Re-evaluation of the stratigraphically important olenellid trilobite *Holmia* cf. *mobergi* from the Cambrian Series 2, Stage 3 and its implications for the lower Cambrian stratigraphy in the Mjøsa area, Norway

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The olenellid trilobite *Holmia* cf. *mobergi*, known from a single cephalon in the upper lower Cambrian strata from a river section in Flagstadelva, Hamar, has played a significant stratigraphic role in interpreting the lower Cambrian informal Series 2, Stage 3 in the Mjøsa area, Norway, since its discovery in the early 1950s. It was considered one of the oldest trilobite taxa in the lower Cambrian of Scandinavia, but the stratigraphic level and biozonation of the cephalon were problematic and a matter of discussion for decades. Moreover, organic-walled microfossil biostratigraphy questioned the supposed age of the trilobite. New specimens of this taxon collected from the type locality show that the species occurs at a different stratigraphic level than first reported, prompting a new description of the species and a re-evaluation of the taxon's biostratigraphic significance. *Holmia* cf. *mobergi* is compared with new and well-preserved topotype material of *Holmia inusitata*, a very rare taxon hitherto known from one single outcrop in an autochthonous setting in Norway. *Holmia* cf. *mobergi* and *Holmia inusitata* are here considered conspecific.

Keywords: Cambrian Series 2, biostratigraphy, *Holmia*, ontogeny, Mjøsa area - Norway

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Introduction

The well-exposed upper lower Cambrian section along the river Flagstadelva on the east side of Lake Mjøsa, Norway, has played a key role in establishing the lower Cambrian lithostratigraphy and biostratigraphy of the Mjøsa area in particular and Baltoscandia in general. The section was presented in a number of publications by Henningsmoen (1956, 1960), later described and interpreted as autochthonous by Skjeseth (1963), but more recently considered as parautochthonous or alternatively the proximal part of the Lower Allochthon (Nielsen & Schovsbo, 2007, 2011). Simplified logs of the section have been published by Moczyłowska & Vidal

(1986), Vidal & Nystuen (1990) and Nielsen & Schovsbo (2007, 2011).

A single cephalon of an olenellid trilobite collected at the Flagstadelva section by the Norwegian geologist Steinar Skjeseth in the early 1950s was initially referred to *Holmia* cf. *mickwitzi* (Schmidt) by Henningsmoen (1956). Based on unpublished observations by Skjeseth, he reported this specimen from the stratigraphically lowermost fossil-bearing unit in the Mjøsa area, below occurrences of the problematic fossil *Discinella* (= *Mobergella*) *holsti* Moberg and established a new faunal zone, 1a_{q1}. Skjeseth (1963, p. 46) later concurred and termed the unit the Brennsæter Limestone. Such a low occurrence indicated a correlation with the *Schmidtellus*

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mickwitzi Zone in Baltica and thus older than what had earlier been regarded as the oldest fossil-bearing Cambrian zone in the Mjøsa area (e.g., Kiaer, 1917; Vogt, 1924).

Daily (1972) questioned the presence of a faunal zone below *M. holsti* in Flagstadelva. Based on his investigation of the section, he found that faulting had duplicated the lower part, suggesting that the zonation introduced already by Henningsmoen (1956) was problematic. Later, Martinsson (1974) referred the Flagstadelva specimen to *Schmidtellus* and found it even older than *S. mickwitzi* in Estonia. This was based on a report of *Platysolenites antiquissimus* Eichwald from a basal section at the shore of Lake Mjøsa, interpreted as time-equivalent to the unit in Flagstadelva. Subsequently, the single cephalon, its presumed antiquity and biostratigraphic significance have been referred to in a number of publications (Bengtson, 1977; Føyn & Glaessner, 1979; Bergström, 1980, 1981; Vidal, 1981a, b; Ahlberg, 1984, 1985; Bergström & Gee, 1985; Ahlberg et al., 1986; Mens et al., 1990; Vidal & Nystuen, 1990; Moczyłowska, 1991, 2002; Jensen, 1997; Liebermann, 1999; Moczyłowska et al., 2001; Ebbestad et al., 2003; Nielsen & Schovsbo, 2007, 2011).

Several ardent attempts have been made to search for more fossil material from the assumed trilobite-yielding, pyrite-rich, silty limestone in the basal part of the section, regrettably without any reported results, e.g., B. Daily and G. Hamar (Daily, 1972), field notes from 1975 by Henningsmoen (stored at the Natural History Museum in Oslo, Norway), and Føyn & Glaessner (1979, p. 41) list K. Bjørlykke, J. Bergström, P. Ahlberg, G. Bylund, J.P. Nystuen, and G. Vidal as researchers who have re-investigated the section during the 1970s.

Recent research by the present authors has revealed new and important information, which forces new attention to the stratigraphy, the lower Cambrian faunal content, and the detailed biostratigraphy and stratigraphy of the Mjøsa area. The aim of this work is to a) clarify the stratigraphic occurrence of *Holmia* cf. *mobergi*, b) revise this stratigraphically important specimen, hitherto described under open nomenclature, c) contribute to the understanding of the faunal zonation of the oldest fossil-bearing strata in the Mjøsa area, and d) constrain the timing of the sea-level transgression postdating the Hawke Bay unconformity in the parautochthonous and autochthonous settings of the Mjøsa area.

Figure 1. Simplified geological map of the Mjøsa area. (A) The Scandinavian peninsula with the Caledonides shaded and the study area marked by a red square. (B) Numbered outcrops of important lower Cambrian sections mentioned in the text. 1 – Flagstadelva, 2 – Sollerud, 3 – Langodden, all parautochthonous. 4 – Risbekken, 5 – Lauselva, both autochthonous. 6 – Redalen, 7 – Ringsaker north, 8 – Ringsaker south, 9 – Bråstadelva and Sæterelva, all Lower Allochthon.

Geological setting and biostratigraphy in the Mjøsa area

The lower Cambrian strata of the Mjøsa area are present in different tectonostratigraphic settings: allochthon, parautochthon and autochthon. The Caledonian nappe front is followed along an eroded border on the west side of Lake Mjøsa and along a main fault line north-eastwards from the east side of the lake (Fig. 1). Sediments in the Lower Allochthon Osen–Røa Nappe Complex were deposited at least 140–150 km to the northwest of the thin autochthonous sedimentary cover, as suggested by palinspastic restoration of the décollement sheet (Nystuen, 1981). The autochthonous strata overlie the peneplained crystalline basement. In addition to the allochthonous and autochthonous deposits, slightly thrust parautochthonous Cambrian to Silurian strata are found southeast of the main fault line on both sides of Lake Mjøsa (Nielsen & Schovsbo, 2007, 2011). The Caledonian Lower Allochthon and parautochthonous fossiliferous strata rest unconformably on the lower Cambrian unfossiliferous (except for trace fossils) thick quartzites of the Ringsaker Member of the Vangsåsen Formation (Fig. 2). The transgressive lower Cambrian successions in the Mjøsa area were deposited during major marine-flooding events from the northwest (Skjeseth, 1963, plate 2) (present-day orientation).

Besides the use of organic-walled microfossils (OWM) as biostratigraphic markers (e.g., Moczyłowska & Vidal, 1986, Moczyłowska, 1991, 2002), trilobites provide the best tool for the detailed Cambrian biostratigraphic framework in Scandinavia. In the Miaolingian and the Furongian, the trilobites (and agnostoids) show a considerably faster radiation than the OWMs, although

less so in the lower part of Cambrian Series 2 that is hampered by rare occurrences of trilobites in the strata below the *Holmia kjerulfi* Zone.

Bergström (1980, 1981) introduced the *Schmidtellus mickwitzi* Zone in the Mjøsa area, which was maintained by Bergström & Gee (1985) and Ahlberg et al. (1986), based on the single occurrence of the trilobite specimen that Skjeseth had collected from the Flagstadelva section (locality 1 in Fig. 1). This specimen was compared with *Holmia mobergi* Bergström from the Norretorp Formation in Scania, southern Sweden, and figured and described for the first time as *Holmia* cf. *mobergi* by Ahlberg et al. (1986, pp. 47–49, fig. 6). The supposed coeval Norretorp Formation in southern Sweden corresponds to the *Schmidtellus mickwitzi* Zone and is, together with the lower part of the Grammajukku Formation at Storuman in southern Swedish Lapland, the lowermost trilobite-bearing unit in Scandinavia (Moczyłowska, 2002).

A new trilobite zone was established by Ahlberg & Bergström (1978, fig. 1) in an interval between the *S. mickwitzi* Zone and the *H. kjerulfi* Zone, based on three olenellid remains from an autochthonous locality at Lauselva west of Lake Mjøsa (locality 5 in Fig. 1, see detailed description in Ebbestad et al., 2003). These remains were formally described as *Holmia inusitata* (Ahlberg & Bergström in Ahlberg et al., 1986) and the zone was named the *Holmia inusitata* Zone. Moczyłowska (1991) included the *H. inusitata* and *H. kjerulfi* zones in a new *Holmia kjerulfi* Assemblage Zone, not to be confused with the *Holmia kjerulfi* Group Zone, established by Bergström & Ahlberg (1981) for a highly condensed sequence in the lower part of the Gislöv Formation in Scania, Sweden. The term '*Holmia* Series'

		Lower Allochthon		Parautochthonous	Autochthonous	Zones	
		Ringsaker N	Bråstadelva	Flagstadelva	Lauselva		
Cambrian Series 2, Stage 3	Stage 4	HIATUS				<i>Ellipsocephalus lunatus</i>	
						<i>Ellipsostrenua linnarsoni</i>	
	Ringstranda Formation	Skyberg Member	HIATUS	<i>Holmia kjerulfi</i>			
		Evjevika Member		?	-----		
		Tømten Member		Tømten Member	Tømten Member	<i>Holmia inusitata</i>	
				Brennsætersaga Member			
		Redalen Member		Bråstadelva Mbr	HIATUS	<i>Mobergella radiolata</i> <i>Schmidtellus mickwitzi</i>	
	Vangsåsen Formation	Ringsaker Member		Ringsaker Member	?		

Figure 2. Different tectonostratigraphic settings of the lower Cambrian strata in the Mjøsa area showing formations, members and zonation. Modified from Nielsen & Schovsbo (2007).

is used for the entire lower Cambrian fossiliferous strata in older publications. Ebbestad et al. (2003) reverted to the original concept of a discrete *H. inusitata* Zone in their redescription of the trilobite species, based on new specimens.

Nielsen & Schovsbo (2007) regarded the *Holmia inusitata* Zone as a local biozone within the *Holmia kjerulfi* Chronozone and later (Nielsen & Schovsbo, 2011) proposed abandoning the *H. inusitata* Zone altogether, because it was based on a few specimens recorded solely from the autochthonous Lauselvå locality. According to their sequence-stratigraphical correlation, the occurrence of *H. inusitata* is age-equivalent with the Evjevika Member and the *Ellipsostrenua linnarssoni* Zone.

