Unravelling a Late Ordovician pentameride (Brachiopoda) hotspot from the Boda Limestone, Siljan district, central Sweden

CHRISTIAN M.Ø. RASMUSSEN^{1,2}, JAN OVE R. EBBESTAD³ and DAVID A.T. HARPER⁴

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Abstract: The correlation of the uppermost Boda Core Member of the Boda Limestone is reassessed and the beds assigned to the upper Katian. This is based on the identification of the brachiopod species Brevilamnulella kjerulfi (Kiær) and Amphiplecia tardicostata Wright & Jaanusson from the highest beds in the unit. The former species is overwhelmingly abundant in the uppermost beds of the Boda Core Member in Osmundsberget quarry, forming an almost monospecific coquina. Also occurring in the coquina, is *Clorilamnulella osmundsbergensis* gen. et sp. nov., which ranges into the overlying Hirnantian Glisstjärn Formation. The new genus is here regarded as a transitional form between Brevilamnulella and Clorinda. The oldest occurrence of this latter genus is here revised and not found in rocks older than the Aeronian. Instead, previous Rhuddanian occurrences of 'Clorinda' are transferred to *Clorilamnulella* based on a dorsal cardinalia that differs from both that of *Brevilamnulella*, as well as that of Clorinda. Moreover, gigantic shells of a new species of Brevilamnulella, B. umbosulcata sp. nov, are described from the nearby Solberga quarry where the species occurs in great abundance in a local fossil pocket, that also is correlated with the upper Katian. These new virgianid and clorindoid occurrences, together with previously described occurrences of Holorhynchus and Costilamnulella, demonstrate that during the late Katian, the Boda Limestone was a virgianid hotspot crucial in the evolution of the earliest pentameroid family, the Virgianidae, as well as a possible early cradle for the evolution of the hitherto exclusively Silurian superfamily, the Clorindoidea.

Keywords: Boda Limestone, Upper Ordovician, Lower Silurian, brachiopods, *Brevilamnulella*, *Clorilamnulella*, *Clorinda*.

¹Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, Øster Voldgade 5-7, DK-1350 Copenhagen K, Denmark; christian@snm.ku.dk

²Nordic Center for Earth Evolution (NordCEE), Natural History Museum of Denmark, University of Copenhagen, Øster Voldgade 5-7, DK-1350 Copenhagen K, Denmark

³*Museum of Evolution, Uppsala University, Norbyvägen 16, SE-752 36 Uppsala, Sweden; jan-ove.ebbestad@ em.uu.se*

⁴Geological Museum, Natural History Museum of Denmark, University of Copenhagen, Øster Voldgade 5-7, DK-1350 Copenhagen K, Denmark; dharper@snm.ku.dk

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Introduction

The Boda Limestone is chiefly known for its spectacularly preserved shelly fossils and for signalling the latest Katian Boda Global Warming Event (Fortey & Cocks 2005). These large mud mounds formed in relatively deep water conditions. Together with other coeval, globally-occurring mud mounds in Estonia, northern England, Ireland, and Kazakhstan, these have been related to a global warming event during the late Katian (Boucot et al. 2003). Benthic faunas apparently moved to progressively higher latitudes during the deposition of these mounds, with an increase in endemic faunas at lower latitudes within the mud mounds (Fortey & Cocks 2005). The warming event has recently been re-assessed by Cherns & Wheeley (2007), who presented an alternative explanation.

Brachiopods from the Boda Limestone mounds have been studied for many years, so far resulting in the description of more than 100 species (Ebbestad & Högström 2007). Most recently the strophomenate brachiopods were revised (Cocks 2005) and the new virgianid genus *Costilamnulella* was described by Wright & Rong (2008). Cocks (2005), whose strophomenide material originated from both core and flank facies of the Boda mud mounds, further demonstrated the fauna to have strong mound-endemism. However, some affinities to the adjacent palaeocontinents of Avalonia, Laurentia, and Siberia were also evident. In addition, other brachiopods and fossil groups, such as the trilobites, support the high mound-endemism (Suzuki & Bergström 1999; Cocks 2005). Together these studies demonstrate the great diversity of species that were able to occupy the increasing number of ecological niches available in the late Katian – notably due to the changing mound/intermound facies of evolving carbonate frameworks such as the Boda mounds.

The present study contributes further to knowledge of the highly specialized niches that strongly controlled the diversity of species, also known as α -diversity (see Harper 2006), within the different facies of the Boda Limestone. It develops three main themes. One clarifies the age of the uppermost Boda Core Member of the Boda Limestone, while the second discusses the significance of new occurrences of two species of Brevilamnu*lella* – a virgianid brachiopod genus that hitherto has only been described on Baltica from the Oslo-Asker district of Norway (Cocks 1982). The third theme discusses the phylogenetic relationship between the Pentameroidea and the Clorindoidea, since the new genus Clorilamnulella from the Osmundsberget quarry, described below, is regarded as a transitional form between Brevilamnulella and Clorinda, which originated in the Lower Silurian. Additionally the current study further speculates that the Virgianidae were probably ancestral to the Clorindoidea.

At least four virgianid species are now known from the Upper Katian Boda limestone. Together with the new clorindoid genus *Clorilamnulella*, this suggests that these deep-water carbonate mound settings were particularly ideal for the early evolution of the Virgianidae and possibly the earliest Clorindidae. This is important, as it implies that the Virgianidae were ancestral to firstly the whole of the Pentameroidea, one of the most successful groups within the middle Palaeozoic Brachiopoda (Rubel 1970; Boucot & Johnson 1979; Mørk 1981; Jin & Copper 2010) and secondly, although speculative, also the Clorindoidea.

Regional stratigraphical units are used in the text where applicable, while the international stages are used in general. International chronostratigraphical units, as defined by Bergström et al. (2009), are indicated where necessary.

Geological setting

The Ordovician rocks in the Siljan district of central Sweden are preserved today in a large circular, faulted structure known as 'the Siljan Ring', situated within the Precambrian Shield (Fig. 1). This is a result of a meteorite impact in the Devonian (Reimold et al. 2005). Originally the Ordovician strata covered vast distances across the region, but were eroded probably during the Mesozoic. In the Siljan region, mud mound development occurred both in the early and the late Katian. The older mounds are referred to the Kullsberg Limestone, whereas the younger are assigned to the Boda Limestone.

The Boda mounds succeed the Katian Fjäcka Shale and/or the Jonstorp Formation (Ebbestad & Högström 2007) and are relatively large structures with a maximum diameter of up to 1,000 metres and a maximum thickness of more than 100 metres (Jaanusson 1982). The Jonstorp Formation also occurs laterally adjacent to the mounds. The inter-mound Tommarp Formation has a similar geographic distribution. This formation is overlain by the Hirnantian Glisstjärn Formation which onlaps the Boda mounds disconformably in both Osmundsberget quarry (Schmitz & Bergström 2007) and Kallholn quarry (Ebbestad et al. 2009; Suzuki et al. 2009). The Boda Limestone also crops out in the nearby Solberga quarry. Here post depositional crevices containing Hirnantian bryozoans indicate that the mound

growth ceased before the end of the Hirnantian (Jaanusson 1982). Thereafter follows a hiatus comprising the Rhuddanian and most of the Aeronian, before graptolitic shales of the Kallholn Formation containing *Monograptus sedgwicki* were deposited (Loydell & Maletz 2004).

