Its age is coeval to the interval from the *Holmia* Superzone to the *Paradoxides oelandicus* Zone in the Baltica trilobite biozonation. Vanguetaine (*op. cit.*) adds that several indices can narrow that age down to the two trilobite zones from the lower Cambrian, but without firm proofs.

The Blanmont Formation is mainly formed of massive quartzite with rare pelitic intercalations where *Oldhamia* were observed by Malaise (1900 p. 190). The very thick Tubize Formation (at least 2000 m) is made of greenish slates, siltstones and rhythmic thick alternation of feldspathic sandstone, siltstone and slate (Verniers et al., 2001). *Oldhamia* is observed in the three members of the formation (Fig. 1), with a preference for the siltstone interval of the turbidite sequence. No other trace fossil has been described in the three lowermost formations of the Brabant Massif. This stratigraphic interval corresponds with the interval of the Les Quatre Fils Aymon and the Belleville formations in the Ardennes Inliers (see above § 2.2 and Fig. 1).

We can conclude that the *Oldhamia* of the Blanmont and the Tubize formations have an upper age limit corresponding to the age of the Oisquercq Formation, which is the interval from the upper part of the lower Cambrian to the lower part of the middle Cambrian (*Holmia* Zone to *Paradoxides oelandicus* Zone). Similarly as for the Deville Group (see above §2.2) we can conclude that in the new global chronostratigraphy of the Cambrian (Peng & Babcock, 2008 fig. 4.4 and 4.5) this age corresponds to the interval from the upper third of Stage 3 to the lower three quarters of Stage 5 (Fig. 2). The environment of deposition changes from a shallow shelf or rift for the Blanmont Formation to a deep sea environment for the Tubize Formation where Herbosch & Verniers (2002) described hemipelagic sediments and low to high density turbidites. The Brabant Massif belongs to West Gondwana (SE side of the future Avalonia microplate).

### 2.4. *Weymouth Formation, Massachusetts, USA (West Gondwana)*

Howell (1922) was the first to describe *O. antiqua* in red shale of the Weymouth Formation, in Weymouth, Massachusetts. The specimen was recently retraced in the collections of the Smithsonian Institution by Dr. Mark McMenamin (pers. comm.) who confirmed the identification. This formation contains grey-green and red shale with limestone nodules and also some beds and lenses of clayey limestone (Goldsmith, 1991 p. E32). Outcrops of the formation are rare with no known complete section. Its thickness can only be estimated to be about 100 m. The covering unit, the Braintree Argillite, consists of shale and massive argillite (300 m) and can be dated to a middle Cambrian age. The two units can be considered as shallow water platform deposits. An outcrop 150 m NW of the locality where the *Oldhamia* was discovered and stratigraphically lower (Landing, 1988 p. 662) contains the trilobites *Callavia broeggeri* and *Strenuella strenua* (Burr, 1900), characteristic species of the *Callavia broeggeri* Zone in W Avalonia. This age of upper part of the lower Cambrian confirms an older study with small shelly fossils (Landing, 1988 fig. 4). Landing (1996, p. 49) demonstrated that the upper part of the Weymouth Formation correspond exactly with the Brigus Formation in SE Newfoundland which also belong to the *C. broeggeri* Zone.

The trilobites and *Oldhamia* being found in close proximity and in the same formation, we can conclude that the *Oldhamia* in the Weymouth Formation have an age coeval with the *Callavia broeggeri* Zone. This biozone is correlated in broad outline with the lower half of the Branchian Series (Geyer & Shergold, 2000 Table 1). In the global chronostratigraphy of the Cambrian (Peng & Babcock, 2008 fig. 4.5) this series is correlated with the interval from the upper third of Stage 3 to the lower third of Stage 4 (Fig. 2). The environment of deposition of this formation is interpreted as a shallow platform, belonging to the future Avalonia microplate (Goldsmith, 1991) (Fig. 3).



**Figure 3.** Distribution of *Oldhamia* occurrences on a palaeogeographic reconstruction at the boundary between middle and upper Cambrian at about 500 Ma (modified after Cocks & Torsvik, 2002). The approximate position of Mongolia is after Cocks & Torsvik (2007). The position of Nova Scotia (Meguma) between Gondwana and Avalonia is after Waldron et al. (2009 fig. 3). Belgium has two occurrences (Brabant Massif and Deville Group). Newfoundland 1 and 2 corresponds respectively to Blow Me Down Brook and Cuslett formations. The doubtful occurrence in Spain is not drawn.

### 2.5. Cuslett Formation, Burin Peninsula, SE Newfoundland, Canada (West Gondwana)

Ed Landing (pers. comm.) authorized us to mention an unpublished discovery of *Oldhamia* in the Cuslett Formation in the SE of the Burin Peninsula, Newfoundland (Landing, 1996 fig. 1, 2). These *Oldhamia* can be observed in Member 4 of the Cuslett Formation, 2-3 meter below the covering formation, which lies in unconformity and belongs to the *Callavia broeggeri* Zone. The Member 4 is thin and consists of red shale with thin cold-water limestone (shell ash), testifying a very shallow shelf deposit. The Cuslett Formation, with a thickness of about 200 m, is situated in the *Camenella baltica* Zone of the W Avalonia zonation.

As *Camenella* and *Oldhamia* are observed in the same formation, we could conclude that the *Oldhamia* belong to the *Camenella baltica* Zone. This zone placed at the top of the Placentian Series, is equivalent in the global chronostratigraphy of the Cambrian (Peng & Babcock, 2008 fig. 4.5) to the lower two thirds of Stage 3 (Fig. 2). The environment of deposition of this formation is interpreted as a shallow platform (Landing, 1996), belonging to the future Avalonia microplate (Goldsmith, 1991).

### 2.6. Kern Nesrani Formation, Sehoul Zone, NW Morocco (Gondwana)

El Hassani & Willefert (1990) described *Oldhamia flabellata* and *O. kernnesraniensis* n. isp. in the Kern Nesrani Formation in the Sehoul Zone, N of Rabat, Morocco. Seilacher et al. (2005), however, put the two species in synonymy with *O. antiqua*. These *Oldhamia* are observed very close to levels where the trilobite *Parasolenopleura* is observed, a species encountered in the *Paradoxides oelandica* Zone of Baltica (determination by G. Geyer same reference) from the lower part of the middle Cambrian.