A few autochthonous sites northeast of the Mjøsa area (Tennåsen, Ena, Kvernbekken and Møra-Andrå) were inferred to be located 60–80 km farther palaeo-downslope from the autochthonous Lauselvå locality by Nielsen & Schovsbo (2011, p. 244) and thus must have been transgressed earlier than the basal layers at Lauselvå containing *H. inusitata*. This assumption contributed to the abandoning of the *Holmia inusitata* Zone (Nielsen & Schovsbo, 2011). However, according to Skjeth's palaeogeographical reconstruction (1963, plate 2), based on observed stratigraphic units, the sea-level transgressed from the northwest (present-day orientation), with an approximately time-equivalent drowning for the autochthonous outcrops at Lauselvå and the sites northeast of the Mjøsa area, resulting in successions of broadly similar age, which undermines the correlation proposed by Nielsen & Schovsbo (2011, p. 244).

Ahlberg et al. (2016) suggested simplifying the current Cambrian Series 2 stratigraphy with four modified and updated zones, each defined by the first occurrence of the zonal species, the *S. mickwitzi*, *H. kjerulfi*, *Strenuaeva? spinosa* and *Chelediscus acifer* zones. In this new scenario, the Brennsætersaga Member and the lower part of the Tømten Member (previously termed the Bråstad Shale) containing *H. inusitata* would be within the *S. mickwitzi* Zone, since the FAD of *H. kjerulfi*, together with the ellipsocephalid *Strenuaeva primaeva*, a proposed secondary marker for the *H. kjerulfi* Zone (Ahlberg et al., 2016), is within the upper part of the Tømten Member (previously termed the *Holmia* Shale).

Stratigraphy of the Flagstadelva section

The section along the Flagstadelva river (Figs. 1 (locality 1) & 3), close to the disused and torn-down Brennsætersaga sawmill in the vicinity of the city of Hamar on the east side of Lake Mjøsa, is the stratotype locality for the Brennsætersaga Member of the

Figure 3. Stratigraphical column of the Flagstadelva river section, close to the disused and torn-down Brennsætersaga sawmill in the vicinity of Hamar on the east side of Lake Mjøsa (WGS 84, 6090162, 1110734). Acritarch data based on Vidal & Nystuen (1990). Older stratigraphical names are given in parentheses.

Ringstranda Formation (Nielsen & Schovsbo, 2007). This upward-coarsening member is divided into a c. 2 metre-thick, silty lower part with thin sandstone layers previously referred to as the Brennsæter Limestone, zone 1a₁, and a sandstone-conglomeratic unit about 1.5 m thick in the upper part referred to as the Bråstad Sandstone, zone 1a₂ (Skjeseth, 1963 and Fig. 4). The thin silt- and sandstone layers of the member are

Skjeseth (1963)		Vidal & Nystuen (1991)		Nielsen & Schovsbo (2007)	
Lower Cambrian	Zone with <i>Strenuella linnarssoni</i> and <i>Torella laevigata</i>	Strenuella Limestone 1b β	Evjevik Limestone	Ringstrand Formation	Evjevik Member
	Zone with <i>Holmia kjerulfi</i>	Holmia Shale 1b α	Holmia Shale		Tømten Member
	Zone with <i>Volborthella tenuis</i> and <i>Callavia</i> n.sp.	Bråstad Shale 1a β	Bråstad Shale		
	Zone with <i>Discinella holsti</i> and <i>Platysolenites</i>	Bråstad Sandstone 1a α 2	Bråstad Sandstone		Brennsætersag Member
	Zone with <i>Holmia</i> cf. <i>mickwitzii</i> and <i>Hyolithus</i> sp.	Brennsæter Limestone 1a α 1	Brennsæter Shale		
Eocamb.	<i>Skolithos</i> , <i>Monocraterion</i> , <i>Diplocraterion</i>	Ringsaker Quartzite	Ringsaker Quartzite Member	Vangsås	Ringsaker Member

Figure 4. Lithostratigraphic units of the lower Cambrian in the Mjøsa area of Skjeseth (1963), Vidal & Nystuen (1990) and Nielsen & Schovsbo (2007). The lowermost Redalen Member and the topmost Skyberg Member of the Ringstranda Formation, present in the Lower Allochthon in the northern part of Lake Mjøsa, are not included in this scheme.

devoid of carbonates, therefore Vidal & Nystuen (1991, p. 195) re-named it the Brennsæter Shale (Fig. 4). The Brennsætersaga Member is not developed in the most distal Lower Allochthon deposits on the palaeoslope present at Redalen and Ringsaker north (localities 6 and 7 in Fig. 1), but comprises the lowermost member in the Ringstranda Formation in the proximal Caledonian Lower Allochthon deposits at Ringsaker south (locality 8 in Fig. 1), and in the parautochthonous and autochthonous settings (Figs. 2 & 5).

The stratigraphically overlying Tømten Member of the Ringstranda Formation has traditionally been divided in two units, the Bråstad Shale and the *Holmia* shale, until Nielsen & Schovsbo (2007) defined them as one, lithologically fining-upward sequence (Fig. 4). At Flagstadelva, c. 9 m of greenish-grey mudstone and siltstone of the lower part of the Tømten Member (previously named Bråstad Shale) is preserved.

The top of the Tømten Member at Flagstadelva is developed as a 30–50 cm-thick limestone bed with an erosional contact to a 10–30 cm-thick phosphorite-bearing conglomerate. The conglomerate is the base of the Alum Shale Formation at this locality, which otherwise is represented here by a few metres of dark shales with limestone nodules. Both the limestone and the conglomerate interval was earlier referred to as the 'Ölandicus-conglomerate' (Skjeseth, 1963).

The Ringstranda Formation rests unconformably on the Ringsaker Member of the Cambrian Vangsåsen Formation in the Lower Allochthon and parautochthonous settings (Fig. 2). *Skolithos*- and *Diplocraterion*-type trace fossils occur at the very top of the Ringsaker

Member in the parautochthonous setting, with the former type present at Flagstadelva and Sollerud (localities 1 & 2 in Fig. 1), and both types are present at Langodden (locality 3 in Fig. 1).

In the Flagstadelva section, the dip is close to 90° and the Brennsætersaga Member is weakly folded in a tectonic contact with the massive quartzite of the Ringsaker Member, but the repetition reported by Daily (1972) was not recognised by the present authors (see also Føyn & Glaessner, 1979, p. 41).

The Bråstad Sandstone of older literature was first described from the Caledonian Lower Allochthon along the River Bråstadelta (locality 9 in Fig. 1) on the west side of Lake Mjøsa (Bråstad, 1915). These beds cannot be correlated with the parautochthonous Brennsætersaga Member in a consistent way and are inferred to be older than the Brennsætersaga Member in the Flagstadelva section (Nielsen & Schovsbo, 2007, p. 67, fig. 8; 2011, fig. 27). The diachronous transgression from the northwest (present-day orientation) resulted in older deposits in the distal Lower Allochthon than in the more proximal parautochthonous area in the southeast (Fig. 5). This is corroborated by finds of *Mobergella radiolata* Bengtson and *M. holsti* Moberg at the Bråstadelta locality (pers. obs. MH; see discussion below), here considered the oldest macrofossils in the Mjøsa area (Fig. 6). Nielsen & Schovsbo (2007, 2011) interpreted the basal layers at Bråstadelta to be the most distally deposited unit, but we follow Skjeseth's (1963, fig. 18) interpretation in considering the northernmost localities at Ringsaker and Redalen to be the most distal deposits on the palaeoslope.

Resolving the fossil occurrences in the Flagstadelva section

New research spanning the entire river section, including the Brennsætersaga Member, the stratigraphically overlying Tømten Member (Bråstad Shale in previous term) and the 'Ölandicus-conglomerate', has resulted in numerous new specimens of an olenellid trilobite that is described herein. The lithology of the new material is comparable to the matrix of Skjeseth's specimen of *H. cf. mobergi*, consisting of pyrite-impregnated silty limestone, but was collected *in situ* from a thin silty limestone facies in the uppermost few centimetres of the previously termed Bråstad Shale at 12.5 m in the section in direct contact with the supposed middle Cambrian 'Ölandicus-conglomerate' of Skjeseth (1963) (Fig. 3). Except for some undeterminable olenellid remains found in the mudstone at 10.5 m in the section, this is the only reliable occurrence of olenellids here. Therefore, the position of the single trilobite find of Skjeseth seems to be misplaced, as the lower part of the section has proved to be barren of shelly fossils despite more than 50 years of search; moreover, the lower part of the section does not contain carbonates.

Skjeseth (1963) also reported the occurrence of *Discinella* (= *Mobergella*), an enigmatic but potentially important fossil for biostratigraphy, from a thin sandstone bed in zone 1a₂, the upper part of the Brennsætersaga Member (formerly the Bråstad Sandstone) in the Flagstadelva river section. These specimens have not been located in the collections of the Natural History Museum in Oslo, Norway, where other samples from Skjeseth's research are housed, nor has the record been confirmed during the numerous later examinations of the section listed above. *Mobergella*-bearing sandstones in Scandinavia correlate with the lower part of the *Heliosphaeridium dissimulare*-*Skiagia ciliosa* acritarch Zone (Moczydlowska, 1991), stratigraphically above the *S. mickwitzi* Zone. On the Siberian Platform, *Mobergella radiolata* Bengtson (also occurring at the Bråstadelta locality, pers. obs. MH), is found in older deposits of early Atdabanian age (e.g., Demidenko, 2016; Zhang et al., 2017) corresponding to the *Schmidtellus mickwitzi* Zone and older age. In earlier publications, prior to the acritarch zonation, *Mobergella*-bearing units have traditionally been considered *S. mickwitzi* Zone in age (e.g., Mens et al., 1990). Considering Skjeseth's erroneous placement of *H. cf. mobergi*, the extensive examinations of the section throughout the years and the lack of material in the collections of the Natural History Museum, Oslo, the recorded occurrence of mobergellans in the Brennsætersaga Member at Flagstadelva should be treated with caution and is most likely erroneous.

The 50–70 cm-thick bed capping the Bråstad Shale at Flagstadelva has been referred to the middle Cambrian 'Ölandicus-conglomerate' (Skjeseth, 1963), but only the

uppermost few centimetres of this bed at approximately 13 m in the section consists of small, well-rounded quartz and phosphorite grains with sporadic coarser-grained pebbles up to 20 mm in diameter (Fig. 3). This thin conglomerate forms the base of the middle Cambrian at this locality. The olenellid-containing calcareous lower part of this bed and the conglomerate at the top of the bed are sharply divided by an erosional surface (Fig. 7A) representing a considerable time-span. Commonly occurring trilobite sclerites in the conglomerate belong to the mid-Cambrian trilobites *Paradoxides paradoxissimus* (Wahlenberg) and *Parasolenopleura spinigera* Westergård (Fig. 7B–F), indicating the *Ptychagnostus atavus* Zone or the *Ptychagnostus punctuosus* Zone. *Hypagnostus parvifrons* Linnarsson, a common taxon in both agnostoid zones, was collected 2 m above the conglomerate. The transgression event following the Hawke Bay unconformity resulted in the earliest deposits distally in the Caledonian Lower Allochthon in mid-Cambrian times. Hence, sediments of the *Acadoparadoxides oelandicus* Superzone are found only in the Caledonian Lower Allochthon strata in the Mjøsa area (Høyberget & Bruton, 2008). Areas in the parautochthonous and autochthonous settings were flooded during the much younger *Ptychagnostus atavus* Zone in the *Paradoxides paradoxissimus* Superzone, based on fossil occurrences at Risbekken (Høyberget & Bruton, 2008) (locality 4 in Fig. 1) and Flagstadelva.