Recently three mound facies of the Boda Limestone were formalized (Suzuki et al. 2009). The bulk of the mounds consists of the massive Boda Core Member, especially characterized by the local abundance or pockets (termed by Suzuki & Bergström 1999; see also Suzuki et al. 2009) of disarticulated trilobites, typically of one type, and brachiopods such as Grammoplecia and Costilamnulella (Jaanusson 1982; Wright & Jaanusson 1993; Wright & Rong 2008). Transitional pelmatozoan beds, deposited laterally, comprise the Boda Flank Member, while the stratigraphically upper unit, laterally capping the two other members, is named the Upper Boda Member (Fig. 1). Suzuki et al. (2009) identified four lithologically distinct beds (A-D) in the Upper Boda Member, each with a distinct trilobite fauna. Beds A-D are only fully developed in Kallholn quarry, while beds A-C can also be found in the Osmundsberget (stratotype section), Jutjärn, and Östbjörka quarries (Fig. 1).

The age of the upper parts of the Boda Limestone has been the subject of some controversy during recent years (Jaanusson 1979; Marshall & Middleton 1990; Middleton et al. 1991; Brenchley et al. 1997; Schmitz & Bergström 2007); Suzuki et al. (2009) ascertain that the Upper Boda Member is of Hirnantian age in its entirety.

Material and methods

The shells investigated for the current study were preserved as a coquina in Osmundsberget quarry and a cluster in a fossil pocket in Solberga quarry. The coquina is found at the south entrance of Osmundsberget quarry (locality Osmundsberget 1, Fig. 1B, E). Here it is about 1.8 m thick and consists of a number of individual bands or beds with shells. The upper limit is only about 0.2 m from the uneven top surface of the Boda Core Member. The Boda Core Member is unconformably overlain by the Hirnantian Glisstjärn Formation, and in the latter a marked cephalopod bed is preserved (Ebbestad et al. 2007). The Upper Boda Member is not developed at Osmundsberget 1, but the type section of the unit occurs at localities Osmundsberget 4 and 5 at the north entrance of the quarry (Fig. 1B, E). The cephalopod bed of Osmundsberget 1 may also be identified at the north entrance (Osmundsberget 5), and also here a brachiopod coquina (0.5 m thick) is developed about 0.5 m below the top of the Boda Limestone, in the C unit of the Upper Boda Member of Suzuki et al. (2009). However, it seems to contain only rhynchonellid taxa (see below).

A large complex pocket is developed in the Boda Core Member at the south wall in Solberga quarry (locality Solberga 2, Fig. 1C), and the material was located in a cluster in the lower part of the pocket. At the north wall (locality Solberga 1, Fig. 1C), markedly large shells of *Holorhynchus giganteus* occur in the Boda Core Member (Ebbestad & Högström 2007), while the Upper Boda Member is not developed or exposed in Solberga. The Solberga material is almost completely preserved as three-dimensional moulds. Although difficult to prepare mechanically, as the limestone easily fractures, this was achieved using air-chisels. The Osmundsberget material was easier to prepare as the associated matrix was a bit softer than the shells.



Fig. 1. Maps of area and localities, stratigraphy and sections studied herein. **A**. Geological map of the Siljan district with mounds discussed in this paper. **B**. Map of Osmundsberget quarry with the sections Osmundsberget 1 (OB1) and Osmundsberget 4 and 5 (OB4, OB5) indicated. **C**. Solberga quarry with localities Solberga 1 (Sol1) and Solberga 2 (Sol2) indicated. **D**. Stratigraphy and tentative cross section of the Boda Limestone mound at Osmundsberget with position of sections indicated. The drawing is not to scale. **E**. The three sections at Osmundsberget quarry, with key fossils horizons and facies units indicated. Insert maps are modified from Ebbestad & Högström (2007), while stratigraphical overview is modified from Suzuki et al. (2009).

The interiors of material from both localities were studied in cross sections using a Unicam serial grinder to cut through the shells. Shells were polished sagittally in slides down to 0.01 mm starting at the posterior margin. In this way internal structures, if preserved, would be viewed perpendicular to the sagittal axis. Once each section was prepared, the surface was washed and placed in citric acid for 90 seconds. This was carried out to enhance

the relief between the softer matrix and the harder shell structures. Following this, the surface was washed again, air dried and then a thin film of acetone was added to the surface before a sheet of acetate paper was carefully placed on the surface. Hereafter the surface was dried for at least one hour before the acetate could be peeled off. The finished acetate peel was then placed under a slide scanner and further enhanced using Adobe Photoshop[®].



Fig. 2. Palaeogeographical reconstruction for the earliest Silurian showing the distribution of *Brevilamnulella*, *Clorilamnulella* and *Clorinda* in the Katian through Llandovery interval. In addition the probable dispersal route of *Clorilamnulella* through the interval is shown in yellow and indicated by an arrow. The positions of larger epicontinental seas are shown in blue. See legend for further explanation of figure. Palaeoprojection is provided by Trond Torsvik (Trondheim) with financial support from Statoil and modified by the authors.

Virgianid brachiopods in the uppermost Ordovician

Although virgianid genera such as Brevilamnulella, Deloprosopus, Disulcatella, Eoconchidium, Holorhynchus, Proconchidium, Prostricklandia, and Tcherskidium experienced a radiation in the tropical regions during the late Katian (Ka4), they came close to extinction during the Hirnantian crisis interval (Jin et al. 2006). Probably the sole survivors within the family, and thereby the whole of the Pentameroidea, were the large, smoothshelled Holorhynchus and the smaller Brevilamnulella (Jin & Copper 2010). The first is known chiefly from the late Katian, but re-appears in the Aeronian of Kazakhstan and South China, whereas Brevilamnulella is relatively widely known from Hirnantian rocks (see Fig. 2) and, as indicated in Fig. 3, has its main radiation in the Rhuddanian probably extending into the lower Aeronian (Rong & Boucot 1998; Boucot et al. 2002; Rong et al. 2004; Rong et al. 2006). The recently discovered genus Costilamnulella Wright & Rong is not well age constrained as its distribution is local. However, it is confined to the very same type of monospecific pockets in Solberga quarry that are here inferred to be upper Katian based on the specimens of B. umbosulcata sp. nov. described in this study. In addition, Costilamnulella may also occur in the studied coquina in Osmundsberget quarry and, thus, is believed to be late Katian in age (see below).

The occurrence of *Brevilamnulella* in Solberga quarry is particularly intriguing. Not only because it occurs together with



Fig. 3. Phylogenetic relationship of *Brevilamnulella* in relation to the evolution of the Clorindoidea within the Upper Katian–Telychian interval. The relative thickness of the generic ranges represent species richness through the interval. Note also that the origination of costae within each genus is shown.

the contemporaneous cluster of *Costilamnulella* mentioned above, but also as the shells are unusually large compared to other species within the genus (Fig. 4). *Costilamnulella* was recently interpreted as a restricted evolutionary sideline to the more widely occurring *Brevilamnulella* (Wright & Rong 2008). This was based on the shared occurrence of both an interarea and palintrope. The new occurrence of *Brevilamnulella* reported in this study thus supports these interpretations as the two genera apparently lived adjacent to each other in the same habitat.

In Osmundsberget quarry *H. giganteus* is found 16.5 m below the top of the Boda Limestone at locality Osmundsberget 4 (Fig. 1A, E; Ebbestad & Högström 2007; locality B of Jaanusson 1982, p. 35, fig. 4) and about a dozen examples are housed in the older collections of the Museum of Evolution in Uppsala, Sweden (recent collections also by DATH and JORE). *Holorhynchus giganteus* has previously been reported from the site (Jaanusson 1979, 1982; Cocks 2005) and was believed to be of Hirnantian age (Jaanusson 1979, 1982; Cocks 1988). However, investigation based on global data on the *Holorhynchus*-bearing strata suggested that they are of late Katian age (Rong & Harper 1988) and even though the genus may be a Lazarus taxon, it has never been recovered from Hirnantian beds (Rong et al. 2004). Furthermore, Brenchley et al. (1997) assigned *H. giganteus* to the pre-Hirnantian based on the isotopic composition of the shells from central Oslo Region, Norway.