The Kern Nesrani Formation, with a thickness of more than 300 meter, is made of decimetric to metric sandstone beds alternating with metric pelitic beds. El Hassani & Willefert (*ibid.*) interpret the environment of deposition as deltaic. However the description of this unit, with sandstone showing structures such as fining upward, oblique stratification, slumps and microbreccias, could suggest also a turbiditic environment. This seems to be corroborated by recent studies showing that the Ediacaran to middle Cambrian deposits of the western margin of Gondwana correspond to turbiditic infillings of rift systems (Vaughan & Pankhurst, 2008; Alvaro et al., 2008).

By their proximity to the trilobite level we can conclude that the *Oldhamia* of the Kern Nesrani Formation belong to the *Paradoxides oelandicus* Zone of the Baltica trilobite zonation. In the W Avalonia zonation it corresponds to the part of the Acadian Series under the *Ptychagnostus gibbus* Zone (Gyer & Shergold, 2000, table 1). In the global chronostratigraphy of the Cambrian (Peng & Babcock, 2008 fig. 4.4) this interval extends from the *Oryctocephalus indicus* Zone (base of Stage 5) to the base of the *Ptychagnostus gibbus* Zone (Zhao et al., 2008). The age of the Kern Nesrani Formation corresponds hence to the lower two thirds of Stage 5 (Fig. 2). The environment of deposition, initially interpreted as deltaic, can be more probably interpreted as deep marine of turbiditic type. The formation was deposited on the NW part of Gondwana (Fig. 3).

### 2.7. *Puncoviscana* Formation, NW Argentina (Gondwana)

Aceñolaza & Durand (1973, 1984) described *O. antiqua*, *O. radiata* and a new species *O. flabellata* in the Puncoviscana Formation from the NW of Argentina. It is the only region on the world where five of the six *Oldhamia* species have been observed (see § 1.2). The formation exhibits a very rich ichnofauna abundantly described in the literature (syntheses by Aceñolaza & Aceñolaza, 2007; Aceñolaza et al., 2009; Buatois & Mangano, 2004; Seilacher et al., 2005). The Puncoviscana Formation *sensu lato* forms one of the largest sedimentary basins of South America, extending at least 1000 km N-S and 250 km E-W. The basin shows a more than 3000 m thick predominantly terrigenous series, which was later metamorphosed and strongly tectonically deformed (Jezek et al., 1985; Aceñolaza & Toselli, 2009). The stratigraphy is poorly known because of the lithological homogeneities and the tectonic complexity, hampering lithostratigraphical correlation. As Aceñolaza & Aceñolaza (2007, p. 1) put it «...lithological correlation, dating and precise identification of sequences in the Puncoviscana basin are highly problematic, with the only clear data points provided by trace fossils and rare geochronological input...».

The sedimentological study by Jezek et al. (1985) could show that most of the infillings correspond to mass-gravity transport bringing in turbidites, debris-flow and conglomerates in an enormous submarine fan, prograding on pelagic sediments in a basin with a very long-lasting subsidence history. The massive red pelitic rocks correspond to pelagic sediments, while the rarely occurring carbonate series were deposited on rises. Directional sedimentary structures prove that the sediments were distributed by currents coming from the east (Jezek et al., 1985 fig. 3). The *Oldhamia* ichnofacies is preferentially encountered in the NW part of the basin in finely laminated distal turbidites (Jezek et al., 1985 fig. 1; Buatois & Mangano, 2003b, 2004).

The age of this formation is strongly debated by the palaeontologists (see for example Aceñolaza, 2005; Buatois & Mangano, 2005). For the majority of the authors

the sedimentation would have started in the Ediacaran or even before (Aceñolaza & Aceñolaza, 2007 fig. 2), and continued until the lower Cambrian. The controversy bears mostly on the age of the Cambrian part, which is restrained by the age of the unconformable covering Meson Group. However, in spite of the absence of arguments based on firm stratigraphical and palaeontological observations these authors arrive to the same conclusions relative to the age of *Oldhamia*: the lower part of the lower Cambrian for Aceñolaza & Aceñolaza (2007 fig. 2) and Adams et al. (2010, fig. 2) and Nemakitian-Daldynian for Mangano & Buatois (2004 fig. 1), Buatois & Mangano (2003b, 2005 fig. 1) and Seilacher et al. (2005). Both ages indeed correspond approximately to the Fortunian of the global chronostratigraphy of the Cambrian (Peng & Babcock, 2008 fig. 4.5).

U-Pb dating on detrital zircons (Adams et al., 2008, 2010) recently added new constrains. On one hand, the maximum age for the deposition of the base of the Meson Group would now be early Late Cambrian. This suggests that the sedimentation of the Puncoviscana Formation might have been continued until the middle Cambrian (Adams et al., 2010 fig. 2). On the other hand, the youngest U-Pb detrital zircon age components in the Puncoviscana Formation greywackes itself, some of which originate from contemporary volcanic sources, indicate a maximum depositional age in the early early Cambrian (JJ2:  $530 \pm 4$  Ma, LRJ1:  $525 \pm 3$  Ma) to late early Cambrian (CAC3:  $522 \pm 4$  Ma, AMP1:  $514 \pm 8$  Ma; Adams et al., 2010 table 1). This range extends down until the base of Ediacaran (8 samples from 545 to 636 Ma). These values prove that sedimentation has really started at the base of the Ediacaran, but, more importantly that it continued much after the lower part of the lower Cambrian, as it is still the opinion of the majority of authors.

Even if it would seem difficult to conclude objectively, seen the many contradictions in the literature, it seems reasonably to use the consensus of the palaeontologists, for whom the *Oldhamia* of the Puncoviscana Formation *sensu lato* obviously belong at the minimum to the Fortunian of the global chronostratigraphy of the Cambrian. But with the new detrital zircon ages it is not at all excluded that the *Oldhamia* can be observed until the top of Stage 3 (~515 Ma; Ogg et al., 2008) or even in Stage 4 (Fig. 2). The best argued interpretation of the environment of deposition is that of a continental slope along the S Pacific margin of Gondwana (Jezek et al., 1985; Do Campo & Guevara, 2005; Aceñolaza & Toselli, 2010).

### 2.8. Mount Wegener Formation, Shackleton Range, Antarctica (Gondwana)

Buggish et al. (1994) describe *O. radiata* and *O. antiqua* in the Mount Wegener Formation in the SE of the Shackleton Range on Antarctica. This formation is made of shale, greywacke and conglomerate and according to its sedimentological features deposited in a deep environment on a continental slope, possibly its upper

part (Buggish & Henjes-Kunst, 1999). This more than 600 m thick formation yields *Oldhamia* in its upper part, unit 6 composed of shale and sandstone. The underlying units 1, 4 and 5 contain carbonate olistoliths and conglomerates with carbonate clasts, in which archaeocyathids, cyanobacteria of the *Epiphyton-Girvanella* group and trilobites have been observed.