Skjeseth (1963, p. 41) refers to worm tracks in the Brennsætersaga Member in the Flagstadelva section as being similar to those found in abundance in the stratigraphically older Redalen Member, but few ichnospecies have been observed during recent investigations, only some simple *Palaeophycus*-type burrows. The Redalen Member in the Caledonian Lower Allochthon setting though yields a range of significant trace fossils in addition to *Palaeophycus* isp. (see below).

Vogt (1924) reported two small fragments (0.7 and 1.5 mm long, respectively) of *Platysolenites antiquissimus* Eichwald from the Lower Allochthon Redalen Member, which was correlated with the Bråstad Sandstone in Flagstadelva by Skjeseth (1963). Some attention has been paid to this specious correlation in later publications (e.g., Hamar, 1967; Martinsson, 1974; Føyn & Glaessner, 1977; Bergström, 1981). The tubular *P. antiquissimus* is an index fossil for considerably older Terreneuvian strata and the occurrence of this taxon in the presumed much younger Redalen Member has not been re-confirmed, nor has it been found in the Flagstadelva section; therefore, its presence in the Ringstranda Formation is considered highly dubious.

Figure 5. Correlation scheme of the different tectonostratigraphic settings in the Mjøsa area showing lithostratigraphy, zonation and important lower Cambrian outcrops. The numbers by each outcrop name correspond to their position on the map in Fig. 1. The white, hachured line indicates the Hawke Bay unconformity and possible denudation. Red bars indicate preserved sections at the different outcrops.

Implications for the lower Cambrian stratigraphy in the Mjøsa area

Early research on acritarch biostratigraphy of the lower Cambrian strata in Scandinavia (Vidal, 1981a, b; Moczyłowska & Vidal, 1986) suggested an age correlative to the Lükati Beds of the East European Platform (EEP) for the 1aa zone in the Mjøsa area (= the Brennsætersaga Member). This age is equivalent to the *S. mickwitzi* Zone. A later publication on acritarchs from the Mjøsa area, including the Flagstadelta river section (Vidal & Nystuen, 1990), showed all recorded species from the Brennsætersaga Member to be long-ranging and biostratigraphically undiagnostic common elements in the *S. mickwitzi* Zone or older deposits, except for a single species: *Heliosphaeridium dissimulare* (Volkova). The age of the lowermost unit at Flagstadelta was therefore considered ambiguous but correlative with the Vergale Beds in the EEP, which is age equivalent to the *Holmia kjerulfi* Assemblage Zone. This new proposal was based on scarce material counting only 1 or 2 recorded specimens of *H. dissimulare*, the only age-diagnostic acritarch species from the unit (Vidal & Nystuen, 1990 fig. 6, and Fig. 3 herein). This indicated a younger age of *Holmia cf. mobergi* than had previously been suggested, a conclusion followed by Moczyłowska (1991, 2002) based on the same scarce acritarch samples. However, this acritarch species' age-diagnostic reliability is questioned by its early occurrences outside Baltoscandia (e.g., Vidal et al., 1994; Jensen et al., 2010). The age-diagnostic acritarch species *Skiagia ciliosa* is found in close proximity to the new olenellid material in the overlying Tømten Member (previously the Bråstad Shale) at Flagstadelta (Vidal & Nystuen, 1990, see also

Fig. 3). These two taxa provided an age-constrain to the *Heliosphaeridium dissimulare*–*Skiagia ciliosa* Zone as presently understood (e.g., Moczyłowska, 1991, 2002), which is equivalent to the *Holmia inusitata* and *Holmia kjerulfi* trilobite zones (*Holmia kjerulfi* Assemblage Zone) of the Tømten Member. Therefore, there is no evidence of fossil-bearing deposits of the *Schmidtellus mickwitzi* trilobite zone in the parautochthonous Mjøsa area (Fig. 2).

The Caledonian Lower Allochthon setting of the Bråstad Sandstone at Bråstadelta (locality 9 in Fig. 1) was referred to as the Cambrian basal unit with *Discinella holsti* by Vogt (1924), and mobergellans are known in abundance in a thin, 5 cm-thick layer (Bråstad, 1915; Vogt, 1924; Skjeseth, 1963) (counting 150 specimens in the collections of the Natural History Museum, Oslo). The Bråstad Sandstone in the Bråstadelta section is here considered time-equivalent to the upper part of the more distally deposited Redalen Member (Fig. 2 & 5) and not equivalent to the upper part of the Brennsætersaga Member as perceived earlier, and is here informally named the Bråstadelta member. The Redalen Member and the Bråstadelta member in the Ringstranda Formation are both confined to Lower Allochthon strata and thereby within the same tectonostratigraphic setting.

The Bråstadelta member and the Redalen Member at Redalen and Ringsaker (localities 6–9 in Fig. 1), may be referred to the *S. mickwitzi* Zone. The Redalen Member is rich in trace fossils and the very common and distinct *Palaeophychus* isp. nov. and the rare *Cheichnus* isp. are also recorded from the lower part of the Grammajukku Formation at Storuman, Sweden, occurring within the *S. mickwitzi* Zone (Moczyłowska et al., 2001). *Gyrolithes*

isp. and *Phycodes palmatus* from the Redalen Member are, in common with occurrences from the Sävovare Formation in Laisvall, southern Swedish Lapland, interpreted to be within the Terreneuvian *Platysolenites antiquissimus* Zone (Moczyłowska et al., 2001) and are also described from the lower part of the Torneträsk Formation at Luovárri in northern Sweden within the *Platysolenites antiquissimus* Zone (Jensen & Grant, 1998). Both ichnospecies are long-ranging.

The Tømten Member is only 9 m thick in the parautochthonous Flagstadelva section and close to 50 m thick in the Lower Allochthon on the west side of Lake Mjøsa, a thickness that may well be underestimated (Bjørlykke, 1979). Several metres of the fossil-rich greenish mudstone in the upper part of the Tømten Member, traditionally termed the *Holmia* Shale, were eroded during the Hawke Bay regression event, or alternatively were not deposited (Fig. 5). The Hawke Bay unconformity is thus significantly more extensive in the parautochthonous strata than in the Lower Allochthon, as already suggested by Nielsen & Schovsbo (2011, p. 244, 2015, p. 315). Consequently, only the lower part of the Tømten Member (previously the Bråstad Shale) is preserved in the Flagstadelva river section (Fig. 5). The absence of the traditionally termed *Holmia* Shale (now upper part of the Tømten Member) and the overlying *Strenuella* Limestone (= Evjevika Member) in the Flagstadelva river section was emphasised by both Skjeseth (1963) and Yochelson et al. (1977). In the Lower Allochthon Bråstad Shale section, the thickness of the previously termed Bråstad Shale is difficult to measure due to complex tectonics and repetition of strata, but is estimated to exceed 20–30 metres (Bjørlykke, 1979).

The *Holmia inusitata* Zone

In the Lower Allochthon, and also in parautochthonous and autochthonous strata on the west and east side of Lake Mjøsa, the alternating mudstone and siltstone facies in the lower part of the Tømten Member contain a low-diversity fossil assemblage, in striking contrast to the younger beds. A single trilobite taxon, *Holmia inusitata* Ahlberg & Bergström, scattered finds of the brachiopod *Magnicanalis* Rowell, the tubular *Torellella* Holm and very common occurrences of the agglutinated, enigmatic *Volborthella* Schmidt are the only recorded microfossils (Fig. 6). The fine-grained mudstone of the upper part of the Tømten Member (the *Holmia* Shale in older terms), however, yields a remarkably more diverse fauna, counting three trilobite families represented by at least eight species including the first appearance of ellipsocephalids, several hyolith- and brachiopod taxa and enigmatic, tubular fossils (Kiær, 1917 and personal observations; Fig. 6). This radiation is also reflected in the significant increase in the diversity of acritarch

species in the *Holmia* Shale (Vidal & Moczyłowska-Vidal, 1997; Moczyłowska, 2002). The fossil content is further diversified with an increase in number of animal groups and species in the overlying Evjevika Member (Høyberget et al., 2015) and unpublished material from the Skyberg Member, both Series 2, Stage 4 in the Ringstranda Formation. This rather sudden faunal diversity in *Holmia kjerulfi*-age sediments and the flourish of ellipsocephalids contrast the low diversity in the older Bråstad Shale, which strengthens the validity of a *Holmia inusitata* Zone at least as a local biozone in the Mjøsa area.

Further research may confirm the *Holmia inusitata* Zone elsewhere in Scandinavia and closer attention should be paid to the interesting finds of *Holmia* sp. described from the Grammajukku Formation at Storuman in southern Swedish Lapland (Moczyłowska et al., 2001). Lower Cambrian strata are preserved in a ~2000 km-long autochthonous unit following the Caledonian nappe front in Scandinavia up to Finnmark in the far north of Norway (Føyn & Glaessner, 1979). A few places have been investigated, but vast areas remain unknown.

Some rare olenellid material collected from the Digermulen Peninsula in northernmost Norway by Henningsmoen & Nikolaisen in the early 1960s, were interpreted as conspecific with *Holmia* cf. *mobergi* by Bergström (1980). The olenellid-bearing strata on the Digermulen Peninsula were subsequently considered

ZONES	BIOTA										COUNTS
	o	M	hyhyhy		X	V	II	Hyo	tutu	X	
<i>E. lunatus</i>	eeee bbb	B phphph									26
<i>E. linnarssoni</i>	ooo eeeeee Eo b	M B ph	hehehehe hy		X						21
<i>H. kjerulfi</i>	oooo eee Eo	M B ph	hyhy		X	V	T	Hyo	tutu	X	20
<i>H. inusitata</i>	o	M	hy			V	T			X	7
<i>Mobergella</i> , <i>S. mickwitzii</i>								mm			2
	ARTHROPODA	BRACHIOPODA	MOLLUSCA	ECHINODERMATA	ANNELIDA	PROBLEMATICA	ALGAE				

Figure 6. Fossil content recorded from the biostratigraphical zonation adopted in this paper: o – olenellids, e – ellipsocephalids, Eo – eodiscids, b – bradoriids, M – *Magnicanalis*, B – *Botsfordia*, ph – phosphatic brachiopods, hy – hyolithids, he – *helcionellids*, V – *Volborthella*, T – *Torellella*, Hyo – *hyolithelminthids*, l – *lapworthellids*, tu – tubular fossils, m – *mobergellans*, X – present. Each abbreviation indicates one species. Based on Kiær (1917), Høyberget et al. (2015) and unpublished data.

Schmidtellus mickwitzii Zone in age in later publications (Bergström, 1981; Ahlberg, 1984, 1985; Ahlberg et al., 1986; Moczyłowska, 1991, 2002; Jensen & Grant, 1998). Extensive new studies yielding acritarchs and a rich collection of trilobites here (Palacios et al., 2015; Ebbestad et al., 2017), including ellipsocephalids (personal observations), have shown that the olenellid-bearing strata in this northernmost area of the Caledonides occur within the *H. dissimilare*–*S. ciliosa* Zone and confirming Nikolaisen & Henningsmoen's (1987) assignment of their scarce Digermulen Peninsula material to the trilobite genus *Kjerulfia* Kiær.

