

Review Article

The key Cambrian succession at Andrarum, southern Sweden – Alum Shales, trilobites and insights from Euan Clarkson's investigations

Per AHLBERG^{1*}  and David Alexander Taylor HARPER^{1,2} 

¹ Department of Geology, Lund University, Lund, Sweden

² Department of Earth Sciences, Durham University, Durham, UK

*Corresponding author. Email: per.ahlberg@geol.lu.se

ABSTRACT: The organic-rich shales and mudstones composing the Miaolingian ('middle' Cambrian) through Tremadocian (Lower Ordovician) Alum Shale Formation have been extensively mined for production of alum at Andrarum in southeastern Scania (Skåne), southern Sweden. Here, the formation was exploited between 1637 and 1912, and a brief account is given of the history of the exploitation. The alum industry had its heyday in the mid-1700s when it was owned by Christina Piper (1673–1752). During this time some 900 people lived within the working area, and it had its own craftsmen, school, hospital and courthouse with a jail annex. The undeformed and virtually continuous succession at Andrarum is generally richly fossiliferous and, albeit largely covered by scree and vegetation, best exposed in the old quarries. The fossil faunas are dominated by trilobites and agnostoids, which form the basis for a detailed biostratigraphical framework. The history of geological and palaeontological research at Andrarum, since the pioneering works in the mid- to late 1800s, is reviewed. The sequence of strata was first elucidated by Alfred Gabriel Nathorst in 1869. Since then, the succession and its fossil content have been studied by a considerable number of influential researchers, such as Gustaf Linnarsson (1841–1881), Sven Axel Tullberg (1852–1886) and Anton H. Westergård (1880–1968). In the decades around the turn of the 21st century, Euan Clarkson initiated a number of projects focusing on the ontogeny, evolution and functional morphology of olenid trilobites from the Furongian at Andrarum, along with two important studies dealing with faunal dynamics and biotic turnovers. His research resulted in a series of pivotal papers on the geology and palaeontology of the Alum Shales.

KEYWORDS: agnostoids, black shales, evolution, faunal dynamics, Furongian, Miaolingian, olenid trilobites, ontogeny

The succession at Andrarum, southern Sweden is of critical importance for elucidating Cambrian geology and palaeontology. Euan N. K. Clarkson (1937–2024), an outstanding geologist and palaeontologist, perhaps best known for his seminal research on trilobites and his benchmark text-book on invertebrate palaeontology and evolution, engaged in studies of this key locality over many years. Already in the early 1970s, Euan became interested in olenid trilobites from the Cambrian Alum Shales of Scandinavia, and in 1973 he published on the morphology and evolution of the eyes of these trilobites (Clarkson 1973). Following a three-month sabbatical at Lund University in 1993, Euan's interest and research on the ontogeny, evolution, functional morphology and life habits of the olenids developed rapidly. He became a frequent guest at the Department of Geology in Lund, pursuing extensive field work and studying the ontogenetic stages and evolution of various olenid species in the Furongian ('upper' Cambrian). This research was largely carried out in collaboration with Per Ahlberg, Kristina Månsson, Cecilia M. Taylor and the late John 'Jompa' Ahlgren (1934–2025). One of the key sites for his research was the old quarries at Andrarum in eastern Scania

(Skåne), southernmost Sweden (Fig. 1); this research generated a series of seminal papers on the Alum Shales together with its olenid trilobites. The present paper describes the Alum Shales and the old alum shale workings at the classical locality of Andrarum, highlighting Euan Clarkson's contributions to the study of olenid trilobites and faunal dynamics in the Furongian.

1. The Scandinavian Alum Shales

The upper Miaolingian ('middle' Cambrian) through lower Tremadocian (Lower Ordovician) Alum Shale Formation of Scandinavia consists predominantly of dark grey to black, siliciclastic mudstones and shales with generally subordinate limestone beds and concretionary lenses, referred to as *orsten* or stinkstone (for general reviews, see Martinsson 1974; Bergström & Gee 1985; Andersson *et al.* 1985; Maas *et al.* 2006; Eriksson & Waloszek 2016). It was deposited in an extensive, sediment-starved and poorly-oxygenated epicontinental sea that covered most of Scandinavia and surrounding areas (e.g., Thickpenny 1984, 1987; Clarkson & Taylor 1995a; Egenhoff *et al.* 2015; Nielsen & Schovsbo 2015; Schovsbo *et al.* 2018). It is therefore



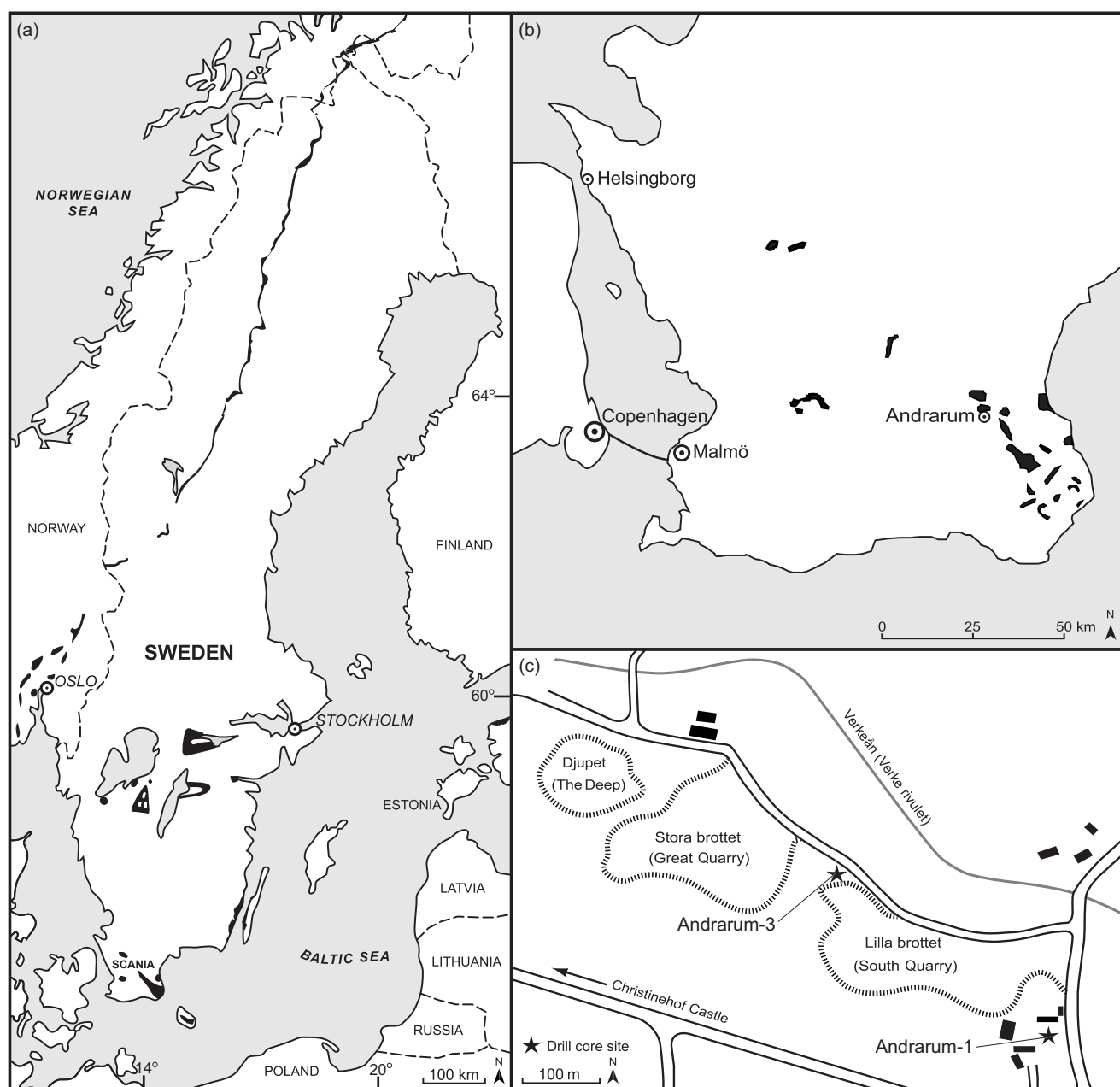


Figure 1 Location of Andrarum and distribution of the Alum Shales, modified from Ahlberg *et al.* (2009, fig. 1): (a) map showing the distribution of Cambrian deposits in Scandinavia; (b) outcrop areas of the Alum Shale Formation (in black) in the province of Scania (Skåne), Sweden, and the location of Andrarum; (c) the old quarries at Andrarum and the location of the drill site for the Andrarum-1 and Andrarum-3 boreholes. The Andrarum-2 borehole is outside the map area, ca. 500 m SE of Christinehof Castle.

rich in organic matter (up to 25 wt. % total organic carbon, TOC) and also enriched in trace elements, such as uranium (U), vanadium (V) and molybdenum (Mo) (Buchardt *et al.* 1997; Schovsbo 2001, 2002).