Buggish & Henjes-Kunst (1999 p. 227) suggest an Atdabanian age by the presence of these fossils and the high diversity of the archaeocyathids. In the global chronostratigraphy the Atdabanian corresponds to the lower half of Stage 3 (Peng & Babcock, 2008 fig. 4.5). Babcock & Peng (2007), Zhu et al. (2007 fig. 1) and Peng & Babcock (2008) all indicate that the archaeocyathids have their appearance at the middle of Stage 2, with their acme in the lower half of Stage 4 and their abrupt disappearance since the middle of the same Stage 4. The oldest trilobites are seen near the base of Stage 3 (Babcock & Peng, 2007; Peng & Babcock, 2008 p. 40). As a consequence a bit larger age interval seems prudent.

Hence we can conclude that *Oldhamia* recovered from the Mount Wegener Formation, just above the archaeocyathids, have an age that could extend from the base of Stage 3 (appearance of trilobites) to about the second half of Stage 4 (extinction of the archaeocyathids). The high diversity of the archaeocyathids hints towards the lower half of Stage 4 (Fig. 2). The environment of deposition of these turbidites and conglomerates is interpreted as a deep marine continental slope on the southern margin of Gondwana (Fig. 3).

### 2.9. *Besonderheid Formation, Vanrhynsdorp basin, South Africa (Gondwana)*

Gresse et al. (1996) mention the presence of *Oldhamia* in the Vanrhynsdorp Basin, forming the southern extremity of the large Nama Foreland Basin in Namibia and South Africa. The study of the rich ichnofossil assemblages in that basin indicates that the new species *O. geniculata* is present in the *Besonderheid Formation* (Knersvlakte Group), while the ichnospecies *Treptichnus pedum* (it first occurrence being used to define the base of the Cambrian, Landing et al., 2007) is present in the seven covering formations (Gresse & Germs, 1993; Buatois et al., 2007; Almond et al., 2008; Aceñolaza et al., 2009). The Knersvlakte Group contains terrigenous sediments deposited in a prograding deltaic succession (Gresse & Germs, 1993), with distal turbidites in the Gannaboos Formation, and more proximal turbidites in the succeeding *Besonderheid Formation*.

The age of the formation itself could not be constrained by fossils or by radiometric ages of interstratified tuffs. However, based on the stratigraphical succession of the observed trace fossils Almond et al. (2008 fig. 1) place the Ediacaran-Fortunian boundary at the base of the *Besonderheid Formation* and the seven covering formations in the Fortunian. In consequence the *Oldhamia* observed in the *Besonderheid Formation* would belong to the extreme base of the Fortunian. The surprising stratigraphical position of the *Oldhamia* below the levels

with *Treptichnus* is explained by the deeper turbiditic nature of the *Besonderheid Formation*.

We can conclude, even in the absence of classic biostratigraphical or radiometric arguments that the *Oldhamia* of the *Besonderheid Formation* belong to the extreme base of the Fortunian (Fig. 2). The deep environment is of a deltaic flysch type. The Vanrhynsdorp Basin is part of the southern margin of the Gondwana (Gresse, 1995).

### 2.10. *Grand Pitch Formation, Maine, USA (Dunnage, peri-Gondwana)*

Smith (1928) found *Oldhamia* in red shale in what is now called the Grand Pitch Formation (Neuman, 1962) in NE Maine (Appalachians). This formation shows an alternation of light-coloured quartzite, darker feldspathic quartzite and grey, green and red shale in variable proportion, deposited in a deep marine environment (Churchill-Dickson, 2007). This formation is covered in major unconformity by the Shin Brook Formation dated as "Arenig" (Neuman, 1997). Neuman (1962) describes other occurrences of *Oldhamia* along the Penobscot River in Grand Pitch and he attributes them to *O. smithi* Ruedemann. But Seilacher et al. (2005) would attribute them rather to *O. antiqua*.

The age of the Grand Pitch Formation is only constrained by the presence of *Oldhamia* and by the "Arenig" age of the covering formation, it is coarsely the whole of the Cambrian. No recent information (Marvinney, pers. comm.) allows narrowing down its age. The environment of deposition is deep marine with turbidites. This formation belongs to an oceanic arc sequence belonging to the peri-Gondwana Dunnage domain (Iapetan Realm of Hibbard et al., 2007b fig.1).

### 2.11. *Church Point Formation, Goldenville Group, Nova Scotia, Canada (Meguma, peri-Gondwana)*

*O. radiata* was recently discovered in the Church Point Formation of the Goldenville Group in SW Nova Scotia, Canada (Waldron et al., 2009; Gingras et al., 2011). It is a part of the Meguma Supergroup in the new nomenclature of White (2008) characterized by a very thick terrigenous succession of more than 10 km, extending from the Cambrian and possibly late Ediacaran to the base of the Tremadocian. The basal Goldenville Group, with a thickness of 6 to 8 km, is composed of a monotonous sequence of thick light-coloured sandy turbidites, while the succeeding Halifax Group is made of dark-coloured silty turbidites.

The *Oldhamia* in the High Head Member is accompanied by abundant other trace fossils as *Helminthopsis*, *Phoebichnus*, *Psammichnites* and *Taenidium*. The 700 m thick sequence of grey-green metasilstone is intercalated in the middle of the Church Point Formation, which is composed of thick to very thick sandstone beds with rare interbeds of siltstone and green or black shale (White et al., 2005; Waldron et al., 2009 fig. 1). The only biostratigraphical constraint is the presence



at the top of the Goldenville Group of a trilobite faunule of middle Cambrian age (Pratt & Waldron, 1991).

In conclusion the age of the High Head Member of the Church Point Formation is only constrained by the presence of *Oldhamia* and the middle Cambrian age of the top of the Goldenville Group. The age of the beds containing the *Oldhamia* could be from basal Cambrian to somewhere in the middle Cambrian. The environment of deposition is deep marine from a turbiditic fan system to a basin-plain (Waldron & Jensen, 1985). The Meguma Supergroup belongs to the peri-Gondwana terranes (Hibbard et al., 2007a, b; Waldron et al., 2009).