Systematic palaeontology

Specimens of *Hyolithus* sp. and *Obolella* sp., previously reported by Skjeseth (1963, p. 48) to co-occur with *Holmia* cf. *mobergi*, were not found in the collections of the Natural History Museum, Oslo, but during recent investigations of the section a single hyolithid shell and a single, damaged, brachiopod specimen were collected together with the new *Holmia* material (Figs. 3 & 7G, H). The hyolithid is collapsed and the shell is mostly peeled off. Shell ornamentation is therefore not preserved. The specimen is 15 mm long and weakly curved, and the internal mould is 1.5 mm across at the widest end. A small preserved shell patch shows a thickness of ~0.2 mm. This specimen is interpreted as a hyolith and not a trilobite genal spine because of the calcite-crystalline wall of the shell patch, quite unlike the trilobite preservation from this locality.

A damaged specimen identified as the brachiopod *Magnicanalis* Rowell (Fig. 7H), previously placed with *Obolella* (e.g., Kiær, 1917), was collected from the silty limestone. The pattern of the growth lines is very similar to *M. rotundata* (Kiær), which commonly occurs in the overlying *H. kjerulfi* Zone and abundantly in the younger *Ellipsostrenua linnarssoni* Zone (Høyberget et al., 2015).

The enigmatic, cone-shaped and agglutinated *Volborthella* Schmidt is repeatedly cited in publications on the Cambrian stratigraphy of the Mjøsa area and figured and described by Bråstad (1915), Kiær (1917) and more thoroughly by Yochelson et al. (1977) from the Bråstad Shale (= *H. inusitata* Zone) and also from the *Holmia* Shale (= *H. kjerulfi* Zone) by Kiær (1917). The latter occurrence was not confirmed by Yochelson et al. (1977), who confined *Volborthella* to the Bråstad Shale only. Attempts have been made to establish a zone with *Volborthella tenuis* Schmidt as the eponymous species (e.g., Vogt, 1924; Skjeseth, 1963). The taxon, though, is long ranging and found throughout the Tømten and Skyberg members of the Ringstranda Formation (unpublished personal observations MH) and is probably of little biostratigraphic value. *Volborthella* is

very common, in places occurring in clusters in the lower part of the Tømten Member (Bråstad Shale), and has been collected throughout this unit in the Flagstadelva river section. The conical specimens show a considerable variation in divergence of the outer margins from the apex to the widest end (Fig. 7L, M), from 26° to 12° and with most specimens around 17°. The length/width ratio varies between 2.3 and 5.3 and is around 3.6 in most specimens. *Volborthella* is by far the most common fossil in the *Holmia inusitata* Zone and is reported from a large number of outcrops in the Mjøsa area. Specimens from Flagstadelva and Lauselva are here figured for the first time (Fig. 7I–M).

Material and methods

We provide here the correct spellings of the Lower Cambrian Norwegian members and formations. The new spellings are in grammatical accordance with the formally described Norwegian Ordovician and Silurian members and formations (Worsley et al., 1983; Owen et al., 1990).

Linear measurements used in this analysis are explained in Fig. 8A.

Bivariate and ordination analyses were undertaken on linear measurements made on suitable material. All measurements were done on images of specimens in Adobe Photoshop. Statistical tests and the PCA analyses were performed with Microsoft Excel and the statistical package PAST, version 3.10 (Hammer et al., 2001).

A new figure of the original specimen (PMO 113.235) collected by Skjeseth (Fig. 9A) is presented and additional material from the Flagstadelva river section is provided, collected during investigations in 2002–2005. This new material consists of partially preserved cephalia, including a series of six meraspid (PMO 234.265–PMO 234.268/1, PMO 234.269 and PMO 234.270/1) and twelve holaspid cephalia (PMO 234.268/3 with counterparts PMO 234.268/3A and B showing the entire length of the occipital spine, PMO 234.270/2, PMO 234.271, PMO 234.272/1, PMO 234.272/2, PMO 234.273/1, PMO 234.273/2, PMO 234.274–PMO 234.278) of different size, four hypostomes (PMO 234.268/2, PMO 234.279–PMO 234.281), nine articulated thoracic segments (PMO 234.282) with a macrospine on the 9th segment, four isolated thoracic segments (PMO 234.283–PMO 234.286), one genal spine with inner spine angle and counterpart (PMO 234.306) and one pygidium (PMO 234.287), all collected at about 12.5 m in the Flagstadelva river section.

Additional well-preserved topotype material of *H. inusitata* was collected from Lauselva between the 1.5 and 2.0 m levels in the section (see Ebbestad et al., 2003, text

Figure 7. (A) Photo showing the sharp erosive surface between the mid-Cambrian basal conglomerate of the Alum Shale Formation with calcite-cemented, rounded, quartz- and phosphorite grains and the lower Cambrian silty limestone of the Tømten Member, containing *Holmia inusitata*. 13 m level, Flagstadelva. (B) Pygidium of *Paradoxides paradoxissimus* (PMO 234.299/1). (C, F) *Parasolenopleura spinigera* (PMO 234.300/1). (D) *Parasolenopleura spinigera*, note occipital spine (PMO 234.300/2). (E) *Parasolenopleura spinigera* (PMO 234.299/2). B–F from basal conglomerate of the Alum Shale Formation, Flagstadelva. (G) *Hyolithid* (PMO 234.301), Tømten Member, 12.5 m level, Flagstadelva. (H) *Magnicanalis* sp. (PMO 234.270/3), Tømten Member, 12.5 m level, Flagstadelva. (I) *Volborthella*, same slab as K. (J) *Volborthella* (PMO 234.303), Tømten Member, 12 m level, Flagstadelva. (K) Cluster of *Volborthella* (PMO 234.302), *Holmia inusitata* Zone, Lauselva. (L, M) Close-up of *Volborthella* cluster (PMO 234.304), note variable tapering, Tømten Member, 12 m level, Flagstadelva. All scale bars = 2 mm.

fig. 3) during investigations in 2000–2009. This consists of three nearly complete specimens (PMO 234.288–PMO 234.290), one showing an *in situ* hypostome and pygidium, one fragmentary cephalon with five attached thoracic segments (PMO 234.291), four partially

preserved cephalons (PMO 234.292–PMO 234.295), one fragmentary cephalon with hypostome attached (PMO 234.296), two articulated thoracic regions, one with 7 segments (PMO 234.297), another with 9 segments (PMO 234.305), both specimens carrying a macrospine

Figure 8. (A) Schematic drawing of the cephalon of *H. inusitata* with the linear measurements used in this analysis. (B) Bivariate plot of glabellar length (GL) against posterior width of the glabella (W5). (C) Bivariate plot of the width across the palpebral lobes (W7) against width of the extraocular area (W10). (D) Bivariate plot of glabellar length (GL) against length of the postocular area (L5). (E) Scatter plot of the PCA analysis.

on the 9th segment, and one partial thoracic segment (PMO 234.298).

The material described or discussed in this paper is housed at the Natural History Museum in Oslo, Norway (PMO), Swedish Geological Survey, Sweden (SGU), Lund University, Sweden (LO) and the Museum of Evolution, Uppsala University, Sweden (PMU).

Suborder Olenellina Walcott, 1890

Family Holmiidae Hupé, 1953

Genus *Holmia* Matthew, 1890

Type species: By original designation of Matthew (1890, p. 160), *Paradoxides kjerulfi* Linnarsson, 1871, p. 790, from the lower Cambrian Tømten Member of the Ringstrand Formation (previously the *Holmia* Shale) at Stein in the Ringsaker district, Norway.

Holmia inusitata Ahlberg & Bergström, in Ahlberg et al., 1986
Figs. 9–19

- 1956 *Holmia* cf. *mickwitzi* (Schmidt) – Henningsmoen (biostratigraphic scheme and listed in the text).
- 1960 *Holmia* cf. *mickwitzi* (Schmidt) – Henningsmoen (biostratigraphic scheme and listed in the text).
- 1963 *Holmia* cf. *mickwitzi* (Schmidt) – Skjeseth (mentioned in text and lithostratigraphic column).
- 1963 *Callavia* sp. n. – Skjeseth (mentioned in text and lithostratigraphic column).
- 1974 *Schmidtellus* cf. *mickwitzi* (Schmidt) – Martinsson (discussion and table with Scandinavian biozones).
- 1974 *Callavia* n. sp. Skjeseth – Martinsson (mentioned in the text).
- 1977 *Schmidtellus* cf. *mickwitzi* (Schmidt) – Bengtson (mentioned in the text).
- 1978 *Holmia* cf. *mobergi* Bergström – Ahlberg & Bergström (table with biozones).
- 1978 *Holmia* n. sp. Ahlberg & Bergström (table with biozones).
- 1979 *Holmia* cf. *mickwitzi* (Schmidt) – Føyn & Glaessner (listed in the text).
- 1980 *Holmia mobergi* Bergström – Bergström (listed in the text).
- 1980 *Holmia* n. sp. – Bergström (biostratigraphic scheme and listed in the text).
- 1981 *Holmia mobergi*(?) Bergström [part.] – Bergström (listed in the text and Baltoscandian correlation chart). Not material from Finnmark = *Kjerulfia* n. sp.
- 1981 *Holmia* n. sp. ("Callavia") Bergström (listed in the text).
- 1981 *Holmia* n. sp. Bergström – Bergström & Ahlberg (correlation scheme).
- 1981a *Holmia* cf. *mobergi* Bergström – Vidal (mentioned in the text).
- 1981b *Holmia* n. sp. Bergström – Vidal (mentioned).
- 1984 *Holmia* cf. *mobergi* Bergström – Ahlberg (mentioned).
- 1984 *Holmia* n. sp. Bergström – Ahlberg (mentioned).
- 1985 *Holmia* cf. *mobergi* Bergström – Bergström & Gee (listed in the text).
- 1985 *Holmia* cf. *mobergi* Bergström – Ahlberg (mentioned in the text and biostratigraphic scheme).
- 1985 *Holmia* n. sp. Bergström – Ahlberg (mentioned in the text and biostratigraphic scheme).
- 1986 *Holmia inusitata* n. sp. – Ahlberg & Bergström (description and fig. 3).
- 1986 *Holmia* cf. *mobergi* Bergström [part.] – Ahlberg et al. (description and fig. 6). Not fig. 8A, B from Finnmark = *Kjerulfia* n. sp.
- 1990 *Holmia* cf. *mobergi* Bergström – Vidal & Nystuen (listed in the text).
- 1990 *Holmia* cf. *mobergi* Bergström – Mens et al. (correlation scheme).
- 1991 *Holmia* cf. *mobergi* Bergström – Moczyłowska (mentioned in the text).
- 1991 *Holmia inusitata* Ahlberg & Bergström – Moczyłowska (mentioned in the text).
- 1995 *Holmia inusitata* Ahlberg & Bergström – Fritz (mentioned in the text).
- 1997 *Holmia* cf. *mobergi* Bergström – Jensen (listed in the text).
- 1999 *Baltobergstroemia inusitata* (Ahlberg & Bergström) – Liebermann (discussion).
- 1999 *Schmidtellus* sp. – Liebermann (discussion).
- 2001 *Holmia* cf. *mobergi* Bergström – Moczyłowska et al. (compared with *H.* sp.).
- 2002 *Holmia* cf. *mobergi* Bergström – Moczyłowska (mentioned in the text).
- 2003 *Holmia inusitata* Ahlberg & Bergström – Ebbestad et al. (description and figures).
- 2003 *Holmia* cf. *mobergi* Bergström – Ebbestad et al. (discussion and line drawing in table with biozones).
- 2007 *Holmia* cf. *mobergi* Bergström – Nielsen & Schovsbo (mentioned in the text).
- 2007 *Holmia inusitata* Ahlberg & Bergström – Nielsen & Schovsbo (mentioned in the text).
- 2011 *Holmia* cf. *mobergi* Bergström – Nielsen & Schovsbo (mentioned in the text).
- 2011 *Holmia inusitata* Ahlberg & Bergström – Nielsen & Schovsbo (mentioned in the text).