Recently a Hirnantian age was re-inferred for the uppermost Boda Limestone based on δ^{13} C isotope excursions (Schmitz & Bergström 2007). However, as stressed by Kaljo et al. (2008), correlation based on isotopes in the latest Ordovician are less convincing as the onset of the major positive δ^{13} C appears to be diachronous, and new data in Ebbestad et al. (2009) suggest the



Fig. 4. Width/length ratios for the specimens in the studied material, as well as selected species of *Brevilamnulella*, *Costilamnulella*, and *Clorilamnulella* from the literature (see legend). *Brevilamnulella* and *Costilamnulella* are illustrated by squares confined by a red line, whereas *Clorilamnulella* is represented by circles and triangles (*C. undata* is also partially represented by squares) bounded by a black line. The different species are then represented by different colour infills. Note the size of *B. umbosulcata* sp. nov compared to the other species of *Brevilamnulella* and further that the species of *Clorilamnulella* become larger up through the interval.

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start of the excursion is above the *H. giganteus* level in Osmundsberget quarry. Suzuki et al. (2009) suggested that unit A of the Upper Boda Member is entirely of Hirnantian age, and at locality Osmundsberget 4, unit A starts stratigraphically above the *Holorhynchus*-bearing strata. We consider the global data on *Holorhynchus* to be well established, and supporting stratigraphical information firmly establish that the *Holorhynchus* giganteus-bearing strata of the Boda Limestone at Osmundsberget are in fact of Pirgu age (late Katian–Ka4).

The Brevilamnulella kjerulfi coquina

Despite thorough investigation of the Boda Limestone brachiopods during the past century or so, a new coquina has recently been recognized. This coquina is located just below the Hirnantian Glisstjärn Formation, in the uppermost beds of the Boda Core Member. The current study presents new identifications of the brachiopod species in this coquina based on samples taken from the south entrance of Osmundsberget quarry (Osmundsberget 1, Fig. 1B).

The coquina is almost monospecific. *B. kjerulfi* (Kiær) is by far the most abundant species in the coquina; however, *Clorilamnulella osmundsbergensis* gen. et sp. nov. also occurs as a minor constituent. Most of the *Brevilamnulella* shells are equal-sized, although there are some variations. Because the ventral and dorsal valves are almost equi-dimensional in *B. kjerulfi*, no apparent differentiation between the two has been observed. Possibly, *Costilamnulella valdari* Wright & Rong also occurs in this coquina (see Fig. 5I). Furthermore, one conjoined specimen of *Amphiplecia tardicostata* Wright & Jaanusson (see Fig. 5M–Q) and fragments of shells probably assignable to species of *Leptaena*? and *Onniella*? occur in the coquina along with fragmented trilobites such as *Flexicalymene*? and bryozoan colonies.

At Osmundsberget 5 the terminal succession seems at first glance to be very similar to that of Osmundsberget 1, based on the relative position of the cephalopod bed and brachiopod coquinas (Fig. 1E). However, the Upper Boda Member is not developed at Osmundsberget 1, and Suzuki et al. (2009) identified the taxa in the Osmundsberget 5 coquina as rhynchonellids. We have not sampled that section in this study.

B. kjerulfi is known from the upper Katian Langåra Formation of the Oslo–Asker district in Norway where it is associated with *H. giganteus*. The genus *Amphiplecia* has a known range from the upper Sandbian or lower Katian to the uppermost Katian (upper Pirgu) in the Ringerike district in Norway and the Siljan district in Sweden. This is based on its occurrence in the Arnestad– Frognerkilen and Bønsnes formations in Norway and the Boda Limestone (Owen et al. 1990; Wright & Jaanusson 1993; Ebbestad 1999). Thus, the occurrence of *B. kjerulfi* and *A. tardicostata* constrain the upper age limit of the coquina in Osmundsberget 1.

Elements of the contemporaneous brachiopod fauna

Above the *Brevilamnulella kjerulfi* coquina at the southern entrance of Osmundsberget quarry (see Fig. 1), the Hirnantian Glisstjärn Formation can be stratigraphically correlated between the northern and southern entrance by a coquina consisting of orthoconic nautiloids (Fig. 1E; Ebbestad et al. 2007). At the southern entrance of the quarry the nautiloid layer is associated with the brachiopods *Cliftonia* aff. *psittacina* (Wahlenberg 1818) and *Clorilamnulella osmundsbergensis* gen. et sp. nov.

At the northern entrance (Osmundsberget 4 and 5) in unit B of the Upper Boda Member, a coquina reported to consist of *Cryptothyrella* occurs. We doubt the presence of this genus; its type species is from the Aeronian and is currently under revision (Paul Copper, *pers. com.*). Instead we concur with Brenchley et al. (1997) and Suzuki et al. (2009) and identify this as *Hindella*, a genus that is a typical element of the *Hirnantia* fauna and also believed by some to be confined to the Hirnantian Stage (Jin & Copper 2008). However, others report *Hindella* from upper Katian strata extending at least into the Lower Aeronian on several palaeoplates (Rong et al. 1994; Rong et al. 1995; Harper 2001; Rong et al. 2002; Kaljo et al. 2008).

At Osmundsberget 4, Holorhynchus giganteus occurs in the upper Boda Core Member, below the Hindella coquina in the Upper Boda Member (Fig. 1E). Suzuki et al. (2009) identified three distinct trilobite faunas in the Upper Boda Member. The brachiopod succession has not been studied in detail, but it is reasonable to assume that these will show a similar pattern. Associated taxa include Coolinia, Dalmanella? and Hindella. These, together with Cliftonia aff. psittacina, all occur in the typical Hirnantia fauna (Rong & Harper 1988). Coolinia is not known from Baltica prior to the Hirnantian. However, in Laurentia Coolinia may extend down to upper Katian beds on Anticosti Island (Dewing 2001). The closely similar Fardenia (see Harper 2006) has also been reported, elsewhere described from lower Katian (Onnian)-lower Telychian strata including Baltica (Cocks 1988; Cocks & Rong 1988; Baarli 1995; Cocks & Modzalevskaya 1997; Rong et al. 2002; Cocks 2005; Harper 2006). Further study is required to establish the distinctions between these two taxa at least during the latest Ordovician (Rong & Li 1999).

The *B. umbosulcata* sp. nov. specimens from Solberga quarry occur in a large complex pocket at locality Solberga 2. The age of the Boda Limestone in Solberga quarry is believed to be not younger than Hirnantian, based on bryozoans (Jaanusson 1982). However, the stratigraphical infilling of such a large pocket as in Solberga may have sampled different aged strata. Nevertheless, as described below, the new species is considered con-specific with *Brevilamnulella* sp. from the *H. giganteus* Zone of the Chu-Ili Range, south-western Kazakhstan (Sapelnikov & Rukavishnikova 1975). Thus, the infill is no younger than latest Katian (Rawtheyan). One further piece of evidence

Fig. 5. Brevilamnulella kjerulfi (Kiær) and *Amphiplecia tardicostata* Wright & Jaanusson from the Boda Core Member, Osmundsberget quarry. A–K. *Brevilamnulella kjerulfi*; A. ventral view of conjoined specimen, MGUH 29209. B. dorsal view of conjoined specimen, MGUH 29210. C. posterior view of conjoined specimen, MGUH 29210. D. anterior view of conjoined specimen, MGUH 29210. E. lateral view of conjoined specimen, MGUH 29210. T. interior view showing interarea, palintrope and spondylium. Note the medial spondylial groove, MGUH 29211. G–I. different varieties of ornament in dorsal valves (compare with b); G. MGUH 29212. H. MGUH 29213. I. Could possibly be assigned to *Costilamnulella* instead; however, this is only based on outline and ornament, MGUH 29214. J. anterior view of dorsal valve. Note the closely-spaced growth lines at the anterior margin, MGUH 29213. K. lateral view of dorsal valve showing pronounced fold in profile. Note growth lines are also present mid-valve, MGUH 29213. M–Q. *Amphiplecia tardicostata*, MGUH 29214; M. ventral view of conjoined specimen. N. posterior view of conjoined specimen. P. lateral view of conjoined specimen. Q. dorsal view of conjoined specimen.



for the age of the sediment infill in locality Solberga 2, is that the size of the shells are striking (see Fig. 4), indicating that the species enjoyed favourable ecological conditions in this setting, compared to other contemporaneous *Brevilamnulella* occurrences. Brachiopod 'gigantism' has been reported from middle-upper Katian rocks of the Laurentian Hudson Bay and Williston basins (Jin et al. 1997; Jin 2001; Jin & Zhan 2001). It may be that a similar increase in shell size occurred on Baltica in contemporaneous strata.