### 2.12. Czarna Shale Formation, Holy Cross Mountains, S Poland (Baltica?)

Kowalski (1983, 1987 plate I) describes *O. antiqua* at the base of the Czarna Shale Formation in the Małopolska block of the Holy Cross Mountains in south-central Poland. This formation consists of an 800 m thick succession of sandstone, siltstone and shale. The Cambrian units start above an unconformity with the 30 m thick Osiek Sandstone Formation in which the ichnospecies *Treptichnus pedum* is found. *Oldhamia* is observed in the more silty lower member of the Czarna Shale Formation at less than about 100 m above the levels with *Treptichnus* (Kowalski, 1987 fig. 2). For Jaworowski & Sikorska (2006), the Holy Cross Mountains were part of a large terrigenous shelf belonging to the passive margin of Baltica.

The age of the Czarna Shale Formation is poorly established with contradicting opinions and no recently published studies (Zylinska, pers. comm.). Pozaryski et al. (1981 in Polish, in Kowalski, 1983 p. 184 and p. 195; 1987 p. 31) dated the lower member using acritarchs as coeval with the *Holmia* and *Schmidtiellus* Baltica trilobite zones, which correspond to the middle part of the lower Cambrian. On the other hand, according to Kowalski (*op. cit.*) the presence of the ichnospecies *Sabellidites cambriensis* shows that these strata belong to the extreme base of the lower Cambrian. What is however well established is the age of the covering formation, the Ocieseki Formation (Orlowski, 1989, 1992): its lower part could be dated with trilobites from the *Holmia* Zone to the *Schmidtiellus* Zone of Baltica. This corresponds in the W Avalonia zonation (Gyer & Shergold, 2000 table 1) to the *Camanella baltica* and *Callavia broeggeri* zones. This interval extends in broad outline from the appearance of the trilobites to the lower half of the Branchian Series.

With these conflicting opinions we can only conclude that *Oldhamia* of the Czarna Shale Formation has an upper age limit corresponding to the age of the Ocieseki Formation, which in the global chronostratigraphy of the Cambrian (Peng & Babcock, 2008 fig. 4.5) corresponds to the interval from the base of Stage 3 to the lower third of Stage 4 (Fig. 2). The environment of deposition is shallow on the distal part of the shelf. The palaeogeography of the Holy Cross Mountains is also debated: either it is a peri-Gondwana terrane (for example Belka et al., 2000) or part of Baltica (Cocks, 2002; Jaworowski & Sikorska, 2006;

Nawrocki & Poprawa, 2006; Nawrocki et al., 2007), with the latter more favoured in recent publications.

### 2.13. Nassau Formation, New York, USA (peri-Laurentia, Dunnage)

The first discovery of *Oldhamia* in the United States was by Walcott (1894) in reddish shale, associated with green shale and thin sandstone beds of the Nassau Formation. Other occurrences are mentioned by Dale (1904 p. 13) and Ruedemann (1929). The species *O. occidens* created by Walcott is attributed by Seilacher et al. (2005) to *O. radiata*. In the allochthon of the Appalachians, the thrust unit of Gidding Brook shows a 600 m thick condensed series extending from the highest Ediacaran to the Late Ordovician (Stanley & Ratcliffe, 1985; Landing, 2007 fig. 5). The Nassau Formation consists at its base of the Bomoseen Member, made of greywacke in grey-green shale, followed by the Truthville Member formed by green and reddish shale with large bioturbations and some sandstone beds. The whole sequence was deposited in a deep marine environment with a turbiditic sedimentation on a continental slope (Stanley & Ratcliffe, 1985; Landing, 2007).

The recent discovery of a trilobite sclerite at the top of the Bomoseen Member (Landing, 2007 p. 18), while *Oldhamia* is observed in the covering Truthville Member (Landing, pers. comm.) provides a lower age limit for *Oldhamia*, because the first trilobites appear at the base of Stage 3. An upper limit is given by the age of the Browns Pond Formation, overlying the Nassau Formation, in which the lower *Elliptocephala assaphoides* assemblage is observed (Landing, 2007 fig. 5). The age of this assemblage is still debated (Landing, 2007 p. 20), but is generally attributed to the middle part of the *Bonnia-Olenellus* Zone, while other authors place it rather at the base of this zone (Landing & Bartowski, 1996; Hollingworth, 2005; Landing, pers. comm.).

In conclusion the *Oldhamia* of the upper part of the Nassau Formation have an age between the appearance of the trilobites and the middle part of the *Bonnia-Olenellus* Zone, which corresponds in the global chronostratigraphy of the Cambrian (Peng & Babcock, 2008 fig. 4.4) broadly taken to the interval from the base of Stage 3 till the lower part of Stage 4 (Fig. 2). This formation is part of a sequence of deep marine deposits on the western margin of the Iapetus Ocean belonging to the peri-Laurentia Dunnage domain (Iapetan Realm of Hibbard et al., 2007b).

### 2.14. Saint-Nicolas Formation, Sillery Group, South Quebec, Canada (Laurentia)

Lapworth (1886) and later Walcott (1894) were the first to report the presence of *Oldhamia* in the Sillery Group in southern Quebec. More recently, Sweet & Narbonne (1993) described there *O. curvata* together with a new species *O. smithi*, but Seilacher et al. (2005) consider *O. smithi* as a junior synonym of *O. curvata*. The Sillery Group consists of the Sainte-Foix, the Saint-Nicolas and the Breakeyville formations (St-Julien & Osborne, 1973).

These 1000 m thick units consist of an alternation of shale and feldspathic sandstone, deposited in a deep marine environment. The *Oldhamia* were observed in the Saint-Nicolas Formation, which consists of an alternation of green, black or red shale with sandstone beds.

The Saint-Nicolas Formation is devoid of fossils, but the overlying Breakeyville Formation contains the inarticulate brachiopod *Botsfordia pretiosa* (Ulrich & Cooper, 1938). In W Avalonia trilobite zonation *Botsfordia* extends from the *Callavia broeggeri* Zone to the top of the lower Cambrian (Sweet & Narbonne, 1993 p. 70). This interval corresponds exactly to the Branchian Series (Geyer & Shergold, 2000 Table 1).

Hence, the *Oldhamia* in the Saint-Nicolas Formation have an upper age limit corresponding to the age of the Breakeyville Formation, which is the upper part of the lower Cambrian or the Branchian Series. In the global chronostratigraphy of the Cambrian (Peng & Babcock, 2008 fig. 4.5) this age extends from the upper third of Stage 3 to the top of Stage 4 (Fig. 2). The environment of deposition is deep marine of turbidite fan type (Hesse & Ogunyomi, 1982).