Holotype: By original designation of Ahlberg & Bergström, in Ahlberg et al., 1986, pp. 43–45, fig. 3A and refigured by Ebbestad et al. (2003). pl. 1, fig. 1. A partially preserved cephalon with three fragmentary thoracic segments (PMO 113.233) collected by S. Skjeseth from autochthonous strata in the Lauselva river section west of Lake Mjøsa in the early 1950s.

Diagnosis: Emended. A species of *Holmia* with a perfectly semi-circular cephalic outline and a broad and convex cephalic border with a well-defined border furrow. The glabella is half as long as total cephalic width and subparallel in outline. S3 is transglabellar and undulating. The occipital spine is stout and broad based, medially placed on the occipital ring (LO) while the intergenal spines are small and node-like, placed in line with or slightly outside the ocular lobes (exsag.). Posterior end of ocular lobes is adjacent to the anterior part of LO. Thorax with 19 segments.

Remarks: *Holmia* cf. *mobergi* described from Flagstadelva is here considered conspecific with *Holmia inusitata*. *Holmia* sp., *sensu* Moczyłowska et al. (2001), although very similar to *H. inusitata*, is in need of a more thorough revision and is still left under open nomenclature.

The only known specimen from the Flagstadelva river section, originally determined *Holmia* cf. *mickwitzi*, has previously been figured and described as *H. cf. mobergi* in Ahlberg et al. (1986). Liebermann (1999) discussed its affinities and transferred the species to *Schmidtellus*

Figure 9. (A) *Holmia inusitata* (PMO 113.233), coll. S. Skjeseth, early 1950s. A diagonal crack and slight clockwise rotation of the cheek region make the occipital lobe appear wider. Note prominent border. Presumably from 12.5 m level, Flagstadelva. (B) *Holmia inusitata*. Retrodeformed large cephalon (PMO 234.271) with strain ellipse showing densely placed compaction cracks, Flagstadelva. (C) *Holmia inusitata*, cephalon (PMO 234.292) with well-preserved posterior margin. a – parafrontal band, b – anterior metaparian suture, c – posterior metaparian suture. Lauselve, 2 m level. (D) *Holmia inusitata*. Retrodeformed, small holaspide cephalon (PMO 234.272/1) with strain ellipse, Flagstadelva. a – parafrontal band, b – anterior metaparian suture. See Fig. 19A for the specimen prior to retrodeformation. (E) *Holmia inusitata*, partial cephalon (PMO 234.274), Flagstadelva. All Flagstadelva specimens from the 12.5 m level. (F) *Holmia mobergi*, holotype (LO 4457T), coll. J.C. Moberg, 1904. *Schmidtellus mickwitzi* Zone, Norretorp Formation, Scania, Sweden (original of Bergström, 1973, fig. 3A). Scale bar on A–C, E & F = 10 mm, D = 5 mm. Note that scale bars in the retrodeformed specimen are prior to retrodeformation.

Moberg in accordance with Martinsson (1974). Ebbestad et al. (2003) described and discussed *Holmia inusitata*, figured all available specimens at that time and sorted out the character variations and distribution within Scandinavian species of *Holmia*. Similarities between *Holmia inusitata* and *H. cf. mobergi* were emphasised in their re-description of *H. inusitata* and both taxa were maintained as distinct species of *Holmia*.

Description

Measurements

The material from both the Flagstadelva and the Lauselva sections shows variable degrees of dorso-ventral compaction and/or tectonic deformation, which introduces problems interpreting the original shape of such specimens (Webster & Hughes, 1999). Length and width measurements on the cephalon of these specimens are therefore uncertain and are here only used as a general guide to highlight certain features of the morphology or individual specimens and better understand the deformation involved.

Generally, specimens from the autochthonous Lauselva section are less compacted and show little tectonic deformation, while specimens from the parautochthonous Flagstadelva section are more dorso-ventrally compacted and usually tectonically deformed. Some of the small meraspid specimens from Flagstadelva show less compaction-related deformation while the two large and fairly complete cephalon from Flagstadelva (Fig. 9A, B) are rather heavily dorso-ventrally compressed. Similar-sized specimens from Lauselva, although dorso-ventrally compacted, typically retain much of the convexity of the glabella area and palpebral lobes (tr., exsag.) whereas the extraocular area is played to various degrees.

Tectonically deformed specimens had to be retro-deformed prior to measurements, which was done based on assumptions at right-angles on the cephalon and comparison of relative proportions from specimens less affected by tectonic deformation (see Żylińska et al., 2013). The elongation of the strain ellipse is 125–135%.

Fifteen specimens from Flagstadelva and ten specimens from Lauselva were suitable for measurements. The morphological variation was captured with a set of 17 linear measurements (Fig. 8A, Table 1) that were subjected to both bivariate and principal component analyses (PCA). Because of missing data, W3, W4 and W8 were omitted in the PCA analysis, leaving 14 measurements and 16 specimens. Although incompletely preserved, measurements of *H. mobergi* Bergström from Scania, southern Sweden (Fig. 9F), are included in Table 1 and some of the bivariate plots.

Glabellar length could be measured in fourteen specimens from Flagstadelva, and eleven of these are smaller than the smallest specimen from Lauselva. The average glabellar length of presumed meraspid specimens from Flagstadelva (glabellar length shorter than 8.0 mm) is 4.18 mm ($n = 5$), while the average glabellar length for presumed holaspid specimens from Flagstadelva is 17.33 mm ($n = 9$). Specimens from Lauselva have an average glabellar length of 25.11 mm ($n = 10$). The standard deviation of the glabellar length measurements of the Flagstadelva specimens is greater than that of the Lauselva specimens (9.57 vs. 3.79) showing that the latter sample is much more homogeneous in its size distribution. The Flagstadelva sample has more specimens in the lower size classes (glabellar length less than 5 mm) and fewer of the large specimens (glabellar length greater than 12 mm). The greatest glabellar length measured on a Flagstadelva specimen is greater than any of the measurements on the Lauselva specimens (Table 1).

Bivariate plots of linear measurements yield for the most part a fairly close relationship between the Flagstadelva and Lauselva specimens, but with some exceptions. Sagittal glabellar length (GL) plotted against the width (tr.) at the occipital lobe (W5) places the Lauselva specimens a bit lower on the y-axis, meaning that the glabellar length is proportionally longer relative to W5 in this sample set (Fig. 8B); a Student's t-test shows that there are no significant differences in the slopes between the regression lines in the two samples. The original *H. cf. mobergi* specimen (Fig. 9A) has the widest posterior width relative to glabellar length of the Flagstadelva specimens, followed by the third largest specimen (Fig. 9B). Both of these show a substantial degree of dorso-ventral flattening. Specimen in Fig. 9C is a fairly representative specimen from Lauselva with regard to these measurements, while specimen in Fig. 10B has a proportionally narrow posterior width and specimen in Fig. 13B is closer to the larger Flagstadelva specimens. In the largest specimen from Flagstadelva (Fig. 10A, B) the anterior margin of the glabella is a bit deformed, which may have affected the length measurement. Otherwise, the original convexity of the specimen in Fig. 10B, D & F is well-preserved.

One of the most variable linear interrelationships is between the width across the palpebral lobes (W7) and the width of the extraocular area (W10) (Fig. 8C). Generally, specimens from Lauselva have a greater width of the extraocular area than the Flagstadelva specimens. See Figs. 11A, B, C, & 13A, B, C, D and also PMO 169.669/1 in Ebbestad et al., 2003, plate 1, fig. 2. Exceptions are specimens shown in Fig. 9C and 10B, which correspond well with specimens from Flagstadelva (compare Fig. 9A & 9C). The differences are most likely due to the different compressional settings of the specimens as discussed above and partly size-related as discussed under ontogeny.

Table 1. Measurements in millimetres on cephalon of *Holmia inusitata* from Flagstadelva and *Lauselv* arranged according to increasing glabella length. Numbers of specimens from Flagstadelva are in bold. *Holmia mobergi* is included. A (H) following the specimen number indicates the holotypes. GL is the glabella length, calculated from L1-L2 or measured directly on the specimen.

Specimen	W1	W2	W3	W4	W5	W6	W7	W8	W9	W10	W11	L1	L2	GL	L3	L4	L5
<i>Holmia inusitata</i>	1.0	0.6	–	–	1.0	2.0	2.8	–	0.7	–	–	–	–	2.1	0.3	1.6	–
<i>Holmia inusitata</i>	1.8	0.8	1.1	1.9	1.6	3.0	4.3	5.3	0.9	0.5	0.5	3.7	0.4	3.3	0.9	2.0	0.3
<i>Holmia inusitata</i>	2.0	1.0	–	–	2.0	3.7	5.3	–	1.1	–	–	–	–	–	–	2.8	0.6
<i>Holmia inusitata</i>	2.7	1.2	–	–	2.1	4.2	6.0	–	1.4	0.5	0.6	4.9	0.4	4.5	1.1	3.0	0.5
<i>Holmia inusitata</i>	2.3	1.1	–	2.1	2.3	4.0	6.0	7.5	1.3	–	–	–	–	4.6	1.1	3.1	0.6
<i>Holmia inusitata</i>	3.9	1.2	–	3.3	3.4	4.7	7.7	9.8	1.9	1.2	0.8	7.2	0.9	6.4	1.9	3.7	0.6
<i>Holmia inusitata</i>	5.1	1.6	–	–	4.5	7.0	10.0	–	1.9	1.1	1.2	8.7	0.7	8.0	2.7	4.3	1.0
<i>Holmia inusitata</i>	4.9	1.8	–	–	4.4	7.4	9.6	–	2.0	–	–	9.4	0.7	8.7	2.8	4.4	1.1
<i>Holmia inusitata</i>	–	2.6	0.0	6.6	6.2	9.1	14.4	19.0	3.3	1.4	1.7	11.8	1.0	10.8	3.3	6.4	1.1
<i>Holmia inusitata</i>	9.3	3.8	3.4	8.9	6.6	11.4	17.6	24.5	3.9	2.6	2.3	14.2	1.4	12.8	4.3	7.5	1.4
<i>Holmia inusitata</i>	10.1	3.7	–	–	8.0	13.7	19.3	–	3.9	–	–	–	–	15.4	4.8	8.7	–
<i>Holmia inusitata</i>	12.1	3.7	–	9.1	10.5	17.4	22.2	28.7	4.2	3.4	1.9	19.3	1.3	18.0	6.7	9.7	1.8
<i>Holmia inusitata</i>	13.2	3.9	4.8	10.4	9.5	16.1	21.7	30.6	4.5	4.5	2.7	20.7	1.3	19.4	7.6	9.9	2.2
<i>Holmia inusitata</i>	12.2	4.7	6.9	12.5	10.3	17.8	24.0	35.3	4.5	4.8	2.2	23.1	1.9	21.3	7.3	11.6	2.2
<i>Holmia inusitata</i>	12.8	4.4	5.8	12.4	10.5	16.9	23.5	35.7	4.8	3.5	2.7	23.0	1.7	21.3	7.5	11.1	2.5
<i>Holmia inusitata</i>	12.9	4.5	–	–	10.3	19.0	24.3	–	5.3	3.6	3.1	25.5	1.7	23.9	7.1	11.7	3.1
<i>Holmia inusitata</i>	14.8	5.1	7.2	15.2	12.1	19.9	27.7	42.8	6.6	4.7	3.5	25.5	1.3	24.2	7.7	13.0	3.2
<i>Holmia inusitata</i>	18.6	6.3	–	15.2	14.9	29.2	35.6	44.9	6.7	4.1	2.8	26.5	2.3	24.2	9.4	13.5	4.3
<i>Holmia inusitata</i>	13.3	4.6	–	–	11.6	18.8	25.1	–	4.8	5.9	3.2	27.2	1.7	25.5	8.5	13.0	3.3
<i>Holmia inusitata</i>	18.6	6.4	5.9	13.6	16.5	23.2	34.0	43.6	6.7	4.2	3.6	27.7	1.5	26.2	7.6	14.7	3.2
<i>Holmia mobergi</i>	16.2	5.8	–	–	13.6	22.0	–	–	–	–	–	28.4	1.4	27.0	10.0	14.3	1.8
<i>Holmia inusitata</i>	–	5.5	8.7	16.3	13.0	21.7	28.9	45.6	6.9	6.2	3.4	29.2	2.1	27.1	9.0	13.5	5.1
<i>Holmia inusitata</i>	16.5	4.9	7.6	14.2	13.8	21.0	28.3	42.3	5.0	6.7	2.7	30.5	2.2	28.3	10.3	13.7	3.0
<i>Holmia inusitata</i>	14.4	5.2	8.1	16.0	15.5	24.8	31.3	49.7	6.1	6.5	3.5	30.9	1.1	29.8	11.7	15.3	3.7
<i>Holmia inusitata</i>	20.3	7.0	–	–	14.6	25.5	34.0	–	5.9	–	–	–	–	30.5	11.1	15.1	5.0
<i>Holmia inusitata</i>	0.0	0.0	–	–	19.1	–	–	–	–	–	–	–	–	31.9	–	–	–