Anoxic and perhaps even euxinic bottom-water conditions prevailed during much of its deposition, but these were interrupted by brief oxygenation events of 600–3000 years duration (Dahl *et al.* 2019). As evidenced by the TOC and the occurrence of redox sensitive trace elements, such as U and Mo, oxygen depletion reached its highest levels during the Furongian Epoch (e.g., Andersson *et al.* 1985; Bian *et al.* 2021). The globally significant Steptoean Positive Carbon Isotope Excursion (SPICE) has been recognized in the lower–middle Paibian Stage of the Alum Shale Formation (Ahlberg *et al.* 2019, 2009; Hammer & Svensen 2017; Zhao *et al.* 2022). This positive $\delta^{13}\text{C}_{\text{org}}$ shift of up to $\sim 3.0\text{‰}$ in shale sequences in Baltica is coincident with a global anoxic episode associated

with enhanced burial of organic carbon and pyrite (Saltzman *et al.* 2000; Gill *et al.* 2011; LeRoy & Gill 2019; see Pulsipher *et al.* 2021 for a general review). Based on the presence of bioturbation in shales throughout the SPICE interval at Andrarum, Egenhoff *et al.* (2015), however, argued for intermittently dysoxic conditions during deposition through the SPICE event.

The thickest and stratigraphically most complete successions of the Alum Shale Formation are in Scania and in the Oslo Region of Norway (Buchardt *et al.* 1997, fig. 2; Schultz *et al.* 2015). In these areas the alum shales were largely deposited in outer-shelf settings, and are up to approximately 100 m thick. In other parts of southern Scandinavia, the Alum Shale Formation is considerably thinner and several stratigraphical gaps of various magnitudes occur within the succession (Martinsson 1974; Schovsbo *et al.* 2018; Nielsen *et al.* 2020).

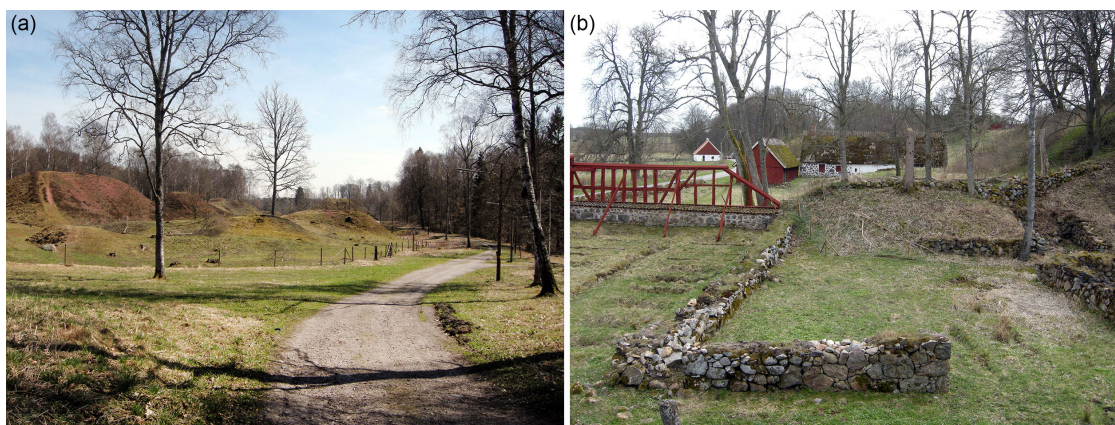


Figure 2 Views of the abandoned alum industry at Andrarum: (a) heaps with burnt Alum Shale at Andrarum; (b) the ruined boiler house (*pannhuset*) at the southeastern end of the South Quarry in Andrarum where the leachate was boiled and then left to cool until alum crystals precipitated. Both photos by Per Ahlberg 2010.

In Sweden, exploitation of the Alum Shale has periodically occurred since the 1600s. The rock has been utilized in calcination, for alum production, for oil extraction, as a raw material in the production of lightweight concrete (aerated concrete or “blue concrete”), and most recently (1965–1969) for uranium extraction (for brief reviews, see Andersson *et al.* 1985; Ladenberger *et al.* 2024). The production of lightweight concrete ceased in 1975 when the construction industry had become sufficiently aware of the risks associated with radiation, but houses built of blue concrete were still appearing until 1980.

2. The alum industry of Andrarum

Along the Verkeån rivulet, about 10 km from the east coast of Scania and 800–900 m east of Christinehof Castle, lie the remains of the old alum works at Andrarum (Figs 1, 2), which in the 18th century were the leading alum producers in the Nordic region and the largest industrial site in Scania. Here, an archive from a long-gone era is preserved—breaking the black shales apart is like flipping through a diary nearly 500 million years old. The old alum works are protected, not only because they are located within the Verkeån Nature Reserve, the largest nature reserve in Scania, but also because they constitute a historical monument—here, cultural history and natural science are combined in spectacular fashion.

Large brick-red waste heaps with crushed and burnt shale (Swedish *rödifyr*; Fig. 2a), a grand, whitewashed warehouse building from the 1740s and a few picturesque, often thatched half-timbered houses are today the only tangible evidence that a significant chemical-technical industrial operation once dominated the region. The foundation of the operation was the black shale, which was mined from the mid-17th century until the early 20th century. The shale is called alum shale because it was quarried for the extraction of alum (potassium aluminium sulphate), a salt that was used as a mordant in dyeing yarn, for tanning leather, production of paper and varnishes, and to fire-proof paper and cloth. In medicine, alum acted as a styptic (to staunch bleeding) and disinfecting agent. It has also been widely used for preserving and bleaching flour.

2.1. Alum and alum production

Alum was known already in ancient times (Stoltz 1932; Levey 1958); the Romans referred to this salt as *alumen*. It was initially extracted mainly from the mineral alunite, which is common in some volcanic regions and was roasted in furnaces, resulting in alum that could be leached from the burnt mass with water (Andersson 1974). The leachate produced alum crystals after

boiling. Eventually, it was discovered that alum could also be extracted by heating black shales that were crushed and then leached (Stoltz 1932; Millard 1999).

The alum shale of Scandinavia was mined in opencast mines and then burned for as long as organic material remained in the shale (up to three months). High temperatures ($\sim 700^{\circ}\text{C}$) resulted in oxidation of the pyrite and the formation of sulphuric acid and iron oxide. During this process, the acid reacted with the silicate minerals and alum salt was formed (e.g., Falk *et al.* 2006). The burnt shale was then leached with water, and after boiling the leachate was left to cool until alum crystals were precipitated. At the Andrarum works, barrels of alum were then transported by horse and cart to the ports in Åhus and Kivik at the east coast and for a period, also to a private port at the mouth of the Verkeån rivulet (Stoltz 1932). When the operations at the works were at their most intense, the yellowish-white, sulphur-smelling smoke hung heavily over large parts of the area (Andersson 1974).

2.2. History of exploitation

The alum industry at Andrarum was founded by a Danish nobleman, Jochum Beck (1604–1682), who understood that the production of alum from alum shale could yield greater returns than using the shale for lime burning (Stoltz 1932; Carlsson 1996). In 1637, he received the Danish King Christian IV’s charter to establish the alum works at Andrarum. However, the production of alum was delayed for a couple of years after diligent experimentation of the processes, but by the early 1640s, the operation had started (Stoltz 1932). Jochum Beck, however, encountered significant technical problems, and the industry suffered during the Danish-Swedish War of 1643–1645.

The alum industry was rebuilt after the war, and production of alum could once again commence, and production was gradually stabilized. However, Beck had large debts and was in the hands of several creditors. After much struggle, this once wealthy man (“Rich Beck”) died disappointed and impoverished in 1682. Despite the complicated ownership relations of the operation with several co-owners, both during and after Beck’s lifetime, alum production steadily increased during the final decades of the 17th century (Stoltz 1932).

The alum industry had its heyday during the 18th century when it was owned by Christina Piper (née Törne; 1673–1752; Fig. 3). This successful entrepreneur and business-minded woman was married to Count Carl Piper, one of the most favoured advisors of the Swedish monarch Charles XII, and brought a very substantial fortune as her dowry (Norrhem



Figure 3 Portrait of Christina Piper in 1715. Photo Jens Mohr, The Royal Armoury (*Livrustkammaren*) and National Historical Museums, Sweden.

2010). In 1710, she began purchasing shares in the Andrarum alum works, and by 1725, she was the sole owner of the works. Under her leadership, there was a community of around 900 people, a school, a hospital, a retirement home, a prison, and its own mint—the coins/currency were only valid within the works (Andersson 1974; Carlsson 1996). Andrarum gradually developed into a self-sufficient state within the state, with its own craftsmen and its own laws. However, during the 19th century, the shortage of forests and firewood became increasingly evident, and by the end of the century, competition from industrially produced alum became increasingly cut-throat, while other chemical products gradually began to replace alum (Andersson 1974). The operations therefore decreased, and the production of alum completely ceased in 1912. However, as late as the 1930s, red paint, a by-product of alum production, was still being produced. Another important by-product was iron vitriol (iron sulphate). More importantly, however, the industry exposed a unique Cambrian succession.