### 2.15. Blow Me Down Brook Formation, Newfoundland, Canada (Laurentia)

Lindholm & Casey (1989, 1990) described *Oldhamia* in numerous outcrops of the Blow Me Down Brook (BMDB) Formation belonging to the Humber Arm Allochthon on the SW coast of Newfoundland. The many species include the very frequent *O. smithi*, *O. flabellata* and *O. curvata* and the rare *O. radiata* and *O. antiqua*. Seilacher et al. (2005) consider that the specimens determined as *O. smithi* belong rather to *O. antiqua*. Several other occurrences are described by Gillis & Burden (2006). The Humber Arm Allochthon has at its base the Curling Group ranging in age from the top of the Ediacaran (?) to the lower Cambrian. This group contains the Summerside and the Irishtown formations but also the BMDB Formation, considered as a more distal equivalent of the two other formations (Burden et al., 2001 fig. 2). The BMDB Formation, about 400 m thick is mainly built up of conglomerate, lithic subarkose, and sandstone in thick grey or green beds interstratified with black, green or red shale. The very abundant sedimentary structures show that these rocks were deposited by gravity-driven processes in a deep marine environment of turbidite fan type, probably in a marginal rift system (Gillis & Burden, 2006).

The only fossil collected in the Curling Group is a trilobite fragment in a limestone clast of the Irishtown Formation (Lindholm & Casey, 1990). Acritarchs were mentioned in the black shale of the BMDB Formation (Palmer et al., 2001; Burden et al., 2005), but the preliminary study does not allow yet an accurate dating (Burden, pers. comm.). Indirect dating is however possible based on the stratigraphical relation with the units in the Humber Arm Autochthon, which are richer in fossils (Burden, pers. comm.). Indeed the Forteau and Hawke Bay formations are partially the lateral equivalents of the

upper part of the BMDB Formation. The very top of the Hawke Bay Formation contains trilobites of the *Plagiura-Poliella* Zone (equivalent to the *Oryctocephalus indicus* Zone; Geyer & Shergold, 2000 Table 1) marking an upper age limit. The Forteau Formation and the lower part of the Hawke Bay Formation contain trilobites and archaeocyathids of the *Bonnia-Olenellus* Zone forming a lower age limit.

We can conclude, under the reservation that the regional correlations can not exactly be proven, that the *Oldhamia* in the BMDB Formation have an age coeval to the interval from the *Bonnia-Olenellus* Zone to the *Plagiura-Poliella* Zone of Laurentia. In the global chronostratigraphy of the Cambrian (Peng & Babcock, 2008 fig. 4.4) this age extend about from the upper third of Stage 3 to the lower third of Stage 5 (Fig. 2). The environment of deposition is of a deep marine turbidite fan type, probably in a marginal rift system. The Humber Arm Allochthon belongs to the margin of the Laurentia continent (Lindholm & Casey, 1990).

### 2.16. Selwyn, Barn and British Mountains from North Yukon, Canada and Brooks Range from NE Alaska, USA (Laurentia)

Hoffman & Cecile (1981) describe *Oldhamia* in the area of Nidderly Lake in the Selwyns Mountains of central Yukon. This study has been completed by new finds in the same area and also in the Neruockpuk Formation of the Barn and the British Mountains from northern Yukon (Hoffman et al., 1994). The *Oldhamia* probably are originating from a comparable stratigraphical level (Lane, 1991) as these found in NE Alaska (Mertie, 1937; Churkin & Brabb, 1965). The sediments from the Nidderly Lake area show numerous trace fossils: *O. radiata*, *O. flabellata*, *O. watsi*, *O. curvata*, *Planolites* isp., *Helminthoidichnites* isp. As in other cases Seilacher et al. (2005) consider *O. watsi* a form close to *O. radiata*.

All *Oldhamia* from the Nidderly Lake area occur in the middle of the Unit ICma, a 100 m thick unit of chestnut brown and green argillite with siltstone intercalations. The discovery of archaeocyathids in the Unit Ca at about 100 m above the argillite with *Oldhamia*, allows dating them as lower Cambrian. The *Oldhamia* from the Barn and the British Mountains are recovered from the same very characteristic argillite and siltstone unit, however, without any other fossils. On the contrary in the Alaskan part of the British Mountains archaeocyathids have been observed at the same stratigraphical level as where the *Oldhamia* occur (Churkin & Brabb, 1965 fig. 3). This unit that comprises turbidites, coarse-grained sandstone, conglomerate and limestone has been deposited in a deep basin (Hoffman & Cecile, 1981). The archaeocyathids appear near the middle of Stage 2, have their acme in the lower half of Stage 4 and there is a consensus that they disappear abruptly from the middle of Stage 4 (Zhu et al., 2007 fig. 1; Babcock & Peng, 2007).

Considering the stratigraphical proximity of the levels with archaeocyathids and with *Oldhamia* we can conclude that the *Oldhamia* in the unit of chestnut brown and green

argillite from northern Yukon and also from NE Alaska have an age only constrained by the time range of the archaeocyathids. In the global chronostratigraphy of the Cambrian this interval is rather long, extending from the upper part of Stage 2 to about the middle part of Stage 4 (Fig. 2). The environment of deposition is deep of a turbiditic type, probably on a prograding margin (MacNaughton et al., 2005). The Selwyn Basin belongs to the passive Pacific margin of the Laurentia continent (Dewing et al., 2004), while the Barn and the British Mountains are part of the Arctic Alaska plate with a still debated origin (Lane, pers. comm.).

### 2.17. Grant Land Formation, Northern Ellesmere Island, Canada (Laurentia)

Hoffman et al. (1994) describe *Oldhamia* in the upper part of the Grant Land Formation on the northern part of Ellesmere Island, Canada. Various species have been observed: *O. radiata*, *O. flabellata*, *O. antiqua*, and *O. curvata*, accompanied by *Didymaulichnus* sp. and *Planolites* sp. The upper member of this approximately 1500 m thick formation is mainly composed of sandstone interstratified with shale of different colour. The environment of deposition is interpreted as a deep submarine fan system. The top of the Grant Land Formation at about 100 or 200 m above the levels with *Oldham* is regionally correlated with the upper part of the lower Cambrian by the occurrence of trilobite of the *Bonnia-Olenellus* Zone of the Laurentia biozonation (Trettin et al., 1991).