Two specimens have a markedly longer postocular length (L5) (exsag.) relative to the glabellar length than in other Flagstadelva and Lauselva specimens (Fig. 8D). *Holmia mobergi* Bergström (Fig. 9F) is included for comparison, demonstrating a very short L5 relative to the glabellar length. The long L5 is found in the specimen in Fig. 9B from Flagstadelva and the holotype of *H. inusitata* (see Ebbestad et al., 2003, plate 1, fig. 1) from Lauselva. In general, L5 tend to be marginally longer in larger specimens (glabellar length > 19 mm), which may relate to ontogeny. However, both the mentioned specimens are tectonically deformed, which likely explains the anomaly in the L5 data.

The first principal component (PC1) in the Principal Component Analysis (PCA) relates to increase in the size of the specimens, becoming larger towards the right on PC1 (Fig. 8E). The second principal component (PC2) reflects a number of morphological variations and ontogeny. Especially the width measurements (W1, W5–W7) have large positive loadings on PC2, while lengths (L1, GL, L4) and the width of the extraocular area (W10) have large negative loadings on PC2 (Table 2).

There is a clear relationship between the glabellar length and the width across the palpebral lobes (W7) for the large specimens from Lauselva (right side of PC1). Specimens with a low score on PC2 have a subequal length/width relationship, whereas W7 progressively becomes proportionally greater higher on PC2. The posterior width of the glabella (W5) is about 50% of the

glabellar length, which is average, and the specimens with the lowest score tend to have a bit longer palpebral lobes (L4) relative to W7. The original *H. cf. mobergi* (Fig. 9A) plots high on PC2 owing to a combination of a wide W7, a proportionally wide W5 and short L4 relative to W7.

Meraspid specimens with a glabellar length shorter than 10 mm are clustered quite closely on the left side of PC1 and have low negative scores on PC2. They do not have the same W7-GL relationship as the large specimens. Instead, the meraspids have long, narrow glabellas with a short frontal lobe (L3), wide W7, and long L4 relative to glabellar length (Figs 9D, 17B, D & 18). Two early holaspid specimens a bit higher on PC2, Figs. 9E & 19C, D, also have long L4 but proportionally much wider W7 than the smaller specimens. A slightly larger and flattened specimen, PMO 234.276 (not figured), compare well with the larger Lauselva specimens. The W7 is slightly larger and the W5 value is high, placing it higher on PC2.

The bivariate and PCA analyses highlight some general aspects of this material. The parameters that most strongly influence variations are the glabellar length, palpebral lobe length, length of the frontal glabellar lobe, width across the palpebral lobes and posterior width of the glabella. Especially the width measurements seem susceptible to compaction-related deformation, but differently among the specimens; small meraspids are largely unaffected, larger specimens from Flagstadelva are flattened, while Lauselva specimens retain convexity but with the extraocular area typically splayed and reflected in larger values for W10. The meraspids stand out with narrow glabellas and long palpebral lobes, changing through the ontogeny to shorter L4 and broader W7. Larger specimens from Flagstadelva typically have wider W7 and W5 relative to GL than the Lauselva specimens, most likely reflecting different degrees of compressional compaction.

Cephalon

Ebbestad et al. (2003) erroneously suggested that the cephalic outline in *H. inusitata* was slightly pointed, which was based on the only known cephalon at that time with the outer margin partly preserved. A pointed cephalic outline is commonly observed in other Baltoscandian olenellids and is here interpreted as a preservational condition. It was also stated, based on the holotype, that L1 is extended postero-laterally onto the palpebral area (Ahlberg et al., 1986, p. 43; Ebbestad et al., 2003, p. 1046), but this is caused by wrinkling of the interocular area. L1 is distinctly outlined laterally by an axial furrow in line with the other glabellar lobes (Figs. 9A, C, 10B, 11C & 13A, B). Furthermore, the cephalic length/width ratio is close to 0.5; the glabellar length being half the cephalic width and not less than two-thirds of the maximum cephalic width as previously stated.

Table 2. PCA loadings for the first three principal components.

	PC1	PC2	PC3
W1	0.25562	0.3453	0.63802
W2	0.083999	0.15114	0.11141
W5	0.23088	0.2471	-0.29897
W6	0.36081	0.11894	-0.52687
W7	0.46433	0.50016	-0.064043
W9	0.090187	0.20416	0.051696
W10	0.099211	-0.25482	0.039365
W11	0.051572	0.043252	0.064938
L1	0.47296	-0.42561	0.27689
L2	0.020874	-0.027837	0.22049
GL	0.45209	-0.39778	0.056406
L3	0.16143	-0.28475	-0.26206
L4	0.22373	0.0095245	-0.061411
L5	0.056849	-0.052525	-0.0091946

Figure 10. *Holmia inusitata*. (A & C) Largest glabella collected (PMO 234.268/3), dorsal and lateral view. Note position of base of prominent occipital spine. Flagstadelva. (B, D & F) Partial cephalon (PMO 234.293) in dorsal, lateral and anterior view, transversally slightly compressed. Note prominent anterior border. Lauselva, 1.5–2.0 m level. (E & G) Large fragmentary and tectonically compacted cephalon (PMO 234.277). Note prominent anterior border. Dorsal and anterior view. Flagstadelva. Flagstadelva specimens collected at 12.5 m level. All scale bars = 10 mm.

Striking characteristics of the Flagstadelva specimens are the prominent and convex cephalic border in front of the glabella that gradually widens laterally. The border furrow is distinct and clearly separates the anterior glabellar lobe from the anterior border.

The extraocular area is wider than the antero-lateral border. These features are in common with *H. inusitata*

from the type locality at Lauselva and to some degree *H. mobergi* from the *Schmidtellus mickwitzi* Zone, Scania, southern Sweden, *H. sulcata* Bergström, 1973 from the *H. kjerulfi* Group Zone, Scania, southern Sweden, *Holmia* sp. *sensu* Moczyłowska (2001) from the *S. mickwitzi* Zone, Storuman area in southern Swedish Lapland, and to some extent *H. grandis* Kiær, 1917 from the *H. kjerulfi* Zone, Mjøsa area. No other Scandinavian holmiids show these features.

The stout spine, medially positioned on the occipital lobe in the Flagstadelva material (Fig. 9A, 10A) corresponds well with *H. inusitata* and *H. sp.* The preserved occipital spine on the counterpart (PMO 234.268/3B, not figured) of the specimen in Fig. 10A is 7.5 mm long. A stout spine is a character not found in *H. mobergi* or *H. sulcata*. In *H. mobergi*, the spine is tiny and positioned closer to the posterior margin (Fig. 9F) and the species is further separated from *H. inusitata* by the longer ocular lobes with the distal ends adjacent to midway on the occipital lobe and S3 is not transglabellar. *H. grandis* is distinguished from all other *Holmia* species by the comparatively short ocular lobes, narrower anterolateral border and wider extraocular area. A well-developed transglabellar S3 is seen in the Flagstadelva material, in *H. inusitata* from Lauselva and seemingly present in the few figured specimens of *H. sp.* from Storuman.

Slight compaction of the cephalon usually exaggerates the glabellar furrows and gives them a transglabellar appearance (Fig. 19E).

The Flagstadelva material has a proportionally less expanded frontal lobe, compared to the stratigraphically younger *H. kjerulfi*, *H. lapponica* Ahlberg & Bergström and *H. cf. lapponica*. This lobe is slightly wider than LO, while L1 and L2 are slightly narrower than LO, giving the glabella a subparallel appearance. The same conditions are seen in *H. inusitata*, *H. sp.*, *H. mobergi* and in species of *Schmidtiellus*, the stratigraphically oldest Baltoscandian olenellid taxa. The new topotype material of *H. inusitata* possesses long and straight posteriorly directed genal spines, extending back to the tenth thoracic segment (Fig. 13A, C). The cephalon is covered with a reticulate pattern in well-preserved specimens.

Figure 11. *Holmia inusitata*. (A) Flattened cephalon (PMO 234.294), making the extraocular area appear wide. (B) Silicone cast of cephalon (PMO 234.295) displaying well-preserved reticulate pattern. (C) Partial cephalon (PMO 169.670) showing exceptionally preserved compound eye consisting of thousands of facets (original of Ebbestad et al. 2003, plate 1, figs. 3,4,6 & 8 and plate 2, Fig. 15). (D & E) Close-ups of specimen in C. Lateral views of compound eye. All specimens collected between 1.5–2.0 m level, Lauselva. Scale bars on A–C = 10 mm, D = 5 mm, E = 1 mm.

A parafrontal band is seen in both the Lauselva and the Flagstadelva material (Fig. 9C, D). Its functional morphology is discussed under the description of the hypostome.

Størmer (1942) drew attention to a pair of faintly raised lines in the cheek region of *H. kjerulfi* and *Kjerulfia lata*. These lines were termed the anterior and posterior eye lines. Harrington (*in* Moore, 1959, figs. 45J and 48B) interpreted the lines as a fused facial suture and named it a metaparian suture; a non-functional suture in a state of complete symphysis. Whittington (1997) doubted this interpretation. Faintly raised metaparian suture-lines are seen in *H. inusitata* from Lauselva and Flagstadelva (Fig. 9C, D).