In summary, based on the co-occurrences of *Brevilamnulella kjerulfi* and *Amphiplecia tardicostata*, it is suggested that the *B. kjerulfi* coquina, constituting the uppermost beds of the Boda Limestone in Osmundsberget quarry, is of latest Katian age. The same age is inferred for the *B. umbosulcata* clusters at Solberga quarry, based on the co-occurrence of the same species from contemporaneous beds in Kazakhstan.

Brevilamnulella in ecological associations

Pentameroid brachiopods are often associated with near-shore settings as they are typically associated with intercratonic seas. Commonly their posteriorly thickened ventral valve provided stability in rough-water zones. Although Brevilamnulella does not display the same degree of posterior thickening as many larger pentameroids, it is often associated with relatively shallow-water associations on several tropical to sub-tropical palaeocontinents. Most are found in carbonate facies ranging within the BA 2-4 interval occurring in rock-forming quantities as is typical for this group of brachiopods. Often the Ordovician faunas occur in the deeper part of the depth spectrum. Commonly Brevilamnulella occurs in great abundance and may even be monospecific as evident in the Solberga and Osmundsberget quarries. This is also seen in the Langåra Formation of the Oslo-Asker district, Norway, where it is associated with sediments filling tidal channels, in relatively shallow water (Cocks 1982). With respect to the type species B. thebesensis from the Laurentian Edgewood Fauna, it may have preferred quieter, more offshore environments as suggested by Amsden (1974). Amsden (1974) illustrated a cluster of B. thebesensis from the Keel Formation (pl. 1, fig. 7a) - very similar to the clusters seen in Solberga quarry. Thus, it is very likely that the Brevilamnulella specimens from the Edgewood Group may have lived in conditions that closely matched those under which the Boda Limestone was deposited. Compared to the shallow water habitats preferred by the early Silurian virgianids, this deeper water setting clearly illustrates the shoreward migration of virgianid genera through the Ordovician-Silurian interface (Sheehan 2008). However, it does not necessarily mean that Brevilamnulella preferred quiet water conditions in the late Ordovician. As can be deduced from Fig. 1D, the Osmundsberget coquina was formed on the exposed seaward side of the Boda mounds. This suggests that though it was deep water, there was still some turbulence locally. These niches appear to have been preferred by both B. kjerulfi and C. osmundsbergensis. The Brevilamnulella-bearing nests in Solberga quarry (like those with Costilamnulella) were found in post-depositional nests that also suggest turbulent conditions.

Therefore this new material possibly suggests, that even though the Virgianidae originated in deep water environments, at least in the case of *Brevilamnulella*, it had already by the late Katian entered specialized niches that were characterized by turbulent settings. This would prove to be a great evolutionary advantage for them once more shallow water niches became vacant as a result of the sweeping end Ordovician mass extinctions. Possibly the direct opposite occurred with *Clorilamnulella* and eventually *Clorinda*, remaining in the deep water environments, where they would specialize in quieter conditions during the Silurian.

A cradle for the Clorindoidea?

The appearance of Clorilamnulella within the upper Katian Boda mounds suggests that these mounds can not only be regarded as a pentameroid hotspot, but also, very likely, a cradle for the Clorindoidea. Prior to the current study this latter superfamily was only known with certainty to have originated in the middle-upper Aeronian with the genus Clorinda. However, the origination of Clorinda has long been enigmatic as Rhuddanian species has also been reported (see Cocks & Rong (2008) for a full reference list of these occurrences). However, these tend to have less divergent or parallel inner plates that further lack carinae. True Clorinda has clearly basomedianly divergent inner plates towards the valve floor and possesses carinae (Johnson & Ludvigsen 1972; Jin et al. 1993). Jin et al. (1993) listed all known Silurian species of the genus, recognizing only two species, C. undata Sowerby and C. becsciensis Twenhofel from Rhuddanian rocks, whereas the other 29 species were at least of Telychian age or younger. Subsequently, C. becsciensis was excluded from Clorinda and assigned to Viridita (Jin & Copper 2000). The current study also suggests the exclusion of C. undata from Clorinda and its transfer to the new genus Clorilamnulella.

The Rhuddanian occurrences were also questioned by Cocks & Rong (2008), who assessed the several reports of Rhuddanian taxa questionably assigned to *Clorinda*. They considered these taxa were not true *Clorinda*, but instead belong to a close relative of *Brevilamnulella*. They suggested that this unnamed genus was concentrated primarily in the relatively narrow Iapetus Ocean with isolated occurrences on Siberia and in some of the Kazakh terranes, mostly within the upper Rhuddanian interval (see Fig. 2). Therefore, our data suggest that the Clorindoidea may have originated as a taxon such as *Clorilamnulella* on Baltica, as illustrated in Fig. 2.

As most of the Aeronian occurrences of *Clorinda* are of *C. undata*, the origination of *Clorinda* itself may, as shown in Fig. 3, not have occurred until the mid–late Aeronian with the species *C. tumidula* and *C. superundata* from Anticosti Island (Jin & Copper 2000).

Distinction between Brevilamnulella and Clorinda has traditionally been problematic. The type species of Brevilamnulella, B. thebesensis, was originally assigned to Clorinda by Savage (1919), while St. Joseph's (1938) original three species of Clorinda may prove to be Brevilamnulella (Cocks 1982) and Clorilamnulella (this study). In addition Temple (1970) originally reported Clorinda from the lower Llandovery of Wales, but later corrected this to Brevilamnulella sp. and Clorinda undata (the latter transferred to Clorilamnulella in the current study). Jin & Copper (2010) have provided a more comprehensive list of these taxonomical complications. Amsden (1974) suggested referral of C. undata to Brevilamnulella, but this was later opposed (Temple 1987), and thus the first appearance of Clorinda (and thereby the origination of the Clorindoidea) remains rather elusive. Figure 3 illustrates our interpretation of these new data with respect to the origination of the Clorindoidea.

Several workers have suggested that *Clorinda* may have originated from *Brevilamnulella* (Boucot 1975; Temple 1987; Boucot et al. 2002; Cocks & Rong 2008; Jin & Copper 2010), but without any firm evidence to support this hypothesis. Except for Jin & Copper (2010), origination of the Clorindoidea was not assumed to have occurred prior to the mid Llandovery. However, Jin & Copper (2010) demonstrated through gradational modifications in a morphoseries that the *Viridita–Virgiana* lineage most likely originated from *Brevilamnulella* and that the *Clorinda* lineage could have been derived from either *Brevilamnulella* or *Viridita* during the late Rhuddanian.

The new genus *Clorilamnulella* gen. nov., established in the current study, presents a possible intermediate form that is almost impossible to distinguish between *Brevilamnulella* and *Clorinda*, without careful study of internal structures. This implies that the clorindoids may already have been split from the pentameroids within the late Katian (Fig. 3).

Systematic palaeontology

The figured and described specimens are reposited at the Natural History Museum of Denmark (MGUH) in Copenhagen.