We can conclude, even if the correlation is at a regional scale, that the *Oldhamia* of the upper part of the Grant Land Formation have an age corresponding to the upper part of the lower Cambrian, more exactly the local stage Dyeran (Gyer & Shergold, 2000). In the global chronostratigraphy of the Cambrian (Peng & Babcock, 2008 fig. 4.4 and 4.5) this age corresponds broadly taken to the interval from the upper third of Stage 3 to the lower half of Stage 4 (Fig. 2). The environment of deposition is a deep submarine turbidite fan system. The sequence was deposited in the Franklinian Basin belonging to the northern margin of Laurentia (Dewing et al., 2004).

### 2.18. Kaili Formation, Guizhou, China (South China)

*O. radiata* in association with a very rich ichnofauna of the *Cruziana* facies has been described by Yang (1994 plate I fig. 7) in the Kaili Formation of Taijing, Guizhou (SW China). The middle part of this formation became famous under the name of the Kaili Biota not only because of its remarkable diversity in ichnofossils (Lin et al., 2010), but also because of the exceptional conservation of the body fossils (trilobites, echinoderms, arthropods, etc...). The Kaili Biota is known as a Burgess Shale-type Fossil Lagerstätte.

The formation, about 200 m in thickness, consists mainly of shale and silty mud rock except at its base and top where carbonate rocks are interstratified with shale. The environment of deposition corresponds to the external

part of the Yangtze platform with depths close to the lower limit of the photic zone and in the zone of distal tempestites (Lin et al., 2010). The Kaili Biota is situated in the terrigenous central part of the Kaili Formation and corresponds to the *Oryctocephalus indicus* trilobite Zone (Lin et al., 2010 fig. 1), characterizing the lower part of Stage 5 in the global chronostratigraphy of the Cambrian (Peng & Babcock, 2008 fig. 4.4). The base of the *Oryctocephalus indicus* trilobite Zone in the Kaili Formation has been proposed as GSSP of Stage 5 (Zhao et al., 2007).

Because of the occurrence of *Oldhamia* in the Kaili Biota (Lin et al., 2010 Appendix A «*Oldhamia* rare in the Kaili Biota») we can affirm that their age is exactly the lower third of Stage 5. This region belongs to the South China terrane, situated to the E of the NE border of Gondwana (Cocks & Torsvik, 2002).

### 2.19. Poorly documented or doubtful occurrences

*O. radiata* was observed in the Bayan Gol Formation in the Zavkhan basin of Mongolia (Goldring & Jensen, 1996 fig. 2). Unfortunately the Tayshir I section where they are found has not been well correlated stratigraphically. Older references seem to indicate that it would belong to the Atdabanian (*op. cit.* p. 411) corresponding in the global chronostratigraphy of the Cambrian (Peng & Babcock, 2008 fig. 4.5) to the lower half of Stage 3. The environment of deposition of the strata is probably shallow due to the presence of limestone levels.

Crimes et al. (1977 plate 6 and p. 121) describe *O. radiata* in the Vegadeo Limestone of the lower Cambrian in Ponferrada (northern Spain). The environment of deposition is certainly shallow. The photos are not demonstrative and the authors state that: “the specimens are fragmentary and the burrows tectonically deformed. While they are provisionally included within this ichnogenus, some specimens bear a slight resemblance to *Zoophycus*”. Hence this occurrence is considered as doubtful.

## 3. Synthesis and discussion

### 3.1. The stratigraphical time range of the genus *Oldhamia*

As enumerated in the previous chapters and as far as the overview is complete, the ichnogenus *Oldhamia* has been encountered in 19 different areas worldwide. Only 16 of them have been dated accurately enough to constrain the stratigraphical time range in which the producers of the ichnogenus have lived in the Cambrian. The three unusable occurrences are: the Grant Pitch Formation (Maine, § 2.10), the Church Point Formation (Canada, § 2.11), both with a too widespread time range and the poorly documented Mongolian occurrence (§ 2.19).

The synthesis of the stratigraphical time ranges of *Oldhamia* is shown graphically in Fig. 2, where the most confident deduced time range is indicated in a grey rectangle for each of the 16 occurrences. This figure is

based on the Cambrian time scale of Peng & Babcock (2008 fig. 4.5), published under the umbrella of the International Stratigraphical Commission (Ogg et al., 2008). Horizontal full lines correspond to well dated lower or upper limits of the time range, horizontal dashed lines to probable limits. Vertical dashed lines with arrows indicate the possible extensions of the time range. For the occurrences where only the age of the covering formation has been established, the words «upper age» were added above the grey rectangle. In this case the upper full line of the grey rectangle corresponds to the upper age limit for the formation with *Oldhamia*. There is no lower line because the real lower limit is unknown and only a dashed line with an arrow pointing down with a question mark is shown. When the covering formation is used to date the *Oldhamia* bearing unit, the grey rectangle gives nevertheless a rough estimation of the age of the lower limit.

We can immediately observe from Fig. 2 that the 16 occurrences are stratigraphically distributed in two distinct age groups: a small group of two “older” *Oldhamia* occurrences in a not very well delimited part of the Fortunian and a second, “younger” group with 14 *Oldhamia* occurrences densely distributed between the base of Stage 3 and the lower three quarters of Stage 5. Both groups are separated by a large interval with no occurrences of *Oldhamia* corresponding to Stage 2. This repartition in two unequal groups separated by an interval devoid of *Oldhamia* is at first sight astonishing and raises questions about its interpretation. Therefore we have to evaluate in detail the value of each of the particular stratigraphic constrains in both groups.

### 3.1.1. The younger group with 14 occurrences

In this group with 14 occurrences, 10 are very well dated by using macro- or microfossils present in the same formation containing the *Oldhamia*: it is formations of Bray Head (Ireland), Ardennes (S. Belgium), Weymouth (Massachusetts), Cuslett (Newfoundland), Kern Nesrani (Morocco), Mount Wegener (Antarctica), Nassau (New York), Kaili (S. China), Blow Me Down Brook (Newfoundland) and Grant Land (Ellesmere). The two latter occurrences are slightly less well dated because indirect stratigraphical correlations have been used (see above §2.15 and 2.17). However the largest stratigraphical interval corresponding to these ten occurrences all stretches as mentioned above from the base of Stage 3 to the lower three quarters of Stage 5. The number and the quality of the stratigraphical constrains allow to ascertain that the *Oldhamia*-maker have lived at least within that given time range.

The other 4 occurrences have an age range clearly less constrained, because either only the age of the covering formations could be used (Brabant, N. Belgium; Czarna, Poland and St-Nicolas, Quebec), or only long ranging fossils (Selwyn, N. Yukon). The upper limit is always very well defined, even when it is an upper age limit, and it is never higher than the lower three quarters of Stage 5 (Fig. 2), confirming and reinforcing the previous value.