One specimen collected from Lauselva (Fig. 11C–E) shows an extraordinarily well-preserved, compound eye. This is among the oldest known visual surfaces in the fossil record of densely packed lenses and shows that *H. inusitata* already had established compound eyes consisting of thousands of hexagonally arranged facets, each with a diameter of ~0.03 mm. Similar structures

of the visual surface are also found in *H. kjerulfi*. *Schmidtellus reetae* Bergström, a stratigraphically older trilobite known from the *Schmidtellus* Zone in Estonia, displays relatively larger lenses counting less than one hundred on each visual surface (Schoenemann et al., 2017).

Hypostome

A hypostome conjoined with the rostral plate is preserved *in situ* in a nearly complete specimen prepared from the ventral side and collected in the Lauselva section (Figs. 12B & 13C). The hypostome is slightly wider than long, and the anterior wings are joined to the ventral side of the cephalon corresponding to where the parafrontal bands are situated dorsally on each side of the glabellar frontal lobe. The furrow between the parafrontal band and the anterior lobe may indicate an apodemal pit corresponding to a ventral process for attachment of ligaments in connection with the hypostome (Figs. 12D & 13C). Whittington (1987, text-fig. 3) questioned a suture separating this sternite

Figure 12. Hypostomes of *Holmia inusitata*. (A) Poorly preserved and tectonically slightly skewed hypostome and rostral plate (PMO 234.279). Flagstadelva, 12.5 m level. (B) Well-preserved and in situ on nearly complete specimen (PMO 234.290), same as in Fig. 13C. Lauselva. (C & D) Ventral and lateral view of articulated hypostome and glabella (PMO 234.296). Note hypostomal anterior wing below the parafrontal band and pit. Lauselva. Lauselva specimens collected from 1.5–2.0 m level. Scale bars on A = 1 mm, B–D = 5 mm.

Figure 13. *Holmia inusitata*. (A) Cephalon with 11 articulated thoracic segments (PMO 234.288). Note very long genal spine. (B) Largest specimen (PMO 234.289), nearly complete, showing 16 articulated thoracic segments (16th segment labelled. See Fig. 14A for detail). (C) Nearly complete specimen (PMO 234.290), ventral side with hypostome in situ and thorax curled posteriorly, showing pygidium (19th segment labelled. See Fig. 14B for detail). Note very long genal spine exceeding the 11th thoracic segment. (D) Large partial specimen (PMO 234.291) with well-preserved cephalic posterior margin, inner genal spine angle and pleural fields. Hypostome slightly displaced beneath anterior glabellar lobe. (E) Close-up of D showing raised terrace lines on the genal spine. All specimens collected at Lauselvå from 1.5–2.0 m level. Scale bars on A–D = 10 mm, E = 5 mm.

from the rostral plate in *H. kjerulfi*, based on reported collections of isolated hypostomes of the species. In *H. inusitata*, the hypostome is conjoined with the rostral

plate in both small and large specimens. The anterior lobe is prominent and almost five times as long (sag.) as the posterior lobe. A pair of maculae is placed adjacent

to the midway on the lateral border and a pair of short spines are situated on the lateral margin opposite the posterior ends of the maculae. The posterior border is uniform in length (sag.) and a pair of short spines are present postero-laterally on the posterior margin. The posterior margin of the hypostome is on level with the glabellar S1. The hypostomal lobes are covered with a fine ornamentation consisting of an irregular reticulate pattern that is co-marginal on the posterior border. Four hypostomes from the Flagstadelva section agree well with those in the topotype material (Fig. 12). The hypostomes in *H. inusitata* and *H. kjerulfi* are very similar when the reticulate surface sculpture is not preserved. In *H. cf. lapponica*, the posterior lobe appears proportionally longer (sag.) and narrower (tr.) and the hypostome and rostral plate are densely ornamented with irregular terrace lines (Høyberget et al., 2015, fig. 6L). A fragmentary hypostome of *H. sp.* (Moczyłowska et al., 2001, fig. 7f) is similar to *H. inusitata* and the seemingly long lateral border in the figured specimen is due to an exsagittal crack of the anterior lobe near the base of the anterior wings.

Thorax

The exact number of thoracic segments is unknown, but 14 visible axial rings are counted in Fig. 13C, where probably some 5 segments are hidden beneath the posteriormost, enrolled tergites. Another specimen has 16 segments preserved (Fig. 13B), but judging from the angle between the pleural field and the axial ring in the last preserved segment, no fewer than 3 segments are missing (compare Fig. 14A and B). Therefore, *H. inusitata* apparently has 19 thoracic segments (*H. kjerulfi* and *H. lapponica* have 16 and 15 segments, respectively). The pleural field is about two-thirds as wide as the axial ring, excluding the pleural spine. The spine is, like in all other *Holmia* species, constricted at its base and the

outline appears thorn-shaped. The pleural spine of *H. mobergi* (Fig. 15F) from Scania, Sweden, has a more convex anterior margin and appears more sickle-shaped. The length of the pleural spine in *H. inusitata*, measured along the anterior margin, is about equal to the length (sag.) of 2 to 2.5 axial rings. The axial spines gradually increase in size towards the 9th segment (Fig. 15A, E, G & H), which has an axial macrospine (Fig. 15I). A macrospine is also seen on the 9th segment in PMO 234.282 from Flagstadelva and PMO 234.305 from Lauselva (not figured herein). In *H. kjerulfi*, the axial spines are gradually increasing backwards, the largest spines being on the 12th and 13th segments. The two posteriormost segments in *H. kjerulfi* and at least the four posteriormost segments in *H. inusitata* appear spineless (Fig. 14).

A pair of bulges is present antero-laterally on each axial ring (Fig. 15A, C & E), except in the posteriormost few rings (Fig. 15G), making the axial rings distinctly wider in the anterior half. These bulges are separated by shallow furrows directed adaxially forward. The furrow separating the articulating half-ring is deep and well-developed. The articulating sockets and processes, posteriorly and anteriorly placed along the axial furrow on each segment (Fig. 15J) are well-developed, as known in *H. kjerulfi* (Whittington, 1990). *H. inusitata* also shows an angular projection (Fig. 15B) similar to that in *H. kjerulfi*, although the articulating flange along the anterior margin on each pleura known in *H. kjerulfi* is not obvious in *H. inusitata*. The axis and pleural fields are covered with the same reticulated ornamentation as the cephalon and hypostome (Fig. 15G).

Pygidium

The pygidium of *H. inusitata* is here figured for the first time (Figs. 13C & 16A, B, D & E). The shield is highly vaulted and wider than long, with steep, almost vertically

Figure 14. *Holmia inusitata*. (A) Detail of posteriormost thoracic segments of PMO 234.289 from Lauselva, showing the angle between the axial ring and pleural field in the 16th segment (labelled, see Fig. 13B for the entire specimen and corresponding label). (B) Detail of posteriormost thoracic segments of PMO 234.290 from Lauselva showing the angle between the axial ring and the pleural field in the 19th segment (labelled, see Fig. 13C for the entire specimen and corresponding label). (C) Isolated posteriormost thoracic segment from Flagstadelva. Note the nearly 90 degree angle between the fragmentary axial ring and the inner margin of pleural field (PMO 234.286). Scale bars = 1 mm.

Figure 15. Thoracic segments of *Holmia inusitata* and *H. mobergi*. (A) Anterior segment (PMO 234.283) with small spine midway on axial ring. Note thorn-like constriction at the base of the pleural spine. Flagstadelva. (B) Close-up of A, arrow points to angular projection. (C) Midway to posteriorly placed segment (PMO 234.284), Flagstadelva. (D) Third segment on large part of an articulated thorax figured in I. Lauselva. (E) Posteriorly placed segment (PMO 234.285) with prominent axial spine and deep articulating furrow. Flagstadelva. (F) Pleural field of posteriorly placed thoracic segment of *H. mobergi* (LO 4461T. Original of Bergström, 1973, fig. 6B). Scania, Sweden. (G, H) Dorsal and lateral view of posteriorly placed segment (PMO 234.298) with large axial spine and reticulated test preserved. Lauselva. (I) Paratype specimen (PMO 113.234). Lateral view of eleven anteriormost segments. Note highly vaulted axial rings and macrospine on 9th ring. Collected by S. Skjeseth in the early 1950s, Lauselva. (original of Ahlberg & Bergström, 1986, fig. 3B and refigured by Ebbestad et al. 2003, plate 2, fig. 10, prior to preparation). (J) Seven articulated segments (PMO 234.297) showing articulating sockets and processes on right side. Lauselva. All Flagstadelva specimens collected at the 12.5 m level. All Lauselva specimens collected between the 1.5 and 2 m levels. Scale bars on A, C, I & J = 5 mm, B, D–H = 1 mm.

inclined and narrow pleural fields. No border or spines are seen. One prominent axial ring with a distinct ring furrow is seen anterior to the terminal axial piece, and runs into a pair of faintly indicated pleural ridges (Fig.

16A). The median posterior margin of the terminal axial piece has a small indentation. Pygidia are hitherto only known from three species of *Holmia*, all being micropygous. The pygidia of *H. inusitata* and *H. kjerulfi*

Figure 16. (A & D) Dorsal and lateral view of partially preserved pygidium of *Holmia inusitata* (PMO 234.287), arrow points to faintly raised pleural ridge (pr). Flagstadelva, 12.5 m level. (B & E) Dorsal and lateral view of pygidium and the posteriormost thoracic segment of *Holmia inusitata* (PMO 234.290). Note indentation on the posterior margin of the terminal axial piece. Same as Fig. 13C. Lauselva, 1.5–2.0 m level. (C) Dorsal view of partially preserved pygidium of *Holmia lapponica* (SGU Type 5225), erratic from Kyrkberget, Lake Storuman, Sweden. (Original of Ahlberg et al., 1986, fig. 5). (F) Pygidium of small *Holmia kjerulfi* (PMO 22970). Note indentation on posterior margin of terminal axial piece. Silicon cast of counterpart of specimen previously figured by Kiær (1917, pl. 8:1). Upper part of Tømten Member (*Holmia* Shale), Tømten Farm, Mjøsa area, Norway. All scale bars = 1 mm.

(Fig. 16F) are very similar, the single pygidium known from *H. lapponica* (Fig. 16C) is poorly preserved but seems to be less vaulted and more effaced with no traces of pleural furrows or ridges.

Ontogeny in *Holmia*

Despite the rather high number of described and figured Baltoscandian olenellid taxa, different ontogenetic moulting stages of protaspids and meraspids specimens are rare. Kiær's (1917) description and figures of a series of stages of *Holmia kjerulfi* from the Tømten Member, Ringstranda Formation in the Mjøsa area and surroundings, together with vast material of holaspids, makes this species the best known olenellid taxon in Baltoscandia. Moczyłowska et al. (2001) figured two small, partially preserved cranidia of *Holmia* sp. from the Grammajukku Formation in the Lake Storuman area, Sweden. Høyberget et al. (2015) figured a nearly complete specimen with fourteen thoracic segments and three cephalae of different meraspid stages of *Holmia* cf. *lapponica* from the Evjevika Member, Ringstranda Formation in the Mjøsa area. The figured specimens of these three *Holmia* species display morphological differences in late meraspids of comparable size. A protaspis stage is hitherto only known from a single specimen of *H. kjerulfi*, which is thoroughly treated by Kiær (1917) and Størmer (1942).