Order Pentamerida Schuchert & Cooper, 1913

SUPERFAMILY PENTAMEROIDEA M'COY, 1844

FAMILY VIRGIANIDAE BOUCOT & AMSDEN, 1963

SUBFAMILY MARIANNELLINAE SAPELNIKOV & RUKAVISHNIKOVA, 1975

Genus Brevilamnulella Amsden, 1974

Type species. – Clorinda? thebesensis Savage, 1913, from the Hirnantian Leemon Formation of Illinois, U.S.A.

Species assigned to Brevilamnulella. - Up to 13 different species of Brevilamnulella are known. From the Katian, the Baltic B. kjerulfi is reported from the Holorhynchus beds of the Langåra Formation (upper Pirgu) and the Boda Limestone in Siljan, Sweden, where also *B. umbosulcata* sp. nov. occurs (this study). This latter species is also reported from the Holorhynchus giganteus Zone of the Chu-Ili Range, Kazakhstan (Sapelnikov & Rukavishnikova 1975). B. laevis is known from the upper Katian? Akdombak Formation (Holorhynchus giganteus Zone) in the Chingiz and Chu-Ili ranges, Kazakhstan (Sapelnikov & Rukavishnikova 1975). Furthermore B. gromotuchaensis (Severgina) is reported from the Upper Ordovician of the Altay-Sayan Region, Russia (Severgina 1978; Jin & Copper 1997; Rong & Boucot 1998) and B. curta from the Ashgill Archlyk Formation in the Zeravshan-Gissar mountains of the Kazakh Tien-Shan terrane (Menakova 1984). Further, Brevilamnulella sp. is known from Peary Land, North Greenland (Rasmussen 2009).

B. thebesensis have been recorded from the Hirnantian *persculptus* Zone of Kolyma, north eastern Russia (Oradovskaya 1983; Sapelnikov 1985) and also from contemporaneous as well as Rhuddanian beds of the Laurentian Edgewood Formation of Missouri and Illinois and the Keel Formation in Oklahoma, USA (Savage 1913, 1917; Amsden 1974). *Brevilamnulella*? sp. was reported from the upper Hirnantian Kuanyinchiao Formation in Tongzi, northern Guizhou, South China (Chen et al. 2000). Further *B. gilianensis* is known from the probably Rhuddanian Xiaoshihugou Formation of Gansu, North China plate (Rong & Boucot 1998). From South China *Brevilamnulella* sp. is recorded from the lower Rhuddanian Shiyang Formation of Jiangxi and the

middle Aeronian Xiangshuyuan Formation of the Yichang region (Rong et al. 2005; Rong & Zhan 2006). Temple (1987) described *Brevilamnulella* sp. nov. from Wales in beds that are late Rhuddanian in age. *B. glabra* has been reported from the Aeronian of the Taimyr Peninsula, but as the interiors are unknown its true generic relationship is difficult to assess (Modzalevskaya 2003). Finally, a species of *Brevilamnulella* was also reported from the Llandovery of Kazakhstan (Sapelnikov 1985).

Species excluded from Brevilamnulella. – *B. undatiformis* Rozman, 1978 from the Hirnantian *persculptus* Zone of Kolyma, north eastern Russia (Oradovskaya 1983; Sapelnikov 1985) and Rhuddanian strata from Podkhamennaia Tunguska River, Siberia (Rozman 1978). Baso-medianly parallel to slightly divergent inner plates suggest this species should be transferred to *Clorilamnulella*.

Genus range. - Late Katian-early (?late) Aeronian

Brevilamnulella kjerulfi (Kiær, 1902)

Figs. 5A-K, 6.

1902 Barrandella kjerulfi n. sp., Kiær, p. 63, figs. 1-7.

- 1938 *Clorinda kjerulfi* (Kiær): St. Joseph, p. 307, pl. 7, figs. 1–6; pl. 8, figs. 1–13.
- 1982 Brevilamnulella kjerulfi (Kiær): Cocks, p. 776, pl. 82, figs. 14–16; pl. 83, figs. 1–11.

1993 Clorinda kjerulfi (Kiær): Jin et al., p. 38

1998 Brevilamnulella kjerulfi (Kiær): Rong & Boucot, p. 459.

2000 Phricoclorinda kjerulfi (Kiær): Jin & Copper, p. 61

Description. - Small to medium sized. Equi-biconvex to slightly ventribiconvex, appears more equi-biconvex in adult growth stages. Outline triangular to pentagonal. Transverse, wider than long. About 85-90 per cent as long as wide, with widest point at acute cardinal extremities in adult specimens. Juvenile specimens appear to have obtuse cardinal extremities and are more subcircular to pentagonal in outline (as opposed to triangularpentagonal) with only obscurely developed costae along the anterior margin. Thus, some shells tend to be longer than wide. The anterior commissure is strongly parasulcate, which becomes progressively more pronounced with shell size. Ventral valve moderately convex with relatively deep sulcus that becomes wider towards the anterior margin where it eventually extends for about one-third of the margin width. Umbonal zone positioned posterior of hinge-line in adult specimens. Very narrow, curved apsacline interarea. Dorsal valve moderately convex, with a pronounced fold that widens to about one-third of entire width of the anterior margin. Interarea not observed. Ornamentation appears to vary from almost smooth in juvenile specimens over a few broad costae at the anterior margin to large, broad costae extending along entire valve length in adult specimens. The variation is ontogenetically related and modified in some cases by preservation. Some specimens even appear to have fine costellae in between the broad costae. However, in general there appears to be 3-4 costae on either side of the sulcus and fold. The costae next to the fold are broader and larger than those farther away from the fold. Within the ventral sulcus, two fine, depressed costae are present, usually one more pronounced than the other. The dorsal fold consists of three costae (commonly not seen in juvenile specimens). Weak growth lines are apparent throughout the valve length and are closely spaced at the anterior margin in well preserved specimens.

Ventral interior with a very short, but wide spondylium, that is supported by an even shorter median septum that extends farthest



Fig. 6. Serial transverse sections of a conjoined specimen of *Brevilamnulella kjerulfi* from Osmundsberget (MGUH 29215). Black strokes indicate internal structures composed of primary lamellar calcite; dark grey indicate secondary prismatic calcite and light grey indicate secondary infill of cement.

along valve floor where it appears to be wedged. The spondylium characteristically narrows towards the anterior extremity and possesses a medial spondylial groove. Prominent teeth are present. Dorsal interior with short, initially sub-parallel inner plates that towards the anterior are extremely abbreviated. The bases of the brachial processes possibly give the impression that the very short inner plates are slightly baso-medianly divergent towards valve floor. The widely divergent outer plates are at least twice as long as the inner plates and thicken distally at the teeth sockets. Brachial processes extend longer anteriorly than the outer plates.

Taxonomical and stratigraphical significance. – Strongly resembles *Brevilamnulella kjerulfi* as illustrated by Kiær (1902), St. Joseph (1938), and Cocks (1982) and is therefore

regarded as being conspecific. Cocks (1982, p. 776) noted that 'The number of lateral ribs on either side of the median fold and sulcus varies within each sample from zero to four, with one or two being the most common'. Precisely the same variation in ornamentation is observed on the Boda specimens described here. This variation led Kiær (1902) to distinguish between a wide and a narrow form. But as observed by Cocks (1982) intermediate forms occur in each assemblage. They should thus be assigned to the same species. Fine concentric growth lines that become closely spaced towards the anterior margin were also noted in the species *B. thebesensis* (Savage 1917). However, these tend to be more pronounced and less closely spaced as they are traced along the margin of the entire shell.