3. Early explorations of the Alum Shale at Andrarum

The Forsemölla-Andrarum district is a classical area for Cambrian rocks in Baltoscandia. Material representing the species *Olenus truncatus* was described and illustrated already by Bromell (1729). Two decades later, Andrarum was visited by Carl von Linné in 1749, and both the operation in the alum works and the shale were briefly described in his “Skånska resa” (Journey through Skåne) from 1751. However, it was not until the second half of the 19th century that a relatively good understanding of the stratigraphy and the fossil content began to emerge, primarily through the pioneering works of Alfred Gabriel Nathorst (1850–1921; Fig. 4a), Gustaf Linnarsson (1841–1881), and Sven Axel Tullberg (1852–1886; Fig. 4b).

Already when a student at Lund University, Nathorst was inspired by Nils Peter Angelin (“Sten-Petter”; 1805–1876; Tersmeden 2018) to study the Cambrian deposits in Skåne. They travelled together through the province in the summer of 1868, during which Nathorst had the opportunity to examine the stratigraphy at Andrarum for an extended period. The year after, he published his first scientific paper in which he subdivided the succession into different biozones and established the relative age relationships of the strata (Nathorst 1869). Eight years later (1877), he provided a more detailed description of the stratigraphy, following a trip to Andrarum in the summer of 1876 in the company of the Norwegian geologist Waldemar Christofer Brøgger (1851–1940). Nathorst later became a prominent and internationally recognized geologist, palaeobotanist, and polar researcher, serving as a professor at the Swedish Museum of Natural History in Stockholm.

Nathorst’s fundamental works were in the 1870s and 1880s followed by more detailed studies by Linnarsson (1875, 1880, 1883) and Tullberg (1880). Gustaf Linnarsson was an eminent palaeontologist at the Geological Survey of Sweden and one of the most original and successful geologists of the 19th century (Lapworth 1882). He authored a large number of publications on the Cambrian–Silurian succession of Sweden, but unfortunately his life was cut short at the age of 39 years by pulmonary tuberculosis. The Lund geologist, palaeontologist, and botanist Sven Axel Tullberg has been described as a highly gifted and passionate scholar, and was obsessively interested in women (Hadding 1942; Henriksson 1994). Despite passing away at a young age and being affected by a serious illness towards the end of his life, he published several influential papers. In his classic graduate thesis (Tullberg 1880) on Cambrian agnostoids from Andrarum, he described some ten new species and provided a detailed account of the succession. The thesis included a map of the quarries and the location of important sections. This map has been reproduced in, or served as a basis for, many later works on the Alum Shales at Andrarum, for example in Westergård’s (1922) comprehensive and classical monograph on the upper Cambrian of Sweden.

4. Succession and fossil content

4.1. Succession and quarries

Although largely covered by scree and vegetation, the undeformed and continuous Miaolingian through Furongian succession is still partially exposed in the old quarries at Andrarum. Sections and localities were described in detail by Tullberg (1880), Moberg (1910) and Westergård (1922). The succession predominantly consists of alum shales interbedded with subordinate concretionary limestone lenses and a couple of prominent limestone beds (Fig. 5), including the Wuliuan Forsemölla and Exsulans Limestone beds, the upper Drumian and/or the lower Guzhangian Hyolithes Limestone Bed, the Guzhangian Andrarum Limestone Bed, and thin equivalents to the upper Guzhangian–lower Paibian Kakeled Limestone Bed. The three main alum shale quarries are: (1) The Deep, in Swedish *Djupet*, (2) the Great Quarry, and (3) the South or Small Quarry, in Swedish *Södra* or *Lilla brottet* (Fig. 1c). These lie in a north-west to south-east sequence parallel to the Verkeån rivulet, and because the strata dip gently towards the south-east, virtually the entire Miaolingian through Furongian succession is present within the quarries (cf. Moberg 1910). Large parts of the quarries are, however, now filled with water and most of the succession is covered by scree and soil, or is overgrown, especially in The Deep and in the South Quarry near the ruined boiler house (*Pannhuset*; Figs 1, 2b).

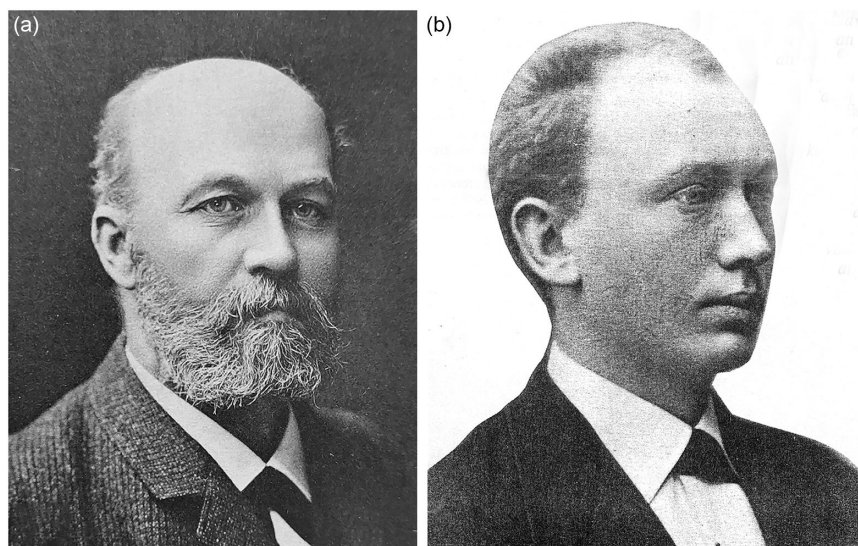


Figure 4 Early explorers of the Alum Shale at Andrarum: (a) already as a student at Lund University and only 19 years old, Alfred G. Nathorst described the Cambrian succession at Andrarum. Photo A. Dahllöf 1903; (b) Sven Axel Tullberg first studied botany but later specialised in geology and palaeontology. One of his first works in the latter field was on agnostoids from the Cambrian succession at Andrarum. From *Svenskt Porträttgalleri*.

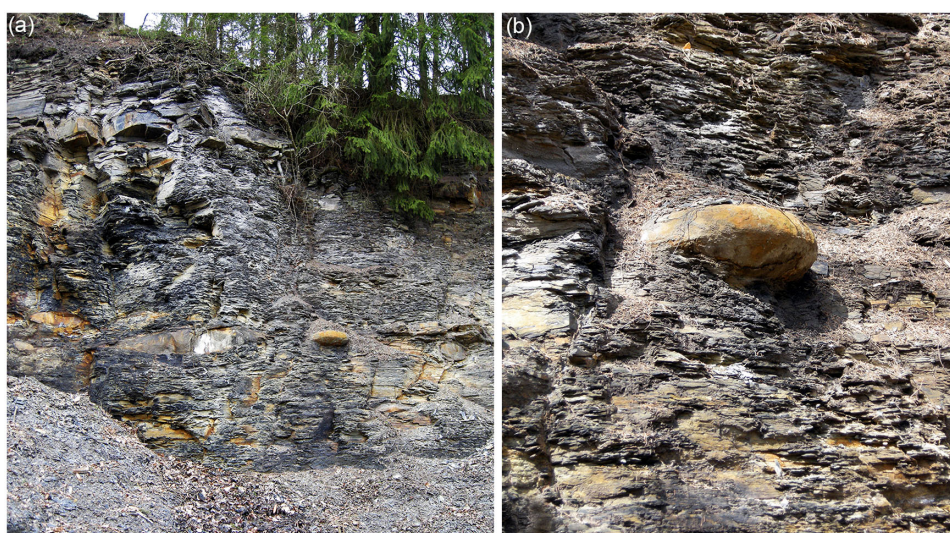


Figure 5 (a) Overview of a section through the uppermost Miaolingian–lower Furongian Alum Shales in the northern part of the Great Quarry at Andrarum. Photo Per Ahlberg 2012; (b) limestone concretion (stinkstone) embedded in alum shale in the northern part of the Great Quarry at Andrarum. The lens is ca 0.7 m in diameter. Photo Per Ahlberg 2010.

Two core drillings (Andrarum-1 and Andrarum-2) carried out in 1941–42 have shown that the Alum Shale Formation in the Forsemölla-Andrarum district has a thickness of at least 76 m (Westergård 1942, 1944). Within this succession, approximately 24–25 m belongs to the Miaolingian, 44 m to the Furongian, and more than 8 m to the Tremadocian portion of the Alum Shale Formation (‘Dictyonema shale’). Cambrian Series 2 and lower Miaolingian strata are exposed at Forsemölla, north of Andrarum (e.g., Bergström & Ahlberg 1981; Cederström *et al.* 2022). The exposed succession in the central quarry (the Great Quarry) spans the upper Guzhangian *Agnostus pisiformis* Zone through the Paibian *Olenus scanicus* Zone. Some of the higher zones in the Furongian were locally exposed in the South Quarry (Westergård 1922; Ahlberg *et al.* 2006).

The best exposures are in the north-central part of the Great Quarry (Fig. 5). In the northernmost end of the quarry, the shales yield abundant flattened olenid trilobites and agnostoids, as well as numerous three-dimensionally preserved specimens in the stinkstones. Here, the lower 7 m comprises the uppermost

zone in the Miaolingian, i.e. the *Agnostus pisiformis* Zone, and the upper 3 m represent the lower Furongian *Olenus gibbosus*–*O. dentatus* zones (Westergård 1922, fig. 4). In addition to *Olenus* species, the upper zones generally yield *Agnostus* (*Homagnostus*) *obesus* in abundance. In the global agnostoid zonation, the *Olenus* zones are equivalent to the *Glyptagnostus reticulatus* Zone (Ahlberg & Terfelt 2012; Nielsen *et al.* 2020).