Meraspid moulting stages of *Holmia inusitata* are presented herein for the first time, collected from the Flagstadelva river section at the 12.5 m level. The present material consists of six, partial, meraspid cranidia with glabellar lengths from 2.1 mm to 6.4 mm and more than twenty partial holaspid cranidia with glabellar lengths ranging from 8.0 mm to 31.9 mm. Although there are no specimens preserved with a complete number of thoracic segments, specimens with a cephalic length of 8 mm or longer have developed mature characters and proportions (Fig. 9D, Table 1). Kiær (1917, p. 68) noted that specimens of *H. kjerulfi* showed mature characters when the cephalic length reached 10 mm. During ontogeny, the relative length of the frontal lobe increases relative to the entire length of the glabella (see discussion of measurements).

The smallest specimen, 2.1 mm in glabellar length (Fig. 17A), has a parallel-sided and narrow (tr.) glabella, distinct transglabellar S3 and occipital furrows. All glabellar furrows are straight and transversally directed, and S1 and S2 are very short. Although not well-preserved, the frontal lobe seems to be short and poorly developed. The base of a small spine or node is medially placed on the occipital lobe and a distinct intergenal ridge is preserved on the left side. The ocular lobes are long, slender and curved, with the posterior ends opposite the anterior part of LO. The interocular area is comparatively wide and the combined width (tr.) of the ocular lobe and the interocular area is as wide as glabellar lobe L2.

Figure 17. (A–E) *Meraspis* stages of *Holmia inusitata*. (A) Smallest collected cephalon (PMO 234.265), 2.1 mm in glabellar length. Arrow points to coarse intergenal ridge. Note transglabellar S3. (B) Small cephalon (PMO 234.266), 3.3 mm in glabellar length showing development of genal spines, occipital spine, intergenal ridge and prominent border. (C) Partial cephalon with well-preserved palpebral lobe (PMO 234.267). (D) Well-preserved cephalon (PMO 234.268/1), dorsal view. Arrow points to anterior metaparian suture. (E) Partial cephalon (PMO 234.269) with distinctly transglabellar S3, posterior border and inner genal angle preserved. All specimens collected at Flagstadelva, at the 12.5 m level. (F) *Holmia* cf. *lapponica*, retrodeformed cephalon (PMO 227.630) of meraspis stage, with strain ellipse. Ellipsostrenua linnarssoni Zone, Evjevika Member, Skyberg. Mjøsa area (original of Høyberget et al., 2015, fig. 6O). (G) *Holmia* sp., cephalon (PMU 24235) of meraspis stage. Schmidtellus mickwitzii Zone, Grammajukku Formation near Storuman, northern Sweden (original of Moczydlowska et al., 2001, fig. 7a), prior to preparation. All scale bars = 1 mm.

A cephalon of *H. kjerulfi* of comparable size, figured by Kiær (1917, pl. 8, fig. 2), shows all glabellar furrows to be transglabellar and the combined width of the ocular lobe and the interocular area is narrower than glabellar lobe L2, and comparatively narrower than seen in *H. inusitata*.

In a complete but flattened cephalon, 3.3 mm in glabellar length (Fig. 17B), the frontal lobe has grown proportionally larger than in the smallest specimen, but is

separated from the border furrow by a short preglabellar field. The intergenal ridge is less pronounced compared to the smaller stage, and reaches the posterior margin in line (exsag.) with the inner part of the posterior end of the ocular lobe. The glabella is parallel-sided and narrow and the posterior end of the ocular lobes is adjacent to the anterior part of LO. The width (tr.) of L2 exceeds the combined width of the interocular area and the ocular lobe at this stage. A concave cephalic border, uniform in

width, is well-developed with a distinct border furrow. The genal spine is approximately half as long as the cephalon. The posterior border is straight between the glabella and the intergenal node, while the distal portion forms an anteriorly directed arch. Cranidia of *H. kjerulfi* (Kiær, 1917, pl. 6, fig. 3) and *H. cf. lapponica* (Høyberget et al., 2015, fig. 6N, O (the latter refigured in Fig. 17F herein)) of broadly similar size, also show an arcuate lateral posterior border. The ocular lobes in these two species are shorter and the cephalic border is less distinct, compared with *H. inusitata* (see Fig. 17F).

The next stage represented in the *H. inusitata* material has a glabellar length of 4.5 mm (Fig. 17D), which can best be compared with a slightly larger cephalon of *H. cf. lapponica* (Høyberget et al., 2015, fig. 6P). The glabella in *H. inusitata* is parallel-sided and narrow and the frontal lobe is short. The base of a distinct spine is medially placed on LO. Metaparian sutures are developed at this stage, which may be interpreted as being important in the species' functional morphology. This is seen as a faint ridge running from the anterior end of the compound eye in a laterally backward direction, crossing the extraocular area (Fig. 17D).

A poorly preserved posterior border in Fig. 17E seems to be weakly arcuate at this size.

H. cf. lapponica has developed a swollen frontal lobe at this size and the posterior border is different from *H. inusitata* by having a zigzagged marginal line. The cephalic border is less pronounced and the border furrow is shallow compared with *H. inusitata*. The smallest specimen of *H. sp.* (Moczydłowska et al., 2001, fig. 7a) has a glabellar length around 5 mm. Preparation of this specimen (PMU 24235) revealed a nearly complete cephalon (Fig. 17G herein). The frontal lobe is slightly expanded and nearly reaches the anterior margin. The frontal lobe and L3 are somewhat wider than the posterior portion of the glabella and the interocular area is narrow compared to the slightly smaller specimen of *H. inusitata*. The ocular lobes are not as curved as seen in other *Holmia* species. Another dissimilarity to *H. inusitata* is the more posteriorly placed occipital spine. The long ocular lobes, extending backwards to a transverse line opposite the midst of the occipital lobe, is also seen in *H. inusitata* at this size (Fig. 17D). An almost complete specimen of *H. cf. lapponica* (Høyberget et al., 2015, fig. 6M) of approximately the same ontogenetic stage has fourteen thoracic segments, which shows that this is a late meraspid stage.

A cephalon with well-preserved right side and glabellar length of 6.4 mm (Fig. 18A–E) probably corresponds to Kiær's 'late neanic stage' (1917, pp. 66–88), representing

Figure 18. *Holmia inusitata*. (A–E) Late meraspid or early holaspid stage. Different views of well-preserved right side of cephalon (PMO 234.270/1), 6.4 mm in glabellar length. Note genal caeca and anterior metaparian suture. Flagstadelva, 12.5 m level. All scale bars = 5 mm.

Figure 19. *Holmia inusitata*. (A) Laterally deformed cephalon (PMO 234.272/1) with genal caeca and anterior metaparian suture. See Fig. 9D for retrodeformed image of this specimen. (B) Detail of fragmentary cephalon (PMO 234.278) with reticulate pattern preserved on palpebral lobe. (C & D) Laterally deformed cephalon, retrodeformed with strained ellipse in D, (PMO 234.273/1) showing long and straight genal spine. (E) Sagittally deformed cephalon (PMO 234.272/2). Note the glabellar furrows that appear transglabellar. All specimens collected at Flagstadelva, at the 12.5 m level. Scale bars on A, C–E = 5 mm, B = 1 mm.

a very late meraspid or an early holaspid stage. At this size, *H. inusitata* has developed several mature characters like the proportionally wider glabella and a longer and weakly expanded frontal lobe almost abutting the anterior border. The L3 has changed into an undulating shape and is slightly widened compared to L1 and L2. The S3 furrow is distinctly undulating and the S1 and S2 show a posterior adaxial direction. The base of the occipital spine is coarse. Further, the cephalic border has developed an uneven width and the combined width of the ocular lobe and the interocular area is markedly narrower than L2. The extraocular cheek is equipped with distinct caeca, best developed close to the border furrow. A larger specimen of *H. sp.* (Moczyłowska et al., 2001, fig. 7c) is quite similar to *H. inusitata* at this or a close stage in having the proportionally wider glabella with an undulating S3, a larger frontal lobe and straight posterior cephalic border. The Swedish specimen differs from *H. inusitata* by the narrower extraocular area. The weaker cephalic border and the flattened cephalic border in *H. sp.* may be due to different degrees of lithological preservation.

In an early holaspid specimen, with a glabellar length of 8.0 mm (Figs. 9D & 19A), the cephalon has developed mature characters. This is seen in the proportionally wide glabella with a rounded and large frontal lobe possessing a parafrontal band, and the glabellar furrows are curved and long and the cephalic border is narrower medially than postero-laterally. This specimen shows genal caeca close to the border furrow.

The largest specimen collected from Flagstadelva (Fig. 10A, C) has a glabellar length of 31.9 mm, indicating a

total width of some ~64 mm of the cephalon. Skjeseth's original specimen (Fig. 9A) has a glabellar length of 26.2 mm and a restored total cephalic width of ~53 mm. The largest specimen collected from the autochthonous strata at the Lauselva locality (the holotype) has a glabellar length of 30.5 mm and a restored cephalic width of around 60 mm. The very large, partially preserved single cephalon of *H. grandis* Kiær, 1917, from the Tømten Member, Mjøsa area, has a restored cephalic width of 80 mm. Among the very rich material of *H. kjerulfi* from the same area, all housed at the Natural History Museum, Oslo, the largest cephalon shows a maximum width of 54 mm.

Conclusions

The previously assumed stratigraphic level of the single specimen of *Holmia cf. mobergi* low in the Flagstadelva section in the Mjøsa area, Norway, is here considered erroneous. Additional material of the taxon figured in this work originates from a much higher stratigraphic horizon, namely the lower part of the Tømten Member, Ringstranda Formation. This is within the *Heliosphaeridium dissimulare*–*Skiagia ciliosa* acritarch Zone, according to Vidal & Nystuen (1990). Comparison of the new material from Flagstadelva and that of new topotype material of *Holmia inusitata* from the Lauselva section in the Mjøsa area demonstrates that *Holmia cf. mobergi* is conspecific with *Holmia inusitata*. The species is recorded from autochthonous and parautochthonous lower Cambrian strata in the Mjøsa area that are very

sparsely fossiliferous with no other trilobite taxa known. It is therefore argued that the *Holmia inusitata* Zone should be maintained as a local biozone in the Mjøsa area, predating the *Holmia kjerulfi* Zone which everywhere in Baltoscandia shows a much higher diversity.

Re-evaluation of other fossil occurrences in the Flagstadelva section also suggests that reports of both the enigmatic fossil *Mobergella* and the rich trace-fossil assemblage are erroneous. The implications are that the Redalen Member of the Caledonian Lower Allochthon in the Mjøsa area, containing abundant trace fossils, and the Bråstad Sandstone (here informally termed the Bråstadelta member) at the Bråstadelta locality in the Mjøsa area, containing mobergellans, belong to the older *Schmidtellus mickwitzi* Zone. Re-interpretation of the traditional lower and middle Cambrian boundary in the Flagstadelva section further suggests that the parautochthonous strata, postdating the Hawke Bay regression event, were developed during the mid-Cambrian *Ptychagnostus atavus* Zone and not during *Acadoparadoxides oelandicus* time or at the age of the *Ptychagnostus gibbus* Zone, as previously stated.

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