Though St. Joseph (1938, p. 309) assigned the species to Clorinda based on baso-medianly divergent inner plates 'as is usual in Clorinda', Cocks (1982) transferred the species to Brevilamnulella apparently based only on its external morphology. The new material of B. kjerulfi seems to support St. Joseph's description in having slightly divergent inner plates in the most posterior transverse sections. However, this is more likely an artefact created partly by the less reliable, posteriorlypositioned sections and partly by the bases of the brachial processes. Therefore, we retain this species within Brevilamnulella based on its extremely abbreviated inner plates, and thus do not follow Jin & Copper (2000) who transferred this species to Phricoclorinda. Amsden (1974) cited the abbreviated inner plates as one of the most important characters for the type species B. thebesensis. Amsden's transverse sections also reveal that even in the type species, the inner plates may be slightly divergent towards valve floor in the most posterior part of the dorsal valve (Amsden 1974, p: 62, text-figure 38A-C). Thus, we are inclined to believe that the same is the case with the current specimens of *B. kjerulfi*. Further characters associated with the dorsal cardinalia that support the placement of this species within Brevilamnulella, are the lack of carinae or hook structures and the longer outer plates. Within the ventral valve, a shallow, wide spondylium with a medial spondylial groove, prominent teeth and the possible wedging of the ventral median septum into the valve floor, are all characters that are typical of the Virgianidae.

Another line of support for this being *Brevilamnulella* is from the costate exterior of the *kjerulfi* species. Though being one of only a few species within the genus, that is costate in adult stages, it is not very likely that *Clorilamnulella* would have developed both costate and smooth forms within the late Katian. Rather the Rhuddanian to early Aeronian forms, like *C. undatiformis* (Rozman) and *C. malmøyensis* (St. Joseph) indicate that ornamentation takes time to evolve. Possibly the same transition is seen in *Clorinda* with the first costate forms appearing with the subgenus *Phricoclorinda* Jin & Copper (2000) in the late Llandovery (see Fig. 3).

On the other hand, the shape of the ventral interarea resembles that seen in *C. osmundsbergensis*, more than it resembles that seen in the Laurentian type species of *Brevilamnulella* or the new species from Solberga quarry. Thus, future work on this species could reveal that it should be transferred to *Clorilamnulella* if, for example, specimens with better preserved inner plates are available.

B. kjerulfi is reported from the Langåra Formation of the Oslo-Asker district, Norway. This formation spans the Ordovician–Silurian boundary. But according to Cocks (1982) the *Brevilamnulella*-bearing beds are situated at the top of the calcarenitic Langøyene Formation of which the limestone–shale

of the Langåra Formation is a lateral equivalent. *Holorhynchus giganteus* occurs at the top of the sequence. This implies latest Katian age for the occurrence of the *B. kjerulfi*-bearing beds in Oslo. Significantly, Cocks (1982) reported the occurrence of this species as almost monospecific, occurring in great numbers, similar to its occurrence in the Boda Limestone.

B. laevis Sapelnikov & Rukavishnikova, 1975 somewhat resembles the Osmundsberget specimens in outline based on the plates in Sapelnikov & Rukavishnikova (1975) and Sapelnikov (1985). However, that species appear to have broader, more pronounced costae on the ventral sulcus and appears to have a weaker ornament. This species, nevertheless, may eventually be assigned to *B. kjerulfi*, when more data on the Chinghiz species are available.]

Brevilamnulella umbosulcata sp. nov.

Fig. 7A–M; Figs. 8–9.

1975 *Brevilamnulella* sp., Sapelnikov & Rukavishnikova, p. 74, figs. 26a,b; pl. 17, figs. 17–18.

Type species. – B. umbosulcata (Holotype: MGUH 29216) from the upper Katian Boda Core Member of the Boda Limestone in Solberga quarry, Dalarna, Central Sweden.

Type material. – Ventral valves: MGUH 29216 (Holotype, Fig. 7A–D), MGUH 29217 (paratype, Fig. 7E, F), MGUH 29218 (paratype, Fig. 7G), MGUH 29221 (paratype, Fig. 7J), MGUH 29222 (paratype, Fig. 7L, M), MGUH 29223 (paratype, Fig. 7N) & MGUH 29224 (paratype, Fig. 8, serial sectioned). Dorsal valves: MGUH 29219 (paratype, Fig. 7H, K), MGUH 29220 (Fig. 7I, subsequently serial sectioned), MGUH 29225 (Fig. 9, serial sectioned).

Derivation of name. – Refers to the very pronounced sulcus in the ventral valve that is strongly developed already within the umbonal region.

Description. – Medium to large. Ventribiconvex, transverse in outline. The specimens are about 70–80 per cent as long as wide, with obtuse cardinal extremities. Anterior commissure strongly parasulcate. Ventral valve strongly convex with wide, deep depression (sulcus) that is developed near the beak and continues through the entire valve length to develop a tongue-like extension of the anterior commissure that occupies almost half of the anterior margin. Medianly, the sulcus is interrupted by a weak elevation. Umbonal zone positioned posterior of hinge-line with small palintrope developed. Interareas are either lacking or well developed as a low, wide and curved surface that does not extend to the cardinal extremities.

Dorsal valve moderately convex to equibiconvex having a pronounced fold, extending to approximately one-third of entire width at the anterior margin. Except for the above mentioned morphological features the material possess a few very characteristic growth rings along the entire shell margin. Except for these, the shells are smooth.

Ventral interior possesses a short, narrow spondylium with a medial spondylial groove (Fig. 7N). Ventral median septum very short and does not extend to the anterior end of the spondylium but the anterior end of the septum is curved so that the attachments to the valve floor and spondylium extend further anteriorly than the middle part of the septum (see Fig. 8).



Fig. 7. Brevilamnulella umbosulcata sp. nov. from the Boda Core Member, Solberga quarry. **A**–**D**. oblique, anterior, posterior and lateral views of ventral exterior, MGUH 29216 (holotype). **E**, **F**. oblique and anterior views of ventral exterior, MGUH 29217. **G**. posterior view of ventral valve, MGUH 29218. **H**. exterior view of dorsal valve, MGUH 29219. **I**. posterior view of dorsal valve, MGUH 29220 (subsequently serial sectioned). **J**. posterior view of ventral valve showing spondylium and the exterior of a dorsal valve inside, MGUH 29221. **K**. cluster of *Brevilamnulella umbosulcata* sp. nov. Three dorsal valves are highlighted, MGUH 29219. **L**. enlarged posterior view of specimen with interarea and palintrope. Note also the two characteristic growth lines seen on the shell margin at the cardinal extremities, MGUH 29222. **M**. close-up of interarea and lower part of palintrope, MGUH 29222. **N**. enlarged specimen showing spondylium and palintrope on specimen without interarea, MGUH 29223.



Fig. 8. Serial transverse sections of a ventral valve of Brevilamnulella umbosulcata sp. nov. (MGUH 29224) from Solberga quarry.

Dorsal interior of the Solberga material is based on probably a juvenile shell affected by recrystallization (Fig. 9). Despite this, the inner plates are noticeably shorter than the outer plates and clearly baso-medianly inclined towards valve floor. Furthermore the inner plates are abbreviated towards the anterior. The outer plates are divergent and thickened distally.

Morphological and stratigraphical remarks. – With respect to the new species assignment to *Brevilamnulella*, the small spondylium and the corresponding dorso-medianly inclined and anteriorly abbreviated inner plates are considered certain characteristics of *Brevilamnulella*. Further, both the medial spondylial groove as well as the curvature of the anterior part of the median septum is also observed in *B. kjerulfi* (see above) and

the type species *B. thebesensis* (as seen on pl. 2, fig. 1b,c and f of Amsden 1974) and also in several other genera within the Virgianidae (Jin & Copper 2000). The latter character is also found in *Clorilamnulella* (see below), as well as in some species of *Clorinda* (Jin et al. 1993, figs. 18, 20).