4.2. Fossil content and faunal diversity

The Alum Shales at Andrarum are generally richly fossiliferous and, collectively, a large biota has been recorded. The fauna is dominated by trilobites and agnostoids, which form the basis for a detailed biostratigraphical framework that to a large extent has been applied also in Poland, England, Wales and eastern Canada. Trilobites and agnostoids are generally confined to the stinkstones; the intervening shales can be largely unfossiliferous. In parts of the succession, however, well-preserved though flattened trilobites and agnostoids are present in vast numbers in the shales. In addition to trilobites and

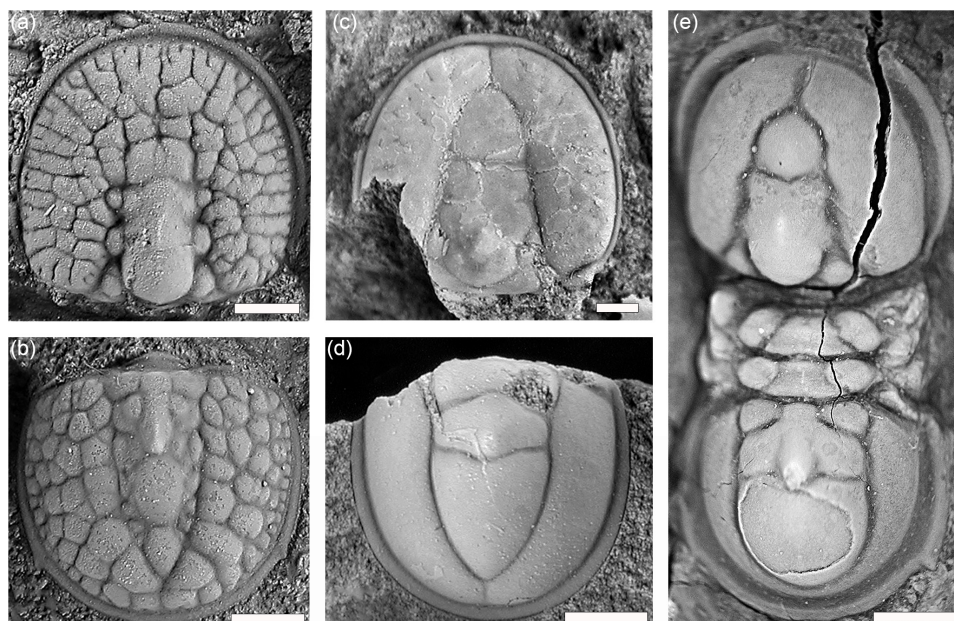


Figure 6 Agnostoids are important for global correlations and chronostratigraphical subdivision of Cambrian strata. All specimens except (e) are deposited in the type collections at the Department of Geology, Lund University (LO). (a) *Glyptagnostus reticulatus*, cephalon from Krokagården, Kinnekulle, south-central Sweden, original of Ahlberg & Ahlgren (1996, fig. 4I), LO 7333t; (b) *Glyptagnostus reticulatus*, pygidium from Krokagården, Kinnekulle, south-central Sweden, original of Ahlberg & Ahlgren (1996, fig. 4M), LO 7337t; (c) *Ptychagnostus atavus*, cephalon from a loose stinkstone at Forsemölla near Andrarum, original of Tullberg (1880, pl. 1, fig. 1a, c) and Westergård (1946, pl. 11, fig. 8), lectotype, LO 354T; (d) *Ptychagnostus atavus*, pygidium from a loose stinkstone at Forsemölla near Andrarum, original of Tullberg (1880, pl. 1, fig. 1b, d) and Westergård (1946, pl. 11, fig. 10), syntype, LO355T; (e) *Aagnostus (Homagnostus) obesus*, nearly complete specimen from the *Olenus wahlenbergi* Zone at Andrarum, original of Westergård (1922, pl. 1, fig. 4a, b) and Ahlberg & Ahlgren (1996, fig. 3G), Swedish Geological Survey (SGU) Type 122a. Scale bars represent 1.0 mm.

agnostoids, brachiopods, hyoliths, phosphatocopines and conodonts (including proto- and paraconodonts) may also be common in certain intervals, particularly in the stinkstones. Noteworthy among the brachiopods is a mass occurrence of the benthic orthide *Orusia lenticularis* in stinkstones of the Furongian *Parabolina spinulosa* Zone in the northwestern end of the South Quarry (Westergård 1922). Its opportunistic occurrence most likely represents intervals when the sea floor was more oxygenated than usual and firm enough to allow colonisation by sessile organisms.

Approximately 190 trilobite and agnostoid species are known from the Cambrian at Andrarum. Of these, at least 110 are from the Miaolingian succession and the remaining (~80 species) from the Furongian. Andrarum is also the type locality for numerous species. Amongst these, can be noted two agnostoids having a wide geographical and nearly global distribution: *Ptychagnostus atavus* (Tullberg, 1880) (Fig. 6c, d) and *Glyptagnostus reticulatus* (Angelin, 1851) (Fig. 6a, b), both of which have been used for defining Cambrian stages. Thus, the Global boundary Stratotype Section and Point GSSP for the base of the Drumian Stage, the middle stage of the Miaolingian Series, coincides with the First Appearance Datum (FAD) of *P. atavus*, and the base of the Paibian Stage, the basal stage of the Furongian Series, coincides with the FAD of *G. reticulatus* (Peng *et al.* 2004; Babcock *et al.* 2007). The highest faunal diversity (more than 30 species of trilobites and agnostoids) has been recorded in the Miaolingian Andrarum Limestone (Westergård 1946, 1953).

5. A renaissance in the 1990s and 2000s

In the decades around the turn of the 21st century, Euan Clarkson (Fig. 7) initiated a number of projects on the ontogeny, evolution, functional morphology and lifestyles of olenid trilobites from the Furongian at Andrarum and elsewhere in southern Sweden. These projects were largely conducted in collaboration with researchers from Lund

University, and the results of the investigations have been elegantly summarised in Clarkson (2011).

In addition to these projects, geochemical and sedimentological evidence along with biofacies analyses in the Furongian of Andrarum have been used in an attempt to build up a more coherent picture of the Alum Shale environment and its inhabitants (Eriksson & Terfelt 2007; Ahlberg *et al.* 2009; Gill *et al.* 2011; Egenhoff *et al.* 2015; Rooney *et al.* 2022). A drill core (Andrarum-3) was carried out in the north-western end of the South Quarry in late September–early October 2004, just northeast of locality 5 of Westergård (1922, fig. 3; Fig. 1c herein). It reached a depth of 31.30 m and penetrated the *Parabolina spinulosa* Zone (Jiangshanian Stage) down into the *Ptychagnostus atavus* Zone (Drumian Stage). A $\delta^{13}\text{C}_{\text{org}}$ curve from the core revealed the presence of the prominent and globally recognised Steptoean Positive Carbon Isotope Excursion (SPICE) in the Paibian Stage, beginning near the FAD of *Glyptagnostus reticulatus* and extending upwards into the lower *Olenus scanicus* Zone (Ahlberg *et al.* 2009).

The Furongian Alum Shale is dominated by polymerid trilobites of the Family Olenidae. They occur in immense numbers from the basal zone, i.e. the *Olenus gibbosus* Zone, and onwards to the top of the Cambrian. They are generally most common in the limestone concretions and beds, where they are usually found as disarticulated specimens. In some parts of the succession, however, notably in Scania, they are also present in the shales and here they are often found complete or near-intact. Usually only one species belonging to a single genus, and very rarely more than three genera, are present at each level (e.g., Clarkson & Taylor 1995b; Clarkson 2011). Since the species turnover rate was very high, a very precise biostratigraphy based on successive olenid species was established by Westergård (1922, 1947) and Henningsmoen (1957). Their zonations have subsequently been revised (Terfelt *et al.* 2008; Nielsen *et al.* 2014) and currently 23 biozones, allocated to six superzones and linked to four agnostoid zones, are recognised (Nielsen *et al.* 2020).



Figure 7 Euan Clarkson and Niklas Axheimer at the northwestern end of the South Quarry, Andrarum. Photo Fredrik Terfelt 2004.

5.1. Olenid ontogenies

Since olenids often are represented at all growth stages in the material from Andrarum, the ontogenies of successive species and genera can be described in detail, allowing assessment of the role of heterochrony in their evolution. Euan Clarkson realised the potential of the Alum Shales for such studies and published a series of papers on the ontogeny of the olenids between 1995 and 2016 (Clarkson & Taylor 1995a; Clarkson & Ahlberg 2002; Bird & Clarkson 2003; Clarkson *et al.* 1997, 2003, 2004; Månsson & Clarkson 2012, 2016). On the basis of excellently-preserved material in stinkstone slabs from Andrarum, the ontogeny of the following species was described in three separate papers: *Olenus wahlenbergi* Westergård, 1922 (Fig. 8), *Parabolina spinulosa* (Wahlenberg, 1818) and *Protopeltura aciculata* (Angelin, 1854).