On the other hand, the lower limit is unknown, because the age is defined in the covering formation (as explained above) and therefore these three occurrences are not very useful to constrain the lower age. However we can observe that the age intervals of the covering formations (the grey zone in Fig. 2) are situated above the base of Stage 3, even largely above in the case of Brabant (N. Belgium) and St-Nicolas (Quebec). Finally for Selwyn (N. Yukon), which dating is only based on the presence of archaeocyathids, the lower age limit corresponds to the appearance of that group near the middle of Stage 2, where they only occur rarely.

In summary we can conclude that the younger group of 14 occurrences with *Oldhamia* occur in a well-constrained time range from the base of Stage 3 to the lower three quarters of Stage 5. The interval is very well constrained by 14 occurrences for its upper limit and by 11 occurrences for its lower limit. We can however not exclude that the lower limit might extend slightly down into the upper part of Stage 2 (Poland, N. Yukon), but it seems unlikely.

### 3.1.2. The older group with two occurrences

The discussion on the oldest group with the two occurrences is particularly delicate, because, as seen above, the ages proposed in the literature are often contradictory, inaccurate or expressed in local chronostratigraphical terms, with unclear correlations with the global chronostratigraphy. These ages are not based on fossils or sure radiometric dating as based for example on interstratified tuffs. And at last, the particular context of the Terreneuvian, where the difficulty to find wide distribution fossils has not yet allowed the construction of a global biostratigraphy, even if the base has formally been defined (Landing et al., 2007).

The absence of a litho- and biostratigraphy in the Puncoviscana Formation (Argentina, § 2.7) is clearly at the origin of many controversies about its deposition age and, by consequence, about the *Oldhamia* age. With the absence of body fossils, only trace fossils deliver the arguments for dating, which are, admittedly rather tenuous or even based on circular reasoning, when based on the presence of *Oldhamia* (even if this is not clearly said so). For the majority of the palaeontologists, the age of *Oldhamia* in this formation seem to correspond globally to the Fortunian. However, the recently obtained U-Pb ages on detrital zircons show, contrary to what was previously thought, that the sedimentation probably continued later than that stage into the upper part of the lower Cambrian. Hence, in the absence of stratigraphical correlations, the *Oldhamia* could probably occur in younger levels than the Fortunian. The presence of five species of *Oldhamia* in this formation goes in the same direction as this hypothesis.

The age of the Besonderheid Formation (South Africa, § 2.9) is better argued and more precise: it is the extreme base of the Fortunian. However again it is an age based solely on the interpretation of trace fossils. The stratigraphic succession is very well known, as is the

sedimentological and tectonic history of the basin, but without any time constraints by fossils or radiochronology.

In summary, the stratigraphical time range in which *Oldhamia* occurred in this older group of two occurrences seems in our opinion poorly constrained, in particular for the Puncoviscana Formation. The published evidence of that interval seems to extend over the whole of the Fortunian. However, because of the weakness of the stratigraphical constraints and the presence of only two occurrences, we can seriously question their stratigraphical position at the base of the Cambrian. This doubt is sharpened in comparison with the younger group of 14 occurrences which are very well constrained in age, and stratigraphy and numerically much more important. Moreover, the absence of *Oldhamia* during Stage 2 remains difficult to explain.

### 3.2. Palaeogeographic distribution and environment of deposition

The *Oldhamia* occurrences plotted on the palaeogeographic map of the top of the middle Cambrian at about 500 Ma (Cocks & Torsvik, 2002), clearly show that these trace fossils had a vast distribution (Fig. 3). They are indeed numerous on margins of the Iapetus Ocean with three occurrences on the Laurentia side, one on the Baltica side and four on the West Gondwana (Avalonia) side of that ocean. The two Belgian occurrences on SE of the future Avalonia and the one on Nova Scotia (Meguma) seem to correspond to the opening of a rift (initiator of the Rheic Ocean) between Gondwana and Avalonia (Nance & Linnemann, 2008; Waldron et al., 2009 fig. 3). They are also present on the margins of the Panthalassic Ocean, north of Laurentia with two occurrences and south of Gondwana with three occurrences. Two isolated occurrences are also observed on the South China and Siberia terranes. They are found at all palaeolatitudes of the southern hemisphere (Fig. 3), from high (Belgium, Morocco, Ireland) to low latitude (Ellesmere, Yukon, Newfoundland, Quebec, New-York, Antarctic). With such a large repartition, *Oldhamia* can be considered to have had a cosmopolitan distribution.

The environment of deposition of the sequences with *Oldhamia* is most often deep marine from continental slope to turbidite plain. The *Oldhamia* bearing sequences are often thick to very thick, measuring several thousands of meters in the cases of the Bray, Tubize, Puncoviscana, Goldenville, N. Yukon and Grant Land formations. They are often deposited by turbidity currents or other gravity driven processes and alternate in variable amount with hemipelagic or pelagic deposits. *Oldhamia* is most often recovered in shale or siltstone of green, red or more seldom black colour. A typical example is the Church Point Formation, in which 600 m of green shale with *Oldhamia* interrupt a 6 km thick turbidite sequence (cf. § 2.10). These series were mostly deposited on passive margins of palaeocontinents, as the Deville Group and Tubize Formation on SE Avalonia, the Puncoviscana and Wegener formations on Gondwana, the Nassau, St

Nicolas, N. Yukon and Ellesmere formations on Laurentia and also the Kaili Formation on S China. Some of the sequences are interpreted to have been deposited in a rift system (Kern Nesrani, Church Point, Blow Me Down Brook) or more rarely in foreland basin (Besonderheid). The present overview confirms, as was emphasized since long and in particular by Seilacher (1974; see also Seilacher et al., 2005), that the large majority of *Oldhamia* occurrences are encountered in deep marine settings, often in thick terrigenous sequences of a flysch facies type, deposited on passive margins.

Nevertheless, this review also shows that a few of the *Oldhamia* occurrences without doubt have been deposited in a shallow or very shallow environment: some of them on an external shelf (Czarna, Poland; Kaili, S. China), some on a shallow or very shallow carbonate shelf (Cuslett, Newfoundland; Weymouth, Massachusetts), some on a shallow shelf or in a rift setting (Blanmont, N. Belgium) or perhaps in a delta (Kern Nesrani, Morocco). The rarity of *Oldhamia* in shallow environments can easily be explained by the poor chance of its preservation in these more strongly bioturbated environments. As shown above (§ 1.1) the Cambrian agronomic revolution started in the shallow environments since about the middle of the Stage 2 to the base of Stage 3 (Seilacher et al., 2005). The majority of *Oldhamia* occurrences are seen later in Stages 3, 4 and 5 (Fig. 2).