Although much larger and possibly more transverse, the Solberga species of *Brevilamnulella* resembles *B. thebesensis* Savage 1913. For example do both species poses characteristically weak growth lines at the anterior margin. Amsden (1974), who synomized Savage's (1913) species of *Clorinda? thebesensis* with *Pentamerus parvulus* and *Whitfieldella? speciosa*, noted that the shells of *B. thebesensis* are transverse, a feature that is not clearly illustrated by Savage (1917). On the other hand, Savage's illustrations of *Whitfieldella? speciosa*



Fig. 9. Serial transverse sections of a dorsal valve of Brevilamnulella umbosulcata sp. nov. (MGUH 29225) from Solberga quarry. Colours as in Figs. 6 and 10.

(pl. 7, fig. 16) clearly show the very pronounced, sharply-defined dorsal fold, a feature that is less obvious on Amsdens's plates and according to Jisuo Jin (pers. com., 2010) this is rarely developed in the North American material of the type species of Brevilamnulella. Thus, the new species differs from the type species in this respect as well as being much larger. With respect to the sharply confined dorsal fold, so characteristic of the new species, only Brevilamnulella sp. from the Holorhynchus giganteus Zone of Chu-Ili (Sapelnikov & Rukavishnikova 1975) and Brevilamnulella sp. from the Upper Rhuddanian of Mathrafal, Wales (Temple 1987), possesses a similar fold. Of these the Kazakh species is here believed to be con-specific, based on its general outline and size (see Fig. 4), as well as the transverse serial sections of the dorsal valve presented by Sapelnikov & Rukavishnikova (1975). The Welsh species, however, is probably much younger than the Solberga species and thus seems unlikely to be the same species.

Sapelnikov (1985) reported *B. thebesensis* from Kolyma. His species appear to be similar in size to the Solberga material (judging from the size compared to the smaller *B. laevis* in his pl. 4, figs. 9-11, 13). The Kolyma species is also notably more transverse than Amsden's species and further appears to have a low, wide ventral interarea (again based on pl. 4, fig. 13d, Sapelnikov 1985). The transverse outline is a consistent feature of the Solberga species, but Sapelnikov's species lack the sharply defined sulcus and corresponding fold.

The specimens of *B. umbosulcata* are mainly separable from *B. kjerulfi* with reference to their smooth shells, larger, more sharply defined dorsal folds and having only a few growth rings

along the entire margin; these are wider spaced compared to the more closely spaced growth rings seen in B. kjerulfi. Further, the B. umbosulcata specimens have a low, wide interarea (when it is not lacking) compared to the narrow, high interarea in B. kjerulfi. Judging from pl. 2, figs. 1a-2c in Amsden (1974), the type material appear to have an interarea that more resembles that seen in *B. kjerulfi* although there seems to be a large variation in the interareas. Amsden noted two forms of B. thebesensis within his material: one with and one without ventral interareas and that the interareas are either narrow and flat or indistinct. Thus, the shape of the ventral interarea in some specimens could indicate that the large species from Solberga quarry may in fact be an entirely new genus, as the interarea more closely resembles that seen in Costilamnulella (Wright & Rong 2008). However, as mentioned above, the specimens of *B. thebesensis* illustrated by Sapelnikov (1985), which also appear large, also appear to have the same low, wide interarea as the Solberga specimens. Although too few specimens within the Boda material have preserved the interarea, it may just as well be that the interareas are fractured and therefore do not resemble Amsden's type material (just as fractured interareas might explain why Amsden found two forms).

The large-sized *B. glabra* from the Aeronian of the Taimyr Peninsula, Siberia (Modzalevskaya 2003) does not possess either a fold or sulcus and further is too young to be considered con-specific. In addition, no interior structures are reported from this species, making it questionable whether it truly belongs to *Brevilamnulella*. If it does, it may be the youngest species within this genus (see Fig. 3).



Fig. 10. Clorilamnulella osmundsbergensis gen. et sp. nov. from the Boda Core Member and Glisstjärn Formation, Osmundsberget Quarry. A-F. ventral, dorsal, anterior, posterior, posterior tilted and lateral views of conjoined specimen from the Boda Core Member MGUH 29226 (holotype). Note the divergent inner plates and the dorsal median ridge in J and K. G-L. ventral, dorsal, anterior, posterior, lateral view of posterior and lateral views of conjoined specimen from the Glisstjärn Formation MGUH 29227. M-Q. ventral, dorsal, lateral, anterior and posterior views of conjoined specimen from the Boda Core Member MGUH 29228 (this specimen was subsequently serial sectioned for Fig. 11).

Superfamily Clorindoidea Rzhonsnitskaia, 1956

Family Clorindidae Rzhonsnitskaia, 1956

Genus Clorilamnulella gen. nov.

Type species. – *Clorilamnulella osmundsbergensis* gen. et sp. nov. (Holotype: MGUH 29226) from the upper

Katian Boda Core Member, Boda Limestone, Siljan, Central Sweden.

Etymology. – '*Clori*' refers to the possible ancestry of the genus to *Clorinda*, whereas '*lamnulella*' both refers to the anteriorly abbreviated inner plates as well as its close affinities to *Brevilamnulella*.

Diagnosis. - Small-sized, equi-biconvex to slightly ventribiconvex with triangular to sub-pentagonal outline and moderately globose convexity in adult specimens. Widest point from mid-valve to anterior one-third of valve. Ventral valve arched with umbo usually protruding posterior of hingeline with an initially low and obscure sulcus that may become very pronounced at anterior commissure. Ventral interarea relatively high, narrow and curved. Dorsal valve less convex, usually with a sharply defined fold in adult specimens, but fold may also be low and obscure, nearly rectimarginate in juvenile specimens. Distinctive growth lamilae seen towards the anterior margin. Ventral interior with short deep and narrow spondylium supported by an even shorter median septum. Dorsal interior with sub-parallel, anteriorly abbreviated inner plates supporting equally short, but very thick, divergent outer plates. Carinae may be developed as bases of brachial processes, though these also could be hook structures.

Species assigned to Clorilamnulella. – St. Joseph (1938) illustrated three species from the Oslo Region, which he referred to *Clorinda*. As already mentioned *C. kjerulfi* was later transferred to *Brevilamnulella* (Cocks 1982). *Clorinda malmøyensis* does not show clearly divergent inner plates, but they are weakly divergent with carinae (or hook structures?) that are well defined and the outer plates are very short. The ventral spondylium is narrow and the supporting ventral median septum is curved. These internal structures resemble more those seen in *Clorilamnulella*. Additionally his form of *Clorinda undata* is here transferred to *Clorinda superundata* by Jin & Copper (2000), but we consider that *C. undata* belongs to *Clorilamnulella*.

Rubel (1970) reported *Clorinda undata* from the upper Rhuddanian Varbola Formation in Estonia. His transverse sections reveal only slightly baso-medianly, divergent inner plates that are again very abbreviated as opposed to those of *Clorinda*. Furthermore the outer plates are very short and strongly divergent towards the ventral spondylium. Therefore, we suggest that Rubel's material of *Clorinda undata* should be transferred to *Clorilamnulella*.

Temple (1970, 1987) questioned the assignment of his own form of *Clorinda* [?undata]. He selected a lectotype from Sowerby's original material and, based on transverse serial sections, he discovered the inner plates to be parallel to weakly baso-medianly inclined. This cast some doubt on whether his material should be assigned to either *Clorinda* or *Brevilamnulella*.

Sapelnikov & Rukavishnikova (1975) described *C. undata* vassiliskii from the lower Llandovery of the Chu-Ili Range, Kazakhstan. This species clearly shows sub-parallel, short inner plates and outer plates that are widely divergent and very short. Furthermore they are considerably thickened distally, just as in the type species of *Clorilamnulella* described herein.

Therefore, based on the above four published studies, which as far as we have been able to find, are the only illustrations that actually show the interior of the species, we assign *Clorinda undata* Sowerby to *Clorilamnulella* based on the slightly basomedianly divergent (commonly parallel) inner plates towards valve floor.