All growth stages in *O. wahlenbergi*, from the anaprotaspis and onwards, were elucidated in a comprehensive paper by Clarkson & Taylor (1995a). In that paper, SEM photographs were used for reconstructions of all smaller stages and for describing cuticular structures, such as tubercles, granules, pits, cell polygons and anastomosing caeca. For the first time, Clarkson & Taylor (1995a) also described a structured median occipital organ in a Cambrian trilobite.

Because *Olenus* is one of the earliest olenid genera and *Parabolina* occurs next in the succession, Clarkson *et al.* (1997) undertook an equivalent study on the ontogeny of the latter genus. The ontogeny of the type species of the genus, *P. spinulosa*, was described, largely on the basis of old collections from the northwestern end of the South Quarry. Protaspides are rare, but the surface of one stinkstone slab is covered with

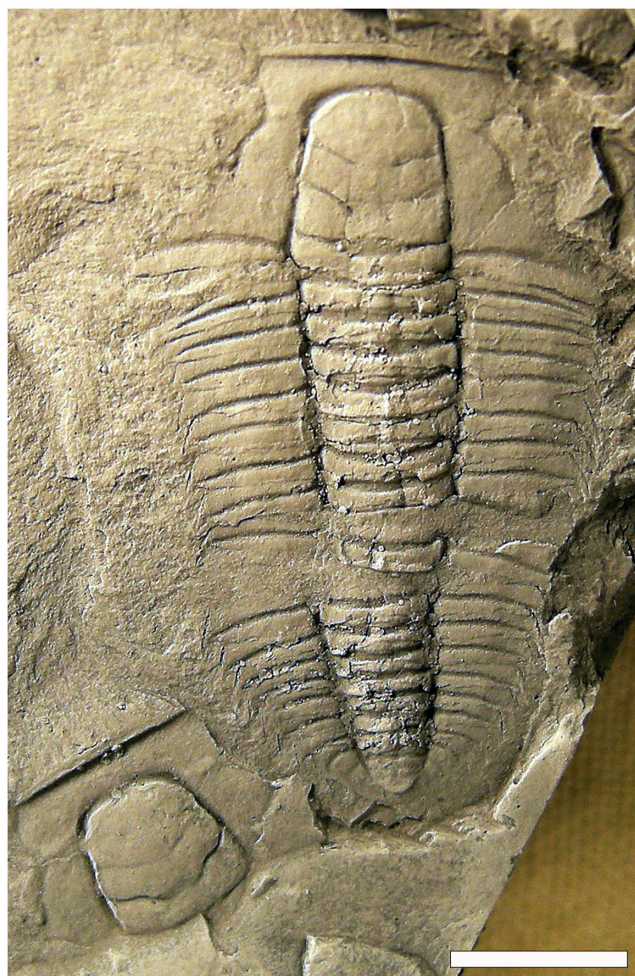


Figure 8 Nearly complete specimen of *Olenus cf. wahlenbergi* from the Great Quarry at Andrarum. Department of Geology, Lund University, No. LO 12537t. Photo Per Ahlberg 2011. Scale bar represents 10 mm.

immature specimens including complete specimens ranging from early meraspides to young holaspides. *Parabolina* is considered to have evolved from the earlier genus *Olenus* (Westergård 1922; Henningsmoen 1957) and, as described by Clarkson *et al.* (1997), their ontogenies are broadly similar. On the basis of comparative ontogeny, they also showed that many, though not all, features of *Parabolina* appear to be of pedomorphic origin and the evolution of the genus is best considered in terms of a mosaic pedomorphocline (Clarkson *et al.* 1997).

The ontogeny of *Protopeltura aciculata*, the earliest known pelturine olenid, was described in the third paper (Månsson & Clarkson 2012). A large proportion of the material was collected in 2008 by the authors at the northwestern end of the South Quarry. Månsson & Clarkson (2012) concluded that *P. aciculata* shows major intraspecific variations throughout development, especially regarding the pygidium where variation is much less constrained than in many other olenids. This high developmental plasticity may have been a survival strategy for a trilobite living in a stressed environment with low oxygen levels (Månsson & Clarkson 2012).

5.2. Microevolution and faunal dynamics

A critical review of microevolutionary transformations and the origin of marine invertebrate species was published by Clarkson (1988). In that paper he emphasised that the most reliable data are based on microstratigraphic sampling through unbroken sedimentary sequences and on a finely resolved biostratigraphy with precise stratigraphical control; a bed-by-bed field strategy

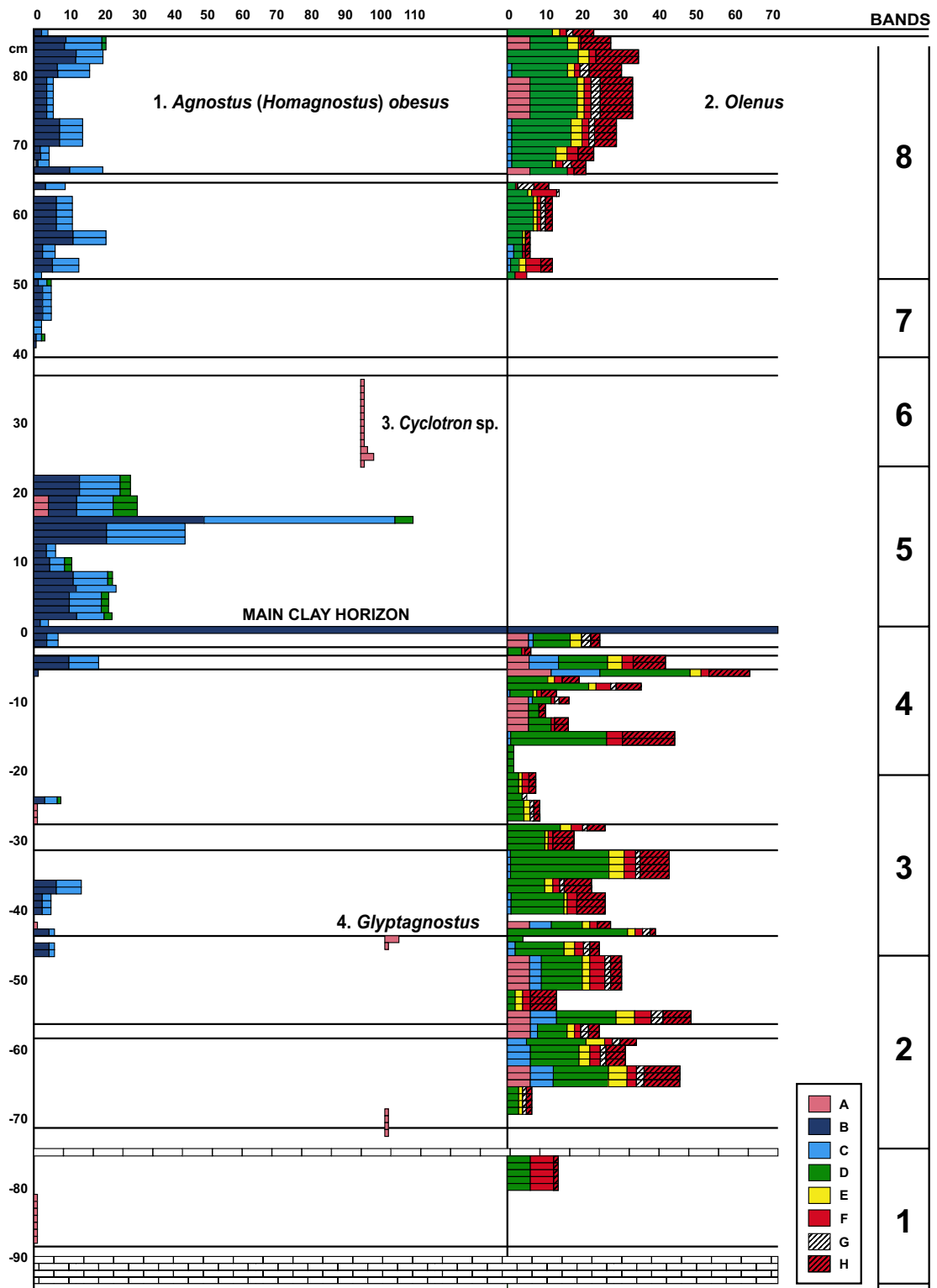


Figure 9 Log showing relative abundance of fossil genera at different levels in a 1.8-m-thick measured section near the north end of the Great Quarry at Andrarum. The lengths of the coloured horizontal scale bars indicate the abundance of individuals for each level, at 1-cm intervals where possible. For each surface trilobite exuvia, and rare complete specimens, were counted within a 5×5 cm quadrat. The counting units and the coloured key are as follows: For *Agnostus (Homagnostus) obesus*, A = complete individual (3 units), B = cephalon (1 unit), C = pygidium (1 unit), D = isolated thoracic tergite (1/2 unit). For *Olenus*, A = complete individual (6 units), C = intact thorax (1 unit), D = cranidium (1 unit), E = pygidium (1 unit), F = isolated thoracic tergite (1/15 unit), G = hypostome (1 unit), H = isolated librigena (1/2 unit). The vertical scale is in centimetres counted below and above the 1-cm-thick Main Clay Horizon. The horizontal scale represents numbers of specimens counted at each level. For fuller explanation, see Clarkson *et al.* (1998). Figure redrawn and slightly amended from Clarkson *et al.* (1998, fig. 2, in Faunal dynamics and microevolutionary investigations in the Upper Cambrian *Olenus* Zone at Andrarum, Skåne, Sweden. *GFF* 120, 257–267, copyright © 1998 Geologiska Föreningen, reprinted by permission of Informa UK Limited, trading Taylor & Francis Group, <https://www.tandfonline.com> on behalf of Geologiska Föreningen).

adopted by Charles Lapworth for his ground-breaking research on the graptolites of the Southern Uplands of Scotland (Lapworth 1879–1880). Since the Alum Shale Formation at Andrarum is generally richly fossiliferous, condensed and virtually complete, the succession is ideal for testing processes and patterns in microevolution. Kaufmann (1933) collected through a 2.5-m-thick section in the Great Quarry and recorded four successive lineages of *Olenus*, each of them showing a narrowing and lengthening of the pygidium. This has been regarded as a classic example of iterative evolution where similar trends arise in successive stocks from a more or less unchanging ancestral stock. However, Hoffmann & Reif (1994) have shown that the Kaufmann's data do not unequivocally support Kaufmann's interpretation of iterative evolution, largely because the number of specimens measured was too small, the species lack clear autapomorphic characters and their interrelationship and lateral distribution is unknown (see also Lauridsen & Nielsen 2005).