We can conclude that the Cambrian *Oldhamia*-maker probably lived in a large spectrum of sedimentary environments from a shallow platform to the abyssal plain, with a majority occurring in a deep oceanic environment. The time lag of the appearance of the Cambrian agronomic revolution according to the depth of deposition gives a rational explication for the rare occurrence of *Oldhamia* in shallow marine environments.

## 4. Conclusions

In our exhaustive review of the literature we show that the ichnogenus *Oldhamia* has been encountered in Cambrian strata from 19 different localities distributed worldwide. We have evaluated the stratigraphic arguments used to determine the time range of occurrence in the global Cambrian chronostratigraphy for each of these 19 sites (cf. chapter 2). We can conclude that in only 16 localities sufficient precision is present to constrain the stratigraphical interval during which *Oldhamia* lived in the Cambrian. Fig. 2 synthesizes all the individual stratigraphic data and it allows establishing that the 16 occurrences are globally dispersed from the base of the Fortunian until the lower three quarters of Stage 5, with a large majority however present from the base of Stage 3 to the top of Stage 4.

More in detail, the occurrences are clearly dispersed in two age groups of unequal size, separated by an interval without *Oldhamia* occupying the larger part of Stage 2. In a first “younger” group of 14 occurrences, the *Oldhamia* show a very well constrained time interval running from the base of Stage 3 to the lower three quarters of Stage 5. A second “older” group with two occurrences shows a

much less constrained time interval with for the Besonderheid Formation the extreme base of the Fortunian and for the Puncoviscana Formation probably the entire Fortunian, even if recent geochronological results open the possibility for an age ranging into the upper part of the lower Cambrian. We hereby raise the question on the reliability of the stratigraphic position of this small group of only two occurrences, isolated at the base of the Cambrian.

With the contrasting situation between on the one hand a group of 14 occurrences of *Oldhamia*, stratigraphically well constrained, and on the other hand, a group consisting of only two occurrences only dated with weak stratigraphical arguments, we would be tempted not to take further into account the second small group. We have however to remain suspicious and stay away from hasty conclusions and particularly here, due to the lacunar nature of the palaeontological recording of the very old sequences and the particular context of the Terreneuvian. Consequently, we propose two alternative interpretations. A first interpretation consists to accept the results from the literature as they are, even if some are less well argued. We can only hope that future research on these sites or on newly discovered ones, will allow clarifying the stratigraphical context of the disputed occurrences. Another more restrictive alternative is to consider the “older” group with only two *Oldhamia* occurrences poorly dated as Fortunian, as scientifically insufficiently substantiated and hence to reject their age determination. In this latter interpretation only the age of the “younger” group of 14 occurrences should be kept as reliable.

In the first interpretation *Oldhamia* would have appeared at the base of the Fortunian, either slowly evolving or only in a few more favourable geographic places, what would explain the low number of discovered occurrences. They would have evolved and slowly dispersed all along the Terreneuvian, the longest of the Cambrian series (about 20 Ma). Subsequently they would have reached their acme, clearly in Stages 3 and 4 (Fig. 2), and disappeared very rapidly before the end of Stage 5. In this interpretation, it is nevertheless rather difficult to explain the very low number of occurrences observed in the Fortunian and then their absence during the larger part of Stage 2. It seems also difficult to explain why the Puncoviscana Formation, supposedly in the basal most Cambrian, would already contain the highest biodiversity of *Oldhamia* (5 of the 6 described species).

In the second interpretation, *Oldhamia* would have appeared, at its earliest, in the second half of the Stage 2 and more probably at its top. Thereafter they would have developed and dispersed rapidly during Stage 3 and 4. Indeed, as can be seen on Fig. 2, nearly the entire group of 14 occurrences has an age between the base of Stage 3 and the top of Stage 4. We interpret this interval (about 11 Ma) as the maximal development or the acme of the ichnogenus *Oldhamia*. At last, they would have disappeared very rapidly during Stage 5 and before the end of it. Only the occurrences of Kern Nesrani (Morocco) and of Kaili (S. China) are entirely present in the Stage 5.

This rapid disappearance is particularly interesting for the question of the dating of the onset of the Cambrian agronomic revolution in deeper marine settings (cf. § 1.1). Indeed, for Seilacher et al. (2005) the disappearance of the *Oldhamia* records the arrival of this revolution in deep marine environment as a consequence of the destruction of resistant microbial mats by bioturbation. Our overview permits to determine more precisely the arrival of this agronomic revolution during the Stage 5 and before the end of it. It is a rather short period of some million years, seen the short duration of the Stage 5 (about 3.5 Ma). This would confirm the middle Cambrian age that was already proposed by Seilacher et al. (*op. cit.*), but now corroborated with much more arguments. However, we can not exclude that the disappearance of *Oldhamia* could also be related to the extinction of the trace-maker taxa itself or to other paleoenvironmental modifications, different than the character of the substrate.

The initial reason to start this review was to check if *Oldhamia* could be used as a biostratigraphical tool. The results of our overview show that this can only be the case in the second interpretation. Indeed, numerous authors (Seilacher, 1974; Sweet & Narbonne, 1993) underline that: a “unit can be correlated with trace fossils that have a short time range, or the first occurrence of long-ranging trace fossils”. In the second interpretation the ichnogenus *Oldhamia* turns out to be a valid fossil to be used in Cambrian biostratigraphy. It appears in the upper part of Stage 2, shows an acme in Stage 3 and 4 and rapidly disappears during Stage 5. This corresponds to a rather large lapse of time (about 15 Ma, Fig. 2), but until now still the only way to date with macrofossils Cambrian deep marine sequences.

Finally from a palaeogeographical point of view, this study shows that *Oldhamia* had a cosmopolitan distribution, which covered the oceanic margins of all major palaeocontinents and some other terranes (Fig. 3). We can also conclude that in the Cambrian the *Oldhamia*-maker were living in a wide variety of depositional environments from shallow platform to abyssal plain, even if in the majority of cases they occurred in a deep marine setting. The rarity of their occurrences in the shallow marine environments, as shown in this review, can easily be explained by the earlier appearance of the Cambrian agronomic revolution in these environments.

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