Clorilamnulella undatiformis (Rozman) from the Hirnantian *persculptus* Zone of Kolyma, north eastern Russia (Oradovskaya 1983) and Rhuddanian strata of Podkhamennaia Tunguska

River, Siberia (Rozman 1978) is here transferred to *Clorilam*nulella based on a longer and higher ventral median septum, the parallel to slightly baso-medianly divergent, abbreviated inner plates, short divergent outer plates and an extremely high dorsal fold that more resembles that seen in *Clorinda undata* than in any species of *Brevilamnulella* (Rozman 1978, pl. VII, fig. 11; Oradovskaya 1983, fig. 20; pl. IX, figs. 4–6). This species is slightly plicate towards the anterior margin and thus is the earliest species within the genus to show ornamentation (Fig. 3).

Overall it appears that shell size and globosity increases from the Katian through to the Rhuddanian within species of Clorilamnulella, as does the dorsal fold and the resultant depth of the ventral sulcus, which in Rhuddanian species are much larger, but less sharply defined than in the Katian type species. Thus, these species may only be separated from Clorinda in having parallel to only slightly divergent inner plates towards the valve floor. Only Temple (1987) reported parallel to slightly inclined inner plates. But it is unclear if the latter should be assigned to Brevilamnulella. The inner plates may display a progressively increasing angle with the valve floor through the Katian-Rhuddanian. As the Rhuddanian species are larger than their Late Ordovician counterparts, these also may be somewhat more transverse in outline, at least in adult specimens. The type species is the oldest known within the genus. The main distribution of the genus is within the Rhuddanian and to a lesser extent it also occurs in the Aeronian (Figs. 2, 3). The youngest occurrence is possibly Clorilamnulella malmøyensis, reported by St. Joseph (1938) from 'stages 8a-8c', now the uppermost Telychian-lowermost Wenlock Skinnerbukta-Malmøya formations in the Oslo Region, Norway. Some uncertainty is associated with this since St. Joseph (1938) in one of his plates (Pl. VIII, figs. 8-9) noted its occurrence in 'stage 6c (lower part)', which is equivalent to the lower-middle Aeronian Solvik Formation of the central Oslo Region. Nikiforova (1978), who apparently only noticed the '6c' occurrence, reported the same species from Tien-Shan, in rocks that can probably be assigned to the upper Rhuddanian (Cocks & Rong 2008).

The most abundantly occurring species is *Clorilamnulella undata* (Sowerby), ranging from Rhuddanian to possibly upper Aeronian rocks in Altai, Avalonia, Baltica, Chinghiz, Chu-Ili, Girvan, Kolyma and Siberia (St. Joseph 1938; Rozman 1970; Rubel 1970; Sapelnikov & Rukavishnikova 1975; Rong et al. 2007; Cocks 2008; Cocks & Rong 2008).

Genus range.- Late Katian-Aeronian (?Wenlock)

Clorilamnulella osmundsbergensis gen. et sp. nov.

Figs. 10A–Q, 11.

Type material. – MGUH 29226 (holotype, Fig. 10A–F) and MGUH 29228 (Fig. 10M–Q) are both conjoined specimens from the Upper Katian Boda Core Member (the latter specimen has been serial sectioned for Fig. 11 subsequently). MGUH 29227 (Fig. 10G–L), is a conjoined specimen from the Hirnantian Glisstjärn Formation. All specimens are from Osmundsberget quarry.

Diagnosis. – Small to medium sized, equi-biconvex to slightly ventri-biconvex with triangular to sub-pentagonal outline and moderately globose convexity. Ventral valve arched in adult specimens with low obscure sulcus most pronounced at anterior commissure. Ventral interarea apsacline, moderately high, narrow and curved. Dorsal valve less convex, usually with a



Fig. 11. Serial transverse sections of a conjoined specimen of *Clorilamnulella osmundsbergensis* gen. et sp. nov. (MGUH 29228) from Osmundsberget quarry. Colours as in Figs. 6 and 9.

sharply defined fold, but fold may also be low and obscure to nearly rectimarginate in juvenile specimens. Distinctive growth lamellae seen towards the anterior margin. Ventral interior with short deep and narrow spondylium supported by an even shorter median septum. Dorsal interior with sub-parallel, anteriorly abbreviated inner plates supporting equally short, but very thick, divergent outer plates. Carinae may be developed as bases of brachial processes, though these also could be hook structures.

Description. - Small to medium size. Ventribiconvex with triangular to sub-pentagonal outline. Juvenile specimens often longer than wide with nearly rectimarginate anterior commissure (Fig. 10C, I). More mature specimens are wider than long, having acute cardinal extremities situated at about mid-valve and a clearly parasulcate anterior commissure with a well defined, sharp fold in the dorsal valve (Fig. 10P). Ventral valve arched with a relatively obscure and shallow sulcus (compared to the well-defined fold in the dorsal valve) that occupies about one third of the anterior margin. Medianly the depression is interrupted by a weak elevation that is wider in the corresponding median elevation in the species of Brevilamnulella described above. In the umbonal region, this elevation gives an impression of a pseudo-fold in the ventral valve. Umbonal zone positioned posterior of hinge-line with small palintrope developed. The ventral interarea is relatively high, narrow and curved confined to the umbonal region and thus not extending to the cardinal extremities. The corresponding dorsal interareas are flat, wider than the ventral interareas.

Dorsal valve moderately convex to equibiconvex with a pronounced, sharply defined fold (in mature specimens), extending to approximately one third of its entire width at the anterior margin. Towards the anterior margin a few very characteristic growth rings are developed along the entire shell margin. Except for these, the shells are otherwise smooth.

Ventral interior with a well-developed, narrow, but deep spondylium. Teeth less well-developed. Ventral median septum not extending to anterior end of spondylium. Instead the anterior end of the septum is curved so that the attachments to the valve floor and spondylium extend further anteriorly than the middle part of the septum (see Fig. 11). The median septum may be wedged into valve floor, but this is difficult to ascertain from the available transverse serial sections.

Dorsal interior with inner plates sub-parallel and strongly abbreviated anteriorly. When viewed from the exterior, a low dorsal median ridge is observed between the inner plates (Fig. 10D, E, J). Outer plates extend further anteriorly than the abbreviated inner plates, but are very divergent, short and excessively thickened laterally. Bases of brachial processes (carinae) are not identified with certainty. These could perhaps be possible hook structures positioned at the proximal part of the outer plates. The latter require serial sectioning of betterpreserved material.

Remarks. - Clorilamnulella osmundsbergensis is distinguished from Brevilamnulella in that the spondylium is very deep and narrow with less prominent teeth, parallel to slightly basomedianly divergent (as opposed to inclined) inner plates towards the valve floor that are anteriorly abbreviated, but less than in Brevilamnulella. The outer plates differ in being very short and considerably thickened. The excessively thickened outer plates seen in Fig. 11 may be a result of secondary thickening of prismatic calcite formed between the teeth sockets and the bases of the brachial processes (these could also be hook structures). However, the same structures are observed in C. undata (Sapelnikov & Rukavishnikova 1975, fig. 49A). Externally, the dorsal fold is restricted and sharply folded, compared to known species of Brevilamnulella. But on the other hand, characters such as the anteriorly abbreviated inner plates and anteriorly

shortened spondylium, with an even shorter ventral median septum similar to those in the two species of Brevilamnulella described above, and also observed in the type species of Brevilamnulella (Amsden 1974, pl. 2, fig. 1f), are all characters typical of Brevilamnulella.

In terms of Clorinda, only the lack of baso-medianly divergent inner plates towards the valve floor that further are anteriorly abbreviated and the short, divergent and thickened outer plates, seem to separate this taxon from that genus.

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