In 1993, Euan Clarkson and co-workers sampled and examined a 1.8-m-thick section near the northern end of the Great Quarry in order to establish how trilobite populations fluctuated through time. The section is still accessible and extends from the top of the *Olenus truncatus* Zone upwards into the lower *O. attenuatus* Zone. Successive bedding planes were examined, at 1-cm intervals where possible, and for each surface all trilobite sclerites, and a few near-intact specimens, were counted within a 5×5 cm quadrat. The shale sequence is lithologically variable suggesting an environment that fluctuated within relatively narrow limits (Clarkson *et al.* 1998). It was shown that *Olenus* spp. and *Agnostus* (*Homagnostus*) *obesus* (Fig. 6e) are very common, but their abundances fluctuate dramatically and in the lower–middle part of the sequence they are almost mutually exclusive (Clarkson *et al.* 1998; cf. Schovsbo 2000; Fig. 9 herein). It was also observed that *Glyptagnostus reticulatus* and the phosphatocopine arthropod *Cyclotron* sp. are rare and confined to particular levels. Clarkson *et al.* (1998) postulated that *Cyclotron* seems to have lived in conditions which no other, or very few, preservable invertebrates could tolerate, perhaps very low oxygen levels. Geochemical evidence suggests, however, that some trilobite- and agnostoid-barren intervals might be the result from an excess in oxygen remobilising the unconsolidated mud and dissolving the calcareous-shelled fossils (Schovsbo 2000, 2001; see also Eriksson & Terfelt 2007).

Fortey (2000) showed that there is a correlation between the presence and abundance of pyrite and the abundance of *Olenus truncatus* and *O. wahlenbergi* in the section measured by Clarkson *et al.* (1998), and also that *Cyclotron* appears and olenids disappear completely when there is no pyrite. This prompted Fortey (2000) to suggest that at least some olenid trilobites were chemoautotrophic symbionts adapted to low-oxygen, sulphur-rich sea-floor conditions.

Another very detailed bed-by-bed study in the *Leptoplastus* Superzone (Jiangshanian Stage) in the western part of the South Quarry (at 'rännil b' of Persson 1904; locality 6 of Westergård 1922, fig. 3) showed that particular faunal associations are often confined to discrete sedimentary packages, or arise after an unfossiliferous interval though some species may range through several sedimentary changes (Ahlberg *et al.* 2006). Thus, the incoming of new genera or species within this succession is apparently linked to abrupt sedimentary changes or follows an unfossiliferous interval. In the lower two zones, the olenid assemblages are monospecific, but at the base of the overlying *Leptoplastus crassicornis*–*L. angustatus* Zone more than one species is present and new morphotypes with long genal spines appear for the first time (Ahlberg *et al.* 2006). As noted by Clarkson in Ahlberg *et al.* (2006), this morphological

innovation presaged the even more dramatic modifications seen in later leptoplastine genera, such as *Ctenopyge* and *Sphaerophthalmus*.

6. Concluding remarks

Geological research in the Forsemölla-Andrarum district dates back as far as the mid-1800s and investigations by many generations of geologists have made it a classical area for Cambrian stratigraphy and palaeontology in Baltoscandia. A particularly active period of research occurred during the last two decades of the 19th century and the early 20th century. Subsequent geological studies in the early–mid 1900s include detailed investigations of both outcrops and drill cores (Westergård 1922, 1942, 1944). Since then, the objective of the research has been to clarify as much as possible about the Alum Shale environment and its faunas. Several of these projects were initiated by Euan Clarkson and focused on studying evolutionary processes and patterns in the olenids, and on faunal dynamics and their relations with environmental fluctuations in the Furongian.

The Cambrian succession at Andrarum is condensed but remarkably complete stratigraphically and not affected by faulting or folding. It was deposited in an outer shelf setting and is dominated by black shales and siliciclastic mudstones. Because there was generally a high rate of faunal turnover and most trilobites and agnostoid species have short ranges, the succession at Andrarum largely forms the basis for the detailed 'middle' and 'upper' Cambrian (Miaolingian–Furongian) biostratigraphy of Scandinavia as outlined by Westergård (1946, 1947, 1953) and revised by Terfelt *et al.* (2008), Weidner & Nielsen (2014), Nielsen *et al.* (2014, 2020) and Weidner *et al.* (2023). Furthermore, the succession has been the subject of a great deal of palaeontological research since the pioneering work of Angelin (1851, 1854), and Andrarum is the type locality for numerous trilobites and agnostoids, several of which have utility for intercontinental correlations. Also, the last four decades have witnessed major efforts to increase our knowledge of the stratigraphy, sedimentology, palaeontology and geochemistry of the Alum Shale, and the Andrarum section is significant in understanding the Cambrian world.

Acknowledgements

We are indebted to Niklas Axheimer for redrawing figure 2 in Clarkson *et al.* (1998, fig. 2), Fig. 9 herein. We are greatly indebted to Alan W. Owen and the journal reviewers Jan Ove R. Ebbestad and Arne T. Nielsen for critically reading and improving the manuscript.

Competing interests

The authors declare no competing interests.

References

- Ahlberg, P., Månsson, K., Clarkson, E. N. K. & Taylor, C. M. 2006. Faunal turnovers and trilobite morphologies in the upper Cambrian *Leptoplastus* Zone at Andrarum, southern Sweden. *Lethaia* **39**, 97–110.
- Ahlberg, P. & Ahlgren, J. 1996. Agnostids from the Upper Cambrian of Västergötland, Sweden. *GFF* **118**, 129–40.
- Ahlberg, P. & Terfelt, F. 2012. Furongian (Cambrian) agnostoids of Scandinavia and their implications for intercontinental correlation. *Geological Magazine* **149**, 1001–12.
- Ahlberg, P., Axheimer, N., Babcock, L. E., Eriksson, M. E., Schmitz, B. & Terfelt F. 2009. Cambrian high-resolution biostratigraphy and carbon isotope chemostratigraphy in Scania, Sweden: first record

- of the SPICE and DICE excursions in Scandinavia. *Lethaia* **42**, 2–16.
- Ahlberg, P., Lundberg, F., Erlström, M., Calner, M., Lindskog, A., Dahlgvist, P. & Joachimski, M. M., 2019. Integrated Cambrian biostratigraphy and carbon isotope chemostratigraphy of the Grönhögen-2015 drill core, Öland, Sweden. *Geological Magazine* **156**, 935–49.
- Andersson, P. G. 1974. *Alun och ark, kalk och krut*. Stockholm: Natur och Kultur, 176 pp.
- Andersson, A., Dahlman, B., Gee, D. G. & Snäll, S. 1985. The Scandinavian Alum Shales. *Sveriges Geologiska Undersökning Ca* **56**, 1–50.
- Angelin, N. P. 1851. *Palaeontologia Svecica. Pars I: Iconographia Crustaceorum Formationis Transitionis. Fascicule I*. Lund, 24 pp.
- Angelin, N. P. 1854. *Palaeontologia Scandinavica. Pars I: Crustacea Formationis Transitionis. Fascicule II*. Leipzig: T. O. Weigel, Academiae Regiae Scientiarum Suecanae, I–IX + 21–92.
- Babcock, L. E., Robison, R. A., Rees, M. N., Peng, S. C. & Saltzman, M. R. 2007. The Global boundary Stratotype Section and Point (GSSP) of the Drumian Stage (Cambrian) in the Drum Mountains, Utah, USA. *Episodes* **30**, 84–94.
- Bergström, J. & Ahlberg, P. 1981. Uppermost Lower Cambrian biostratigraphy in Scania, Sweden. *Geologiska Föreningens i Stockholm Förhandlingar* **103**, 193–214.
- Bergström, J. & Gee, D. G. 1985. The Cambrian in Scandinavia. In Gee, D. G. & Sturt, B. A. (eds) *The Caledonide Orogen—Scandinavia and Related Areas*, 247–71. Chichester, UK: John Wiley and Sons.
- Bian, L., Schovsbo, N. H., Chappaz, A., Zheng, X.W., Nielsen, A. T., Ulrich, T., Wang, X., Dai, S.F., Galloway, J. M., Malachowska, A., Xu, X.H. & Sanei, H. 2021. Molybdenum-uranium-vanadium geochemistry in the Lower Paleozoic Alum Shale of Scandinavia: Implications for vanadium exploration. *International Journal of Coal Geology* **239**, 103730.
- Bird, C. & Clarkson, E. N. K. 2003. Observations on the ontogeny of the upper Cambrian trilobite *Peltura scarabaeoides westergaardi* Henningsmoen, 1957. *GFF* **125**, 177–90.
- Bromell, M. von 1729. Lithographiae svecanae continuatio. Specimen II. Sectio II. Articulatus primus. De lapidibus insectiferis Scanicis & Gothicis. Acta Literaria Sveciae 1729, 493–7, 524–34.
- Buchardt, B., Nielsen, A. T. & Schovsbo, N. H. 1997. Alunskiferen i Skandinavien. *Geologisk Tidsskrift* **1997**(3), 1–30.
- Carlsson, K. 1996. *Bruksbygdsliv—Andra alunbruksboken*. Kristianstad: MonitorFörlaget, 121 pp.
- Cederström, P., Geyer, G., Ahlberg, P., Nilsson, C. H. & Ahlgren, J. 2022. Ellipsocephalid trilobites from Cambrian Series 2 and Stage 4, with emphasis on the taxonomy, morphological plasticity and biostratigraphic significance of ellipsocephalids from Scania, Sweden. *Fossils and Strata* **67**, 1–131.
- Clarkson, E. N. K. 1973. Morphology and evolution of the eye in Upper Cambrian Olenidae (Trilobita). *Palaeontology* **16**, 735–63.
- Clarkson, E. N. K. 1988. The origin of invertebrate species: a critical review of microevolutionary transformations. *Proceedings of the Geologists' Association* **99**, 153–72.
- Clarkson, E. N. K. 2011. The life and times of the olenid trilobites. *Geologické výskumy na Morave a ve Slezsku, Brno* **2011/1**, 11–7.
- Clarkson, E. N. K. & Ahlberg, P. 2002. Ontogeny and structure of a new, miniaturised and spiny olenid trilobite from southern Sweden. *Palaeontology* **45**, 1–22.
- Clarkson, E. N. K. & Taylor, C. M. 1995a. Ontogeny of the trilobite *Olenus wahlenbergi* Westergård, 1922 from the upper Cambrian Alum Shales of Andrarum, Skåne, Sweden. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **86**, 13–34.
- Clarkson, E. N. K. & Taylor, C. M. 1995b. The lost world of the olenid trilobites. *Geology Today* **11**, 147–54.
- Clarkson, E. N. K., Taylor, C. M. & Ahlberg, P. 1997. Ontogeny of the trilobite *Parabolina spinulosa* (Wahlenberg, 1818) from the upper Cambrian Alum Shales of Sweden. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **88**, 69–89.
- Clarkson, E. N. K., Ahlberg, P. & Taylor, C. M. 1998. Faunal dynamics and microevolutionary investigations in the Upper Cambrian *Olenus* Zone at Andrarum, Skåne, Sweden. *GFF* **120**, 257–67.
- Clarkson, E. N. K., Ahlgren, J. & Taylor, C. M. 2003. Structure, ontogeny, and moulting of the olenid trilobite *Ctenopyge* (*Eoectenopyge*) *angusta* Westergård, 1922 from the upper Cambrian of Västergötland, Sweden. *Palaeontology* **46**, 1–27.
- Clarkson, E. N. K., Ahlgren, J. & Taylor, C. M. 2004. Ontogeny, structure and functional morphology of some spiny *Ctenopyge* species (Trilobita) from the upper Cambrian of Västergötland, Sweden. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **94**, 115–43.
- Dahl, T. W., Siggaard-Andersen, M.-L., Schovsbo, N. H., Persson, D. O., Husted, S., Hougård, I. W., Dickson, A. J., Kjær, K. & Nielsen, A. T. 2019. Brief oxygenation events in locally anoxic oceans during the Cambrian solves the animal breathing paradox. *Scientific Reports* **9**, 11669.
- Egenhoff, S. O., Fishman, N. S., Ahlberg, P., Maletz, J., Jackson, A., Kolte, K., Lowers, H., Mackie, J., Newby, W. & Petrowsky, M. 2015. Sedimentology of SPICE (Steptoean positive carbon isotope excursion): A high-resolution trace fossil and microfabric analysis of the middle to late Cambrian Alum Shale Formation, southern Sweden. *The Geological Society of America Special Paper* **515**, 87–102.
- Eriksson, M. E. & Terfelt, F. 2007. Anomalous facies and ancient faeces in the latest middle Cambrian of Sweden. *Lethaia* **40**, 69–84.
- Eriksson, M. E. & Waloszek, D. 2016. Half-a-billion-year-old microscopic treasures—the Cambrian ‘Orsten’ fossils of Sweden. *Geology Today* **32**, 115–20.
- Falk, H., Lavergren, U. & Bergbäck, B. 2006. Metal mobility in alum shale from Öland, Sweden. *Journal of Geochemical Exploration* **90**, 157–65.
- Fortey, R. A. 2000. Olenid trilobites: The oldest known chemoautotrophic symbionts? *PNAS* **97**, 6574–78.
- Gill, B. C., Lyons, T. W., Young, S. A., Kump, L. R., Knoll, A. H. & Saltzman, M. R. 2011. Geochemical evidence for widespread euxinia in the later Cambrian ocean. *Nature* **469**, 80–3.
- Hadding, A. 1942. Lunds universitets geologisk-mineralogiska institution. Dess ursprung, tillkomst och utveckling. In *Lunds Geologiska Fältklubb 1892–1942*, 31–68. Lund: Carl Bloms Boktryckeri.
- Hammer, Ø. & Svensen, H. H. 2017. Biostratigraphy and carbon and nitrogen geochemistry of the SPICE event in Cambrian low-grade metamorphic black shale, southern Norway. *Palaeogeography, Palaeoclimatology, Palaeoecology* **468**, 216–27.
- Henningsmoen, G. 1957. The trilobite family Olenidae with descriptions of Norwegian material and remarks on the Olenid and Tremadocian Series. *Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo, I. Matematisk-Naturvidenskapelig Klasse* **1957**(1), 1–303.
- Henriksson, B. 1994. S. A. Tullberg—sorgligt men sant geologöde. *Geological Survey of Sweden, SGU information No. 1*, 14–7.
- Hoffmann, A. & Reif, W.-E. 1994. Rudolf Kaufmann's work on iterative evolution in the Upper Cambrian trilobite genus *Olenus*: A reappraisal. *Paläontologische Zeitschrift* **68**, 71–87.
- Kaufmann, R. 1933. Variationsstatistisches Untersuchungen über die ‘Artabwandlung’ und ‘Artumbildung’ an der Oberkambrischen Trilobitengattung *Olenus* Dalm. *Abhandlungen des Geologischen-Paläontologischen Institut der Universität Greifswald* **10**, 1–54.
- Ladenberger, A., Blomskog, L., Morris, G., Camitz, J. & Pitcairn, I. 2024. Sampling and characterisation of burnt shale waste (*rödifyr*) in southern Sweden. *SGU-rapport* **2024:08**, 1–56.
- Lapworth, C. 1879–1880. On the geological distribution of the *Rhabdophora*. *Annals and Magazine of Natural History, Series 5* **3**, 245–57, 449–55; **4**, 333–41, 423–31; **5**, 45–62, 273–85, 358–69; **6**, 16–29, 185–207.
- Lapworth, C. 1882. The life and work of Linnarsson. *Geological Magazine* **9**(4), 1–6, 119–22, 171–6.
- Lauridsen, B. W. & Nielsen, A. T. 2005. The Upper Cambrian trilobite *Olenus* at Andrarum, Sweden: a case study of iterative evolution? *Palaeontology* **48**, 1041–56.
- LeRoy, M. A. & Gill, B. C. 2019. Evidence for the development of local anoxia during the Cambrian SPICE event in eastern North America. *Geobiology* **17**, 381–400.
- Levey, M. 1958. Alum in ancient Mesopotamian technology. *Isis* **49**(2), 166–9.
- Linnarsson, G. 1875. Två nya trilobiter från Skåne alunskiffer. *Geologiska Föreningens i Stockholm Förhandlingar* **2**, 498–501.
- Linnarsson, J. G. O. 1880. Om förtolningarna i de svenska lagren med *Peltura* och *Sphaerophthalmus*. *Geologiska Föreningens i Stockholm Förhandlingar* **5**, 132–61.
- Linnarsson, J. G. O. 1883 [dated 1882]. De undre Paradoxideslagren vid Andrarum. *Sveriges Geologiska Undersökning C* **54**, 1–48.
- Linné, C. von (Linnaeus, C.) 1751. *Skånska resa, på Höga Öfwerhetens befallning förrättad år 1749. Med rön och anmärkningar uti oeconomien, naturalier, seder, lefnadssätt*. Stockholm: L. Salvius, 468 pp.
- Maas, A., Braun, A., Dong, X.-P., Donoghue, P. C. J., Müller, K. J., Olempska, E., Repetski, J. E., Siveter, D. J., Stein, M. & Waloszek, D. 2006. The ‘Orsten’—More than a Cambrian Konservat-Lagerstätte yielding exceptional preservation. *Palaeoworld* **15**, 266–82.
- Månsson, K. & Clarkson, E. N. K. 2012. Ontogeny of the upper Cambrian (Furongian) olenid trilobite *Protopeltura aciculata* (Angelin, 1854) from Skåne and Västergötland, Sweden. *Palaeontology* **55**, 887–901.

- Månsson, K. & Clarkson, E. N. K. 2016. Early ontogeny of the Furongian (Cambrian) olenid trilobites *Sphaerophthalmus alatus* (Boeck, 1838) and *Ctenopyge (Mesoctenopyge) tumida* Westergård, 1922 from Bornholm, Denmark. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **106**, 171–83.
- Martinsson, A. 1974. The Cambrian of Norden. In Holland, C. H. (ed.) *Lower Palaeozoic Rocks of the World. 2. Cambrian of the British Isles, Norden, and Spitsbergen*, 185–283. London: John Wiley & Sons.
- Millard, A. R. 1999. Geochemistry and the early alum industry. *Geological Society, London, Special Publications* **165**, 139–46.
- Moberg, J. C. 1910. Guide for the principal Silurian districts of Scania (with notes on some localities of Mesozoic beds). *Geologiska Föreningens i Stockholm Förhandlingar* **32**, 45–194.
- Nathorst, A. G. 1869. Om lagerföljden inom kambriska formationen vid Andrarum i Skåne. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar* **1869**(1), 61–5.
- Nathorst, A. G. 1877. Om de kambriska och siluriska lagren vid Kiviks Esperöd i Skåne, jemte anmärkningar om primordialfaunans lager vid Andrarum. *Geologiska Föreningens i Stockholm Förhandlingar* **3**, 263–72.
- Nielsen, A. T. & Schovsbo, N. H. 2015. The regressive Early-Mid Cambrian ‘Hawke Bay Event’ in Baltoscandia: Epeirogenic uplift in concert with eustasy. *Earth-Science Reviews* **151**, 288–350.
- Nielsen, A. T., Weidner, T., Terfelt, F. & Høyberget, M. 2014. Upper Cambrian (Furongian) biostratigraphy in Scandinavia revisited: definition of superzones. *GFF* **136**, 193–7.
- Nielsen, A. T., Høyberget, M. & Ahlberg, P. 2020. The Furongian (upper Cambrian) Alum Shale of Scandinavia: revision of zonation. *Lethaia* **53**, 462–485.
- Norrhem, S. 2010. *Christina och Carl Piper—en biografi*. Lund: Historiska Media, 288 pp.
- Peng, S. C., Babcock, L. E., Robison, R. A., Lin, H. L., Rees, M. N. & Saltzman, M. R. 2004. Global Standard Stratotype-section and Point (GSSP) of the Furongian Series and Paibian Stage (Cambrian). *Lethaia* **37**, 365–79.
- Persson, E. 1904. Till kännedom om oleniderna i ‘zonen med Eurycare och Leptoplastus’ vid Andrarum. I. *Geologiska Föreningens i Stockholm Förhandlingar* **26**, 507–28.
- Pulsipher, M. A., Schiffbauer, J. D., Jeffrey, M. J., Huntley, J. W., Fike, D. A. & Shelton, K. L. 2021. A meta-analysis of the Steptoean Positive Carbon Isotope Excursion: the SPICEraq database. *Earth-Science Reviews* **212**, 103442.
- Rooney, A. D., Millikin, A. E. G. & Ahlberg, P. 2022. Re-Os geochronology for the Cambrian SPICE event: Insights into euxinia and enhanced continental weathering from radiogenic isotopes. *Geology* **50**, 716–20.
- Saltzman, M. R., Ripperdan, R. L., Brasier, M. D., Lohmann, K. C., Robison, R. A., Chang, W. T., Peng, S. C., Ergaliev, E. K. & Runnegar, B. 2000. A global carbon isotope excursion (SPICE) during the Late Cambrian: relation to trilobite extinctions, organic-matter burial and sea level. *Palaeogeography, Palaeoclimatology, Palaeoecology* **162**, 211–23.
- Schovsbo, N. H. 2000. Environmental fluctuations in the *Olenus* Zone (Upper Cambrian), southern Scandinavia: A geochemical approach. *Bulletin of the Geological Society of Denmark* **47**, 53–61.
- Schovsbo, N. H. 2001. Why barren intervals? A taphonomic case study of the Scandinavian Alum Shale and its faunas. *Lethaia* **34**, 271–85.
- Schovsbo, N. H. 2002. Uranium enrichment shorewards in black shales: a case study from the Scandinavian Alum Shale. *GFF* **124**, 107–115.
- Schovsbo, N. H., Nielsen, A. T., Harstad, A. O. & Bruton, D. L. 2018. Stratigraphy and geochemical composition of the Cambrian Alum Shale Formation in the Porsgrunn core, Skien–Langesund district, southern Norway. *Bulletin of the Geological Society of Denmark* **66**, 1–20.
- Schultz, H.-M., Biermann, S., van Berk, W., Krüger, M., Straaten, N., Bechtel, A., Wirth, R., Lüders, V., Schovsbo, N. H. & Crabtree, S. 2015. From shale oil to biogenic shale gas: Retracing organic–inorganic interactions in the Alum Shale (Furongian–Lower Ordovician) in southern Sweden. *AAPG Bulletin* **99**, 927–56.
- Stoltz, E. 1932. Andrarums alunbruk. En försvunnen bruksbygd. *Svensk Geografisk Årsbok* **1932**, 65–121.
- Terfelt, F., Eriksson, M. E., Ahlberg, P. & Babcock, L. E. 2008. Furongian Series (Cambrian) biostratigraphy of Scandinavia—a revision. *Norwegian Journal of Geology* **88**, 73–87.
- Tersmeden, F. 2018. Professor utan att ha disputerat—Historien om den lärde överliggaren Nils Peter Angelin. In *Professorsinstallation Lunds universitet, 12 oktober 2018*, 36–53. Lund: Media-Tryck.
- Thickpenny, A. 1984. The sedimentology of the Swedish Alum Shales. In Stow, D. A. W. & Piper, D. J. W. (eds) *Fine-grained Sediments: Deepwater Processes and Facies*, 511–25. Geological Society of London Special Publication 15.
- Thickpenny, A. 1987. Palaeo-oceanography and depositional environment of the Scandinavian alum shales: sedimentological and geochemical evidence. In Leggett, J. K. & Zuffa, G. G. (eds) *Marine Clastic Sedimentology—Concepts and Case Studies*, 156–71. London, UK: Graham & Trotman.
- Tullberg, S. A. 1880. Om Agnostus-arterna i de kambriska aflagringsarna vid Andrarum. *Sveriges Geologiska Undersökning C* **42**, 1–37.
- Wahlenberg, G. 1818. Petrificata telluris svecanae. *Nova Acta Regiae Societatis Scientiarum Upsaliensis* **8**, 1–116.
- Weidner, T. & Nielsen, A. T. 2014. A highly diverse trilobite fauna with Avalonian affinities from the Middle Cambrian *Acidusus atavus* Zone (Drumian Stage) of Bornholm, Denmark. *Journal of Systematic Palaeontology* **12**, 23–92.
- Weidner, T., Nielsen, A. T. & Ebbestad, J. O. R. 2023. Middle Cambrian agnostoids and trilobites from the Lower Allochthon, Swedish Caledonides. *Fossils and Strata* **68**, 1–121.
- Westergård, A. H. 1922. Sveriges olenidskiffer. *Sveriges Geologiska Undersökning Ca* **18**, 1–205.
- Westergård, A. H. 1942. Stratigraphic results of the borings through the Alum Shales of Scania made in 1941–1942. In *Lunds Geologiska Fältklubb 1892–1942*, 185–204. Lund: Carl Bloms Boktryckeri.
- Westergård, A. H. 1944. Borrningar genom Skånes alunskiffer 1941–42. *Sveriges Geologiska Undersökning C* **459**, 1–45.
- Westergård, A. H. 1946. Agnostidea of the Middle Cambrian of Sweden. *Sveriges Geologiska Undersökning C* **477**, 1–140.
- Westergård, A. H. 1947. Supplementary notes on the Upper Cambrian trilobites of Sweden. *Sveriges Geologiska Undersökning C* **489**, 1–34.
- Westergård, A. H. 1953. Non-agnostidean trilobites of the Middle Cambrian of Sweden. III. *Sveriges Geologiska Undersökning C* **526**, 1–59.
- Zhao, Z., Ahlberg, P., Thibault, N., Dahl, T. W., Schovsbo, N. H. & Nielsen, A. T. 2022. High-resolution carbon isotope chemostratigraphy of the middle Cambrian to lowermost Ordovician in southern Scandinavia: Implications for global correlation. *Global and Planetary Change* **209**, 103751.

MS received 21 June 2025. Revised 11 September 2025. Accepted for publication 29 September